Ecology and Conservation of the Kagu *Rhynochetos jubatus* of New Caledonia

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A thesis presented in partial fulfilment of the requirements

for the degree

Doctor of Philosophy

in Ecology

at Massey University

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1997

**To my parents for their
continued support...**

"Je suis pas naturaliste, je n'ai jamais aimé à m'occuper des oiseaux, je n'en ai jamais eu en ma possession ; mais celui-ci est tellement en dehors de toute la race des bipèdes emplumés, si affectueux, si intelligent, que je m'y suis attaché comme à un ami qui peuple ma solitude et qui ne manque pas un seul jour de venir, dès qu'il m'aperçoit, me souhaiter le bonjour et recevoir une caresse amicale."

Pouget 1875

Abstract

I carried out two phases of an internationally co-ordinated recovery project for the kagu *Rhynochetos jubatus* of New Caledonia between June 1991 and March 1995.

In Phase One, between June 1991 and January 1992, I established kagu abundance and distribution on Grande Terre in the first comprehensive survey of the species outside Parc Rivière Bleue, where kagu distribution was known through Yves Létocart's work there. In 177 different listening areas, I recorded a total of 491 adult kagus, including 208 pairs, in 84 of the areas, mostly in Province Sud (403 birds; 177 pairs). Low kagu numbers (1-4 birds) were recorded in 56% (n = 47) of the areas. More than nine kagus were recorded in each of 19 areas, which accounted for 57% (n = 282) of all birds. In these 19 areas, virtually all birds sang from intact forest. Kagus occurred in 'patches' over a large area of the island, but mostly in inland mountainous regions. Analyses indicated that larger numbers of kagus were likely to be found on volcanic rock types and with increasing distance from human settlements.

In Phase Two, from August 1992 to March 1995, I carried out a 32-month field-research programme at two high altitude study areas, Pic Ningua and Mt Cindoa, with the main objective of investigating if food supply was limiting annual fecundity of kagus. I found that kagu pairs probably lived on relatively fixed territories year-round where independent offspring may also be present, as was the case at Parc Rivière Bleue. At Pic Ningua, one pair nested in early December 1994, and another also probably around that time in 1993, which contrasted with the main breeding period of June-August at Parc Rivière Bleue. I recorded no breeding at Mt Cindoa, where kagus' bodyweights were generally lower than those of birds at Pic Ningua, probably due to poorer food supplies at Mt Cindoa. Kagus appeared to moult their primary feathers annually between approximately December and May, starting in close association with hot, wet conditions in the wet season, as they appeared to do at Parc Rivière Bleue. Moult may be delayed or suspended in parents feeding chicks in the wet season. After dogs *Canis familiaris* killed most of the kagus I knew at Pic Ningua (see below), remaining birds quit or extended the territories they held before the attacks. This behaviour in widowed birds may have been mostly related to a search for mates.

I found distinct seasonal patterns in kagu food supplies at high altitude closely related to seasonality in climate, especially temperature, and probably highly similar year-to-year. Food supplies peaked in the wet season and were lowest around late October when conditions were driest, and were also relatively spatially uniform in forest. It is not clear why birds do not generally use the period of peak food supplies for breeding, but it may be better for birds to moult their primary feathers at that time. Kagus were generalists in the types of the larger-sized soil and litter fauna they ate, and I recorded many new taxa not previously known to be eaten by the birds. Birds' diets were strongly influenced by seasonality in climate and food supplies, but they did not just track changing patterns in food availability. They were probably also a result of birds approaching local optima in the efficient use of available prey in response to changing environmental and physiological conditions. Birds appeared to use larger prey items when food was more abundant, and be least selective at times of greatest food scarcity in the driest periods. Birds used larvae at high frequencies in the early dry season; larvae might provide energy assimilation benefits in cold conditions.

Bodyweights of mostly non-breeding kagus at Pic Ningua and Mt Cindoa varied seasonally in close positive association with temperature and food supplies, and varied negatively with use of sheltered roosts. Bodyweights peaked at the end of the wet season around April and were lowest in the driest period of the late dry season around late October. Lack of other factors likely to be affecting the kagus' bodyweights like competition, parasites and reproduction indicated that climate and food supplies were closely linked to the seasonal variation in them. The close association between variation in temperature and kagu bodyweights and roosting behaviour appeared to be clear evidence of phenotypic adjustment in roosting behaviour for energy conservation in response to cold conditions, particularly wind chill, and food shortage.

There is little direct evidence that food supply is limiting the kagu's annual fecundity, but indirect support for this comes from, for example, the difficulty birds have in finding and capturing prey present in the soil and litter, and that they generally breed outside the period of peak food supplies and forage for long hours each day. More research is needed on whether food is limiting for aspects of kagu reproduction like egg formation and chick provisioning. Data suggest that the kagu's food supplies are independent of pair densities, thus the kagu's life history characteristics may have been strongly influenced by selection to maximise energy resources through interaction with the environment rather than by competition. This is consistent with aspects of the kagu's life history like for example its relatively non-competitive social organisation which means that birds can devote most of their time to foraging. I propose that density-independent food limitation has played an important role in shaping annual fecundity and other life history characteristics like social organisation in tropical, and possibly south temperate, forest birds.

At Pic Ningua in 1993, I described the first documented case of multiple kagu deaths caused by dogs. Twenty kagus were found dead (15) or wounded (5; one survived) from dog attacks in four distinct episodes over a 14 week period from late April to early August. Older remains of two other birds were also found. Eighteen of the 22 birds wore radio-transmitters, and the four non-radio-tracked birds were found by chance. Dogs errant from a nearby tribal village were strongly implicated in carrying out most, if not all, of the attacks. The events on the peak showed that dogs are dangerous predators of adult kagus, and dog predation may have been important in shaping kagu distribution patterns.

Four other important implications of my study for kagu conservation management are (1) the kagu's reproductive success may be greater in low altitude compared to high altitude rainforest; (2) because the kagu's clutch size is low and invariable, and the number of successful broods per year is also low and seems to be more influenced by density-independent factor(s), birds are especially vulnerable to predation because they cannot respond to lower densities by lifting their reproductive output; (3) feral pigs *Sus scrofa* at sufficiently high densities could potentially reduce prey availability for kagus; and (4) at least two additional managed reserves like Parc Rivière Bleue protecting up to 200 kagus are required to ensure that birds remain in the wild for the long term.

Acknowledgements

My kagu research was the result of an international recovery project to help ensure New Caledonia's bird emblem remained in the wild for the long term. I thank the Service de la Recherche, des Etudes et du Traitement de l'Information sur l'Environnement for financing the Phase One survey, and the Royal Society for the Protection of Birds and BirdLife International for financing my fieldwork for Phase Two.

Many individuals and organisations played a part in the project's development and implementation, in Britain, France, New Caledonia and New Zealand. Most of those who attended the I.C.B.P. conference in Hamilton, New Zealand, in 1990 and discussed setting up the project played an important part in its realisation. These included Jean-Louis d'Auzon, Alistair Gammell, Rod Hay, Yves Létocart, Serge Sirgouant, Jean-Marc Thiollay and Peter Thomas. Colin Bibby, Michael Rands and Tobias Salathé at BirdLife International were also subsequently involved in organisational work on the project. I appreciate the support of Alison Duncan from the Ligue pour la Protection des Oiseaux who was closely involved in overseeing the project for BirdLife International from late 1993.

I was fortunate enough to become involved in the project because Rod Hay, my second supervisor, put considerable faith in a new post-graduate and recommended me to carry out the survey for kagus in 1991. The Association pour la Sauvegarde de la Nature Néo-Calédonienne managed both Phases of my research work in New Caledonia, and I am indebted to the people who I worked closely with at the organisation for their help and assistance throughout my research. I especially thank the hard-working President Jean-Louis d'Auzon, who continually tried, through good and some bad times, to educate me in the 'French way' of doing things. I leave it to him to judge if he succeeded. I thank the other members of the Association's Committee who I came to know and who were always happy to listen to my poor French accent, particularly Jean Broudissou, Alain Houdain, Serge Sirgouant, Madam Geiller and Tony Wilmott. I particularly thank the ASNNC secretaries, the 'three Nathalies' and Olivia, who were a great help to me on my weekly visits to the office in Nouméa.

I thank the Province Sud authorities who supported the project and allowed it to go ahead, particularly Marcel Boulet (Manager of the Service de l'Environnement et des

Parcs et des Réserves de la Province Sud) for his help with permits and other administrative matters, and for allowing me to work in the Pic Ningua Botanical Reserve and at Parc Rivière Bleue.

I owe much to Yves Létocart (M. Cagou, numéro un) and Serge Sirgouant (President of the Société Calédonienne d'Ornithologie) for their support and help throughout my stay in New Caledonia. Yves's help and considerable knowledge of kagus was invaluable, and I thank him for always being willing to answer my questions about the birds and for providing me with information on them at Parc Rivière Bleue when I needed it, for example his moult data. Yves also instructed me how to change the batteries in the radio-transmitters, allowed me to copy his many kagu references and use his recording of a duetting kagu pair. Serge was a great help with information on New Caledonian birds in general, and I particularly thank him for his time when I needed to visit the captive breeding unit at Parc Forestier, and for his data on the kagus there.

I thank Peter Thomas for his friendship when I was new to New Caledonia and for his encouragement and assistance during the 1991 kagu survey. I am grateful to Simon Bulman for his company and help during two months of survey work in often trying conditions associated with difficult terrain and I'm sure at times with a difficult companion. Staff from the Direction du Developpement Rural and Direction du Developpement Rural et Pêche helped with information on kagu whereabouts and with logistical support, especially Martine Berger, Serge Blanchet, Yves Bruireu, Christian Harbulot, Catherine Latreille, Christian Papineau and Pham Robert. I particularly thank Mireille Pandolfi for her friendly assistance and encouragement. Staff at the Service Topographique du Territoire were always helpful in meeting my constant demands for maps, especially Jean-Yves Fabre whose help I called on many times throughout my time in New Caledonia. The Montagnat Mining Company kindly flew us by helicopter onto Mt. Kouakoué, and tribal authorities and private landowners willingly allowed me access to their land. Many other local people who helped me during the 1991 survey remain unnamed, for example those that gave me directions, and provided me with accommodation or information on possible kagu whereabouts.

I thank the SLN (Société le Nickel) mining company for their help in this project, and permission to use their access road to Pic Ningua. I especially thank Georges Miret (then Manager of SLN at Thio) for his enthusiasm and support for my wish to work at

Pic Ningua, and for allowing me to present a display on the kagu at the Thio Mining Museum. I also thank him and his replacement Christophe Thomas for use of accommodation at the mine site in the study area. I thank the mine staff in Thio and at Pic Ningua who were always friendly, helpful, and interested in my research, particularly Joseph Guillo. I am grateful to the personnel of the Vigilant Security Company for letting me share their accommodation at Pic Ningua for over two years, and for their friendly company and interest in my research during my weekly stays in the field. I also thank the Manager of Vigilant Security at Thio for his willing assistance with gate keys to Pic Ningua.

The period of the dog attacks at Pic Ningua between April and August 1993 were especially difficult as I lost most of my study birds then. During this period I thank those that offered their support or helped me, especially Marcel Boulet, Sidney Brochot, Michael Bull, François Christophe, Alison Duncan, Rod Hay, Alain Van Heck, Yves Létocart, Jacques Locque, Christian Matton, Mireille Pandolfi, Serge Sirgouant, Clare Veltman, Tony Wilmott, and SLN staff at Thio. I thank Joseph Guillo who found (dead) bird 134. I also greatly appreciate the friendship of Jacques Locque, and his help in tracing the origin of the stray dogs who attacked the kagus at Pic Ningua.

I thank those who helped me in various ways during my Phase Two research. Philippe Serre was a great help on my first trip to Mt Cindoa, and with the capture of kagus at Pic Ningua and Mt Cindoa. Etienne DuTailly and Ken Cole took photographs of kagus for me at Pic Ningua, and Léonard Droulliard and Serge Sirgouant let me use their kagu photographs for the display panels. I thank the staff at C.I.R.A.D. who I worked closely with and who were always extremely helpful. I thank Dominique Dulieu (then C.I.R.A.D. Manager) and Frédéric Beugnet (C.I.R.A.D. Parasitology Laboratory), for use of the binocular microscope and digital balance, respectively. I also thank Frédéric Beugnet and C.I.R.A.D. for the chance to become involved with the parasite study on kagus, and those in the parasitology laboratory who were involved in that work, namely Laurent Chardonnet, Cyril Bonnault, and Renaud Gadat. Sidney Brochot, then Manager of the Parc Forestier, allowed me to present a display on the kagu in the Maison de la Nature at the Parc. Jean Chazeau gave me advice on pitfall trapping methods. Rod Hay (Department of Conservation, New Zealand) gave the coloured leg bands I used. I thank Michael Ménézo, O.R.S.T.O.M., for access to, and use of the email computer network there. I am grateful to Jacques Mermoud (Nouméa Meteorological Service) for his friendly assistance and the loan of the hand spun hygrometer and instructions on its use, and for supplying me with weather data. The Service de l'Environnement et des Parcs et des Réserves de la Province Sud contributed to the cost of the soil analyses. The Department of Ecology, Massey University gave the Pesola balance and paid for the import licence when I brought my samples back to New Zealand. I thank Olivia Sausset, Philippe Serre, and Etienne DuTailly for their help with translation of English into French for the kagu display panels, and Philippe Serre for help with much other translation work.

I thank Sidney Brochot and Christian Matton at Parc Forestier for access to the kagus there, and information about them, for my research on a possible new method to sex the birds. I greatly appreciate the help of Serge Sirgouant who also helped me with this research aspect, including photographing kagus' wing patterns there. I also thank the other S.C.O. members who helped catch kagus at the Parc one morning. I thank Yves Létocart and Sekine Mitsuo (Director of the Nogeyama Zoo) for supplying me with photographs of kagus at Parc Rivière Bleue and the Nogeyama Zoo, respectively.

I am greatful to Alison Duncan, Rod Hay, Jean-Marc Thiollay, and Clare Veltman for their comments on one or several of the early copies of my reports and/or manuscripts during my field research.

On a more personal level, I owe much to those friends who I flated with in Nouméa - Léonard Droulliard, Etienne DuTailly, Jean-Carl Lambert, and Philippe Serre, who taught me much about the French way of life and made my weekly visits to Pic Ningua much less daunting, especially Etienne DuTailly who continually encouraged to me 'be myself' and to paint!

In New Zealand, I thank Brian Gill for identifying the lizards that unfortunately fell into my pitfall traps, and for helping me import samples into New Zealand. Jay McCartney identified many of the invertebrates in my reference collection from the pitfall traps. I thank Ian Henderson, Greg Arnold and Steve Haslett for statistical advice, Ed Minot for letting me copy a paper from his Journal of Avian Biology, and my flatmate Adam Matich for help with graphing problems. Heather Outred assisted with trying to identify the possible seeds I found in kagu faeces. The Graduate Research Fund at Massey University and The Royal Society in New Zealand funded my attendance at the Behavioural Ecology Congress in Canberra in 1996 where I presented a poster on the kagu. Jenny Edwards (Computer Centre) allowed me to use SAS on my computer which saved an enormous amount of my time. I also thank the technical and office staff in the Department of Ecology who assisted me at one time or another: Paul Barrett, Liz Grant, Shelia Hardy, Tracy Harris, Jens Jorgensen, Barbara Just, Cathy Lake, Jodi Matenga, Steve Pilkington, Erica Reid, and Petra Van Kan. I especially thank Robin Fordham who was always keen to know how my research was going, and the great bunch of Ecology post-graduates for just being there.

I kindly thank Susan Roux and the C.I.P.O. (Conseil International pour la Protection des Oiseaux) for allowing me to reproduce the drawing of the kagu parent and chick in my thesis.

Last but certainly not least I thank my two supervisors, Clare Veltman and Rod Hay, whose help and support during my fieldwork in New Caledonia and write-up has been invaluable. I especially thank Clare for her help and friendship throughout my research, and whose unenviable task it was on occasions to encourage and motivate me during my write-up. I am extremely grateful for her ‘hands on’ attitude and for her continual attempts to make her students achieve their full potential. This thesis owes much to Clares supervision and her time spent reading and commenting on drafts of its chapters.

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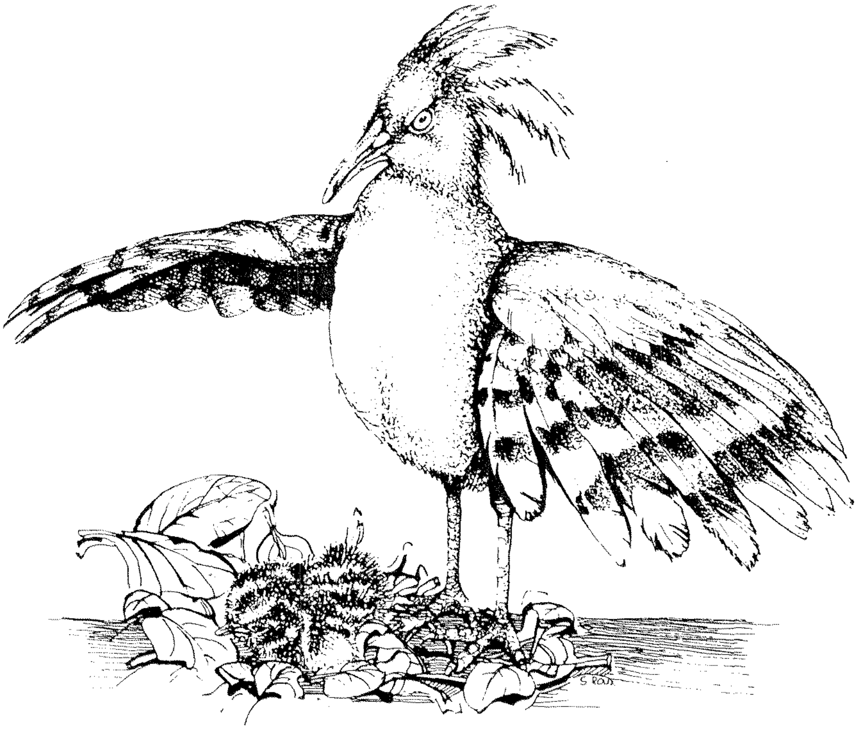
General Introduction



1.1 Research for kagu conservation

I was contracted to carry out two phases of an internationally coordinated recovery project for the kagu *Rhynochetos jubatus* of New Caledonia.

Phase One was a survey of mainland New Caledonia (Grande Terre) to find kagus in areas outside Parc Rivière Bleue (see Fig. 2-2), where kagu distribution was already known (Létocart 1992), which I carried out between June 1991 and January 1992 (Hunt 1996a, *Chapter* 2). This work was funded by the Service de la Recherche, des Etudes et du Traitement de l'Information sur l'Environnement (S.R.E.T.I.E.), a Department of the French Environmental Ministry. Phase Two was a 32-month field research programme from August 1992 to March 1995 (*Chapters 3-6*). The majority of this research was funded by the Royal Society for the Protection of Birds as a centennial project, along with the proceeds from BirdLife International's 'Project Island' (section 1.2). BirdLife International (previously the International Council for Bird Preservation) had overall responsibility for management of Phase Two, but the Ligue pour la Protection des Oiseaux (L.P.O.), France, was delegated much of this work from late 1993. Management in New Caledonia for Phases One and Two was by the Association pour la Sauvegarde de la Nature Néo-Calédonienne, in consultation with other interested parties there like the Société d'Ornithologie Calédonienne and the Province Sud authorities.

The main conditions for my 32-month field research under the terms of my contract were that it be a descriptive conservation-related study like the one Yves Létocart had undertaken on kagus at Parc Rivière Bleue, and that it be carried out in an area different from the Parc. The principal objective was to compare kagu life styles and threats in different areas of Grande Terre to increase knowledge about the birds and better enable appropriate management decisions about future kagu conservation to be made, so I planned my research accordingly (sections 1.5 and 1.6).

In common with that of many endangered endemic species, the kagu decline was probably mainly related to two factors: (1) direct threats to survival of the birds; and (2) a relatively low intrinsic rate of reproduction (Bennett and Owens 1997). My field research for Phase Two principally investigated if food supply was limiting annual fecundity of kagus. The rationale for this (section 1.5) was based on the idea that supplies of time and energy are major selection pressures shaping and linking an individual's life history characteristics (King 1974), which largely determine its reproductive success (Begon *et al.* 1996), and that food supply is a major factor determining the amount of energy resources available for reproduction (Martin 1995). This enabled me to learn about kagu life style and record incidental data on predation threats to kagus outside Parc Rivière Bleue, investigate reasons for low reproductive output in a tropical bird and therefore address an important theoretical area of research in much need of study (Boutin 1990, Martin 1996, Young 1996), and finally comply with my contractoral obligations for a conservation-based field research programme.

1.2 Factors leading to the implementation of the recovery project

There was concern about the kagu's increasing rarity from soon after European settlement (e.g., Bennett 1863, Sarasin 1913, Warner 1948, Béland 1975a, Jeggo 1978, Thiollay 1989), and it is internationally recognised as a threatened species (Barrau 1963, King, 1981, Collar *et al.* 1994, Hunt 1994 1996b). Authors cited a range of factors responsible for the species' decline like habitat destruction, introduced predators and trade, but it was unclear what the principal ones were. The kagu has been listed on Appendix I of CITES since 1973 (King 1981), with full legal protection in New Caledonia since 1956 (Barrau 1963).

The first efforts to reverse kagu decline were in 1974 when the Société Calédonienne d'Ornithologie organised a survey by questionnaire (Béland 1975a). The questionnaires were distributed through local brigades of the Gendarmerie Nationale to people knowledgeable about local fauna, and focused on kagu abundance, movements, habitat, reproduction, diet and threats. The 115 people who returned questionnaires generally reported that kagus were rare, and that the main threats to the birds were from humans, cats *Felis catus* and dogs *Canis familiaris*. This survey was followed soon after by the establishment of a captive breeding unit in sclerophyll forest at Parc Forestier, Nouméa, in 1976 (Brégulla 1987). Since 1977, four permanent breeding pairs have been kept in separate enclosures (1 ha total area) at the Parc, and from 1977 to late 1994, 61 kagus were raised with a 44% egg-to-adult success rate (S. Sirgouant pers. comm.). Since 1989, the Nogeyama Zoo, Yokohama, has also been developing a captive breeding programme for kagus (Hara and Hori 1992).

Létocart (1989 1991 1992) began research on kagus at Parc Rivière Bleue in 1980 with the main aim of increasing the population there, as well as learning about the biology and ecology of wild birds (section 1.3). By 1991, the number of birds in the Parc (163) had almost tripled from an estimated 60 in 1980 (Létocart 1992). This was achieved through a combination of management measures like control of introduced predators, a halt to hunting game (e.g., pigs *Sus scrofa* and deer *Cervus timorensis*), and introductions of kagus (Létocart 1992). In the continuing successful introduction programme, 32 kagus bred at Parc Forestier were released at Parc Rivière Bleue between 1983 and 1992, after about 12 weeks adjustment to natural conditions in a 1 ha enclosure there. Some of these captive-bred birds paired with wild ones (Y. Létocart pers. comm.).

Little was known about kagu numbers or distribution outside Parc Rivière Bleue. Thiollay's (1989) preliminary six-week field survey of Grande Terre was the most extensive up to then, and he recorded 39 birds. BirdLife International had begun Project Island to raise funds for kagu conservation (Rands 1987), and Thiollay's survey suggested that some urgency was needed to ensure kagus persisted outside the Parc. A four-year recovery project was drawn up by Salathé (1991) following a meeting of interested parties at the BirdLife International conference in New Zealand in 1990, consisting of the two Phases that I was contracted to carry out (section 1.1).

1.3 New Caledonia

New Caledonia is a French Overseas Territory lying just within the tropical latitudes (between 19° and 23° south) in Melanesia in the southwest Pacific, and at the shortest distances to them is approximately 1,200 km southeast of Australia and 1,400 km northwest of New Zealand. Grande Terre (*c.* 16,890 km^2) is about 390 km long and 50 km wide. It is of continental origin having been part of Gondwanaland and separated from Australia roughly 80 mya (Holloway 1979). Much of the island is mountainous. A central mountain chain runs along much of its length, and most of the flatter areas are along the leeward, southwest coast. The highest peak is Mt. Panié (1,628 m) in the north of Grande Terre. Peaks, which are commonly over 1,000 m, are mostly formed by ultrabasic rocks which now cover approximately one third of Grande Terre and result from sea floor overthrust that took place between the end of the Eocene and the end of the Oligocene (26 to 38 mya) (Holloway 1979). These rocks are very basic but highly mineralised, especially in nickel, and give rise to unusual soil types relatively poor in nutrients like calcium (Jaffré 1980). These soils appear to be more ancient and weathered, and thus poorer, compared to those studied on ultrabasic rocks in Malaysia (Proctor *et al.* 1988).

Although situated in the tropics, New Caledonia has a relatively temperate climate that Pesin and Thomas (1993) divided into three main seasons: the wet season (December to March), the cool season (June to August), and the 'saisons de transition' (April to May and September to November). Two-thirds of the annual rainfall in New Caledonia falls in the wet season, with the transition months of September to November receiving the least rainfall. Rainfall tended to increase slightly in the cool season after the transition period of April to May. Because of the prevailing southeast tradewinds, rainfall decreases across the island from the northeast coast (up to 4,000 mm annually) to the southwest coast (up to 1,000 mm). Mean annual temperatures at lower altitudes vary from 21° to 25°C, and the absolute maxima and minima recorded on Grande Terre were 38.8°C and 2.8°C, respectively (Chazeau *et al.* 1994).

Most of New Caledonia's rainfall in the wet season is usually associated with the passage of one or more tropical cyclones or depressions originating in the southwest Pacific. The frequency of cyclone activity, and the Territory's climate in general, is probably strongly influenced by the Southern Oscillation (the rising and falling of the pressure gradient across the Pacific; Biggs 1995). Between 1951 and 1993, many localities in New Caledonia had distinct cyclical rainfall patterns, varying from months to years of low and high rainfall (Pesin and Thomas 1993), probably in association with the alternating El Niño (warm) and La Niña (cool) phases of the Southern Oscillation (Philander 1983). The effect of the El Niño phase in the Pacific varies depending on the location, but it generally brings warmer, wetter weather to the east Pacific (e.g., along the western coast of South America) and cooler, drier conditions to the southwest (e.g., in eastern parts of Australia) (Biggs 1995). An unusually long El Niño phase (bringing drier conditions) was present in the southwest Pacific throughout the period of my study (Biggs 1995).

Four main native vegetation types on Grande Terre and their approximate areas are: rainforest (3,350 km^2), sclerophyll forest (100 km^2), niaoulis *Melaleuca quinquenervia* savanna (5,500 km^2) and 'maquis' (shrubland on the ultrabasic rocks;

5,250 km^2) (Schmid 1981, Bouchet *et al.* 1995). Thus rainforest, where kagus live (Létocart 1991), covered approximately 20% of the island.

1.4 Kagu taxonomy, biology and ecology

The kagu *Rhynochetos jubatus* Verreaux and des Murs (1860) is an endemic, ground-nesting flightless bird from New Caledonia (Délacour 1966, Hannécart and Létocart 1980, Hunt 1996b). Kagus have an appearance of something between a small heron and a rail (Plate 1-1) (Jeggo 1978). An obvious feature is their ash-grey and white plumage, somewhat unusual for ground-living forest birds which tend to be cryptically coloured. The long crest feathers which extend to the lower back are a distinguishing characteristic, but often difficult to detect unless displayed (see Plate 3-2). Weights of adult wild birds vary between about 700 and 1,000 g (Létocart 1991), probably depending on seasonal and individual size variation as no significant sexual size-dimorphism was known (Brégulla 1987). Kagus only occurred on Grande Terre.

The kagu is the only extant species in the monotypic family Rhynochetidae, in the order Gruiformes. Another, larger, kagu species *R. orarius* has been described from sub-fossils (*c.* 2000-4000 years B.P.) in New Caledonian coastal Holocene deposits (Balouet and Olson 1989). From examination of data in Balouet and Olson (1989), Trewick (1996) showed that *R. jubatus* is a smaller scaled-down version of *R. orarius,* which raises doubts that it is a separate species.

Verreaux and des Murs (1860) placed the kagu with the Ardeidae because of similarities in plumage coloration to herons and egrets, although they, as well as later authors (e.g., Bartlett 1862, Murie 1871, Parker 1864 1869) noted that it had characteristics similar to both Ardeidae and Gruiformes. For example, the kagu's extensive powder-down is characteristic of members of the Ardeidae (Bartlett 1862). Since 1862, taxonomists placed the kagu closer to the Gruiformes because of greater similarities in anatomy, agility of movement on land, chick and egg coloration, and the change in coloration between chick and adult (see Beddard 1891 for an early taxonomic review). Among the Gruiformes, the Eurypygidae of South America, the Mesitornithidae of Madagascar, and, recently, extinct Messelornithidae of Europe and Northern America (placed in the same sub-order Rhynocheti as the kagu) have been cited as near kagu relatives (Parker 1869, Murie 1871, Burckhardt 1901, Hesse

Plate 1-1. Female 119 (right) and male 120 (left) in forest at Pic Ningua at approximately 1,200 m a.s.l.. The pair's young chick is hiding close by. The long crest feathers of 119 are just visible down her upper back region.

1988). These associations suggested a close link between the kagu and original Gondwanaland fauna.

Determination of the kagu's actual affinities within the Gruiformes has been problematic. It has features not shared with the other birds: a unique blood composition (two-thirds fewer red blood cells and three times more haemoglobin than other birds; Vassart 1988), nares which are separated and not pierced left to right, unique 'flaps' or possibly functional values (as kiwis *Apteryx* spp. have; Reid *et al.* 1982) covering the nasal openings, and relatively large eyes (Pandolfi 1986). DNA-DNA hybridization analysis did not establish clear relationships because of the poor quality of the material used (Sibley and Ahlquist 1990). Karyotype (Wada *et al.* 1993) and mtDNA (Trewick 1997) comparisons suggested that within the Gruiformes the kagu might be closer to the Gruidae which are hypothesised to be representative of the ancestral Gruiformes (Belterman and De Boer 1984). Thus, the Rhynochetidae as a family do not appear to have evolved recently.

Kagus adapt well to captivity (many captive birds have lived for over 20 years; Pandolfi 1986) and most early knowledge published on their behaviour was learnt from birds in aviaries outside New Caledonia (e.g., sex-specific song, Pouget 1875). To my knowledge, the first live kagus to be exported arrived in Australia on 11 December 1861 (Bennett 1862a), soon followed by birds being sent to England (in 1862; Bennett 1862b) and France (in 1864; Pouget 1875). Kagu pairs commonly produced eggs in captivity, and females have done so without males present (S. Sirgouant pers. comm.). Campbell (1905) described egg-laying by one pair in Sydney who failed to hatch a chick. In 1902 three eggs were laid: the first on 6 April and the last on 3 October; in 1903 four eggs: the first on 16 April and the last on 16 November); in 1904 four eggs: 14 April, 23 June, 15 September (the egg was removed and placed in an incubator), and 4 October. Klös (1966) reported that one pair at the West Berlin Zoo laid six eggs over a period of nine months (October 1964, November, December, date not given but probably January, February and June 1965). The first complete description of kagu eggs was by North (1901-1903), and Burckhardt (1901) apparently first described a kagu chick (see also Campbell 1905).

Most of what was known about wild kagus came from Létocart's continuing study at Parc Rivière Bleue, actively managed for kagu conservation since its establishment in 1980 (Létocart 1992). He concentrated on kagu singing and roosting behaviour, diet, social structure and breeding biology, using radio-tracking methods on colour banded birds living at altitudes between approximately 150-450 m. He found that kagu pairs lived in long-term relationships year round on relatively fixed territories. For example, one pair had lived on the same territory for at least ten years. Although he never observed fighting between neighbouring pairs, from kagu calls and observations of birds' behaviour on the boundaries between territories, it appeared that disputes occurred. Fighting appeared to be only between males. The sizes of the combined home ranges of partners for each of four pairs that Létocart followed for several years were approximately 5, 20, 25 and 30 ha. He recorded one case of pair dissolution in these four pairs, which occurred after the pair had shared the same territory for 2.5 years.

Létocart (1989) suggested that kagu duet song, (rarely sung outside the early morning period unless provoked by taped song) maintained the pairbond and also functioned as territorial behaviour. Pairs duetted year round, but appeared to do so more often in the drier months of the dry season (September-November), although this was not statistically tested. For the 101 songs he recorded in Mois de Mai valley (see Fig. 5-2) over one year from one listening site, males sang alone more frequently than females (*c.* 70% and 30%, respectively) and always initiated duet song.

Kagu partners at Parc Rivière Bleue generally moved within well defined and overlapping home ranges, the boundaries of which Létocart (1991) suggested were formed by forest limits and the presence of neighbouring pairs. He noted that partners spent much more time apart outside the breeding season, only coming together infrequently to sing or forage. He also noted that females might be more prone than males to leave their home ranges because of disturbance, and reported one female which left her partner on several occasions (once for 7 months), but returned each time to her old territory and the male who was always resident there. The reason for the female's behaviour was unclear.

Létocart (1991) recorded 19 one-egg clutches laid by six kagu pairs between 1986 and 1990. There appeared to be little attempt by pairs to conceal their nests, but they were often up against objects like fallen trees or living tree trunks, and some were in open areas in the forest. Two of the 18 nests Létocart observed showed no signs of nest building, the 16 others were simple constructions of layered leaves, 10-35 cm in diameter. Pairs bred mainly between June-August (*c.* 83% of known first nesting attempts recorded, n = 10) with most eggs laid in July (n = 7). Two first nesting attempts were after August (October), but none occurred between January and May. Two different pairs laid successful replacement eggs (one in October, and one in December) after the loss of the first chicks from eggs laid in July. In 1987, one pair laid two successful clutches, the first was in July and the second in December (the same pair also laid two successful clutches in 1995; Y. Létocart pers. comm.). The four remaining eggs were laid in October (n = 3) and November (n = 1), but it was unclear if they were first or replacement nesting attempts, although Létocart thought they were the latter. At Parc Forestier, the incubation length of four clutches was 33, 34, 35 and 37 days, and the weight range of 11 eggs laid there was 60-75 g (mean = 69.2) (Brégulla 1987). The incubation period for wild kagus at Parc Rivière Bleue was around 34 days (Létocart 1991).

At Parc Rivière Bleue, kagu parents generally contributed equally to incubation, chick provisioning and protection (Létocart 1991). As well, after offspring became independent at about four months of age they remained on the natal home range for sometimes many years, but often made excursions away from it of up to many months. When on the natal home range they assisted with territory defence and the protection of younger offspring. Létocart (1991) did not report that older juveniles helped in feeding their younger siblings, in fact one was observed to take food from its parent who was about to feed a young chick. In captivity, two older offspring did assist their parents in feeding a chick (J. Begaud pers. comm. cited in Pandolfi 1986).

From 1988 to 1995, Létocart recorded the presence of primary moult in five male and three female kagus between January and May (Y. Létocart in litt.). Incubation never overlapped with moult, although chick rearing did but only when chicks were raised from second or replacement eggs late in the year. Primary moult was observed in a male of a pair with a chick aged 30 days (in 1988), and in 1995 the female of the same pair was moulting when her chick was aged 70 days. The range of bodyweights for four female and four male wild kagus weighed at various times of the year in the Parc were 700-980 g and 810-940 g, respectively (Létocart 1991).

Létocart (1991) documented the use of roosts by one kagu pair over 12 months (1/4/86-31/3/87). He recorded 113 roost records on a total of 26 different roosts (no data were given on the way that each partner used the roosts) and divided them into three classes according to the frequency that they were used (roosts used 10-22 times:

n = 6; used 2-9 times: n = 11; used only once: n = 9). The 26 roosts were located throughout the pair's home range. Twenty-four of the 26 roosts were trunks (mostly dead) inclined at angles up to 20 degrees, on which the birds perched at heights from 0.4-1.5 m above the ground. The remaining two roosts were on a liane and a rock.

Little was known about the diet of wild kagus before Létocart's (1989) investigation, but prey cited by various authors included beetles, earthworms, frogs, grasshoppers, larvae, lizards, slugs, small fish, and snails (Bartlett 1862, Pouget 1875, Sarasin 1913, Jeggo 1978, Brégulla 1987). Létocart (1989) found that birds foraged for most of the day except when food appeared to be superabundant in the wet season when birds often stopped foraging at times during the day because they appeared to be satiated, and carried out other activities like preening (Y. and H. Létocart pers. comms.). Preening is generally carried out when birds are roosting (pers. obs.), but kagus might undertake this activity during forced 'leisure' time when they must wait to assimilate and digest food (Weathers and Sullivan 1993). From 30 hrs of watching three male kagus forage in wet and dry conditions, Létocart (1989) observed the birds take prey off the accessible parts of tree trunks and rocks, on bare soil, on litter, under litter and in the soil. His analysis of kagu faeces showed that kagus ate species of Coleoptera (8 families), Phasmatoidea (1 family), Hemiptera (2 families), Dermaptera (1 family), Diplopoda, Diptera larvae, Araneae, Gastropoda (snails) and Reptilia (geckos and skinks). He knew from observing birds that they commonly fed on earthworms, and also ate Athoracophoridae (terrestrial forest slugs), but suggested that they could not catch the abundant Orthoptera and Amphipoda species because of their rapid springing movements. The 155 kagu excrement samples he collected were from ten different kagus over 12 continuous months and combined for diet analysis, thus there were no data on seasonal variation in their diets. Létocart (1989) also used pitfall traps to obtain qualitative (presence only) data on what prey were available for kagus at the Parc.

As occurs in most other bird species (Murton and Westwood 1977), important energy-demanding phases of the kagu's annual cycle at Parc Rivière Bleue appeared to be partitioned. Breeding mostly took place between June and August, but nesting could occur up until December. Primary moult appeared to begin in the wet season after incubation finished, and continue into the early dry season but finish before breeding began again in June.

1.5 Rationale for my principal field research objective

Kagus are at one extreme of a fast-slow continuum of birds from those with short life spans that produce large numbers of offspring annually, to those long-lived with a low annual fecundity; the adaptive basis for this continuum is unclear (Sæther 1996). Two main, not necessarily mutually exclusive, hypotheses attempt to explain this diversity in birds' life histories: food availability (Lack 1968), and nest predation (Skutch 1949, Slagsvold 1982, Martin 1995). Martin (1995) suggested that the negative correlation between annual fecundity and survival (Bennett and Harvey 1988) meant that effects of food availability on fecundity should be only minimal, and looked to see if nest predation rather than food availability might be mostly responsible for the life history diversity in birds. Martin (1995) found that fecundity in 123 North American Passeriformes and Piciformes was more related to nest sites and nest predation than foraging site; increased nest predation was associated with higher annual fecundity resulting from production of smaller but more broods per year. As Martin (1995) had, Owens and Bennett (1995) also found that the association between higher fecundity and increased nest predation in 250 bird species from 17 orders better explained birds' life histories than food availability.

There are several potential problems with the nest predation hypothesis. First, the scoring of food limitation by Martin (1995) and Owens and Bennett (1995) was very imprecise. Martin used five foraging sites (bark, ground, shrub and canopy gleaners, and aerial insectivores) that he thought differed in food resources, and Owens and Bennett used food type (distinguishing between predominantly herbivorous birds and others) and foraging range (distinguishing between species that obtained food for their chicks within and outside their nesting territories). Food availability though, may be affected by many factors like competition, climate, prey densities and the difficulty of finding and/or capturing prey. Second, the negative correlation between annual fecundity and adult survival could be a consequence of density-dependent effects in a stable population (Sutherland *et al.* 1986), where food might be the important limiting factor. Third, Martin (1995) suggested that the nest predation hypothesis was more likely to be important for the evolution of fecundity because the response to nest predation was probably 'fixed' (genetic) rather than phenotypic. Julliard *et al.* (1997), however, recently found that great tits *Parus major* adjusted clutch size in response to nest predation. Last, nest predation does not appear to be a good explanation for the latitudinal variation in annual fecundity (Martin 1996, see below).

Support for Lack's food availability hypothesis comes from the considerable evidence suggesting that food supply influences clutch size and the numbers of fledged young and broods per year (Drent and Dann 1980, reviewed by Martin 1987, Sæther 1994, Brinkhof and Cavé 1997). This is most graphically seen in seabird populations who can experience high mortality and breeding failure when their food supplies decline sharply (e.g., Ashmole 1963, Barber and Chávez 1986, Cairns 1992, Hamer *et al.* 1993). The importance of food supply is also seen in many birds that appear to time their breeding to coincide with peak food abundance for reproductive activity (Moreau 1950, Perrins 1970, Murton and Westwood 1977, Daan *et al.* 1988), although climatic factors such as heavy rain may force some tropical birds to breed outside periods of peak food supplies (e.g., Foster 1974, Gaston *et al.* 1979). The role of food in shaping life histories is controversial (Boutin 1990), and Martin (1995) pointed out that within-species phenotypic adjustments to reproductive parameters like clutch size associated with food availability may not mean that food had been important in evolving fecundity.

Jouventin *et al.* (1996) showed that the nature of the food supply was closely associated with variation in a range of life history characteristics in sheathbill *Chionis minor* populations. Sheathbills breeding on islands where food was abundant in summer had high bodyweights just prior to producing many offspring from large clutches, and food scarcity in winter saw many pairs leave their territories. On Kerguelen Island, food was less abundant but available year round, and sheathbill pairs remained on their territories, had lower bodyweights and produced fewer offspring from smaller clutches. Their study provided support for the ideas that (1) reproductive success is closely linked to the environment, particularly the food supply (Drent and Dann 1980); (2) reproductive success depends on an individual's condition (e.g., bodyweight) which reflects its food supply (Drent and Dann 1980, McNamara and Houston 1996); and (3) the nature of the food supply influences birds' social organisation (Emlen and Oring 1977) through factors such as social competition and the temporal and spatial variation of these resources (Davies and Hartley 1996).

Jouventin *et al.*'s (1996) study also demonstrated two other important points: (1) investigating a range of life history characteristics and environmental conditions simultaneously, and not just those directly related to reproductive activity, can increase understanding about the factors behind reproductive success; and (2) within-species investigations of birds in different habitats might provide clues about the underlying processes shaping life history characteristics. Another important aspect of life history which may be strongly influenced by a bird's food supply is the annual cycle, particularly the timing of energy-expensive phases like breeding and moult (Perrins 1970).

Annual fecundity of tropical and south temperate (southern) birds is apparently lower than that for north temperate (northern) birds (Yom-Tov 1987, reviewed in Martin 1996). Martin's (1996) review showed that the available evidence provided more support for the food availability hypothesis than the nest predation hypothesis as a reason for this difference in reproductive output. Because food is thought to have a large influence on birds' life histories and the level of annual fecundity in birds appears to show a latitudinal gradient, the main hypothesis for the lower fecundity in the tropics is that the milder climate there causes greater food limitation (e.g., Ashmole 1963, Cody 1966, Fogden 1972, Woinarski 1985, Thiollay 1988). Arthropod biomass in the tropical rainforest understorey for insectivorous birds may be relatively low compared to that in north temperate forests (Elton 1973, discussed by Thiollay 1988 and references therein). If this is the case it may be related to the greater spread of productivity throughout the year because of warmer conditions rather than being condensed into a shorter period because of colder conditions as happens in north temperate regions. The increased diversity of prey in the tropics, along with the higher occurrence of cryptic and toxic prey, may also make their capture difficult for predators thereby further reducing food availability (Owen 1977, Marcotullio and Gill 1985, Thiollay 1988). Thiollay (1988) provided rare quantitative support for the greater food limitation hypothesis when he showed lower foraging success for tropical compared to northern foliage gleaners.

Kagus have many of the life history characteristics exhibited more often in tropical compared to northern birds which have been attributed to greater food limitation, like low clutch size (Lack 1968), long incubation and slow development (Ricklefs 1976, 1993), extended parental care (Fogden 1972), lack of second broods

(Fogden 1972, König and Gwinner 1995), and long life spans (the evidence for this is controversial; Martin 1996). Factors associated with life on oceanic islands with reduced predation might also lower reproductive output for birds compared to those on continents because of greater resource shortage due to density-dependent (e.g., increased intraspecific competition; Grant 1968) and/or density-independent (e.g., reduced resource base; Janzen 1980, McNab 1994a 1994b) effects. Lack (1947) reported that clutch size for some bird species tended to be lower on Mediterranean islands compared to the adjacent mainland.

The kagu appeared an ideal study species on which to investigate if food supply was limiting annual fecundity. First, it is an ancient endemic species with no close relatives so it has probably largely evolved in response to New Caledonian (tropical) conditions. Second, its flightlessness and relatively open-ground-nesting behaviour strongly suggested that the kagu had lived without any serious predation threat for some considerable time. The two points above appear to reduce, at least, the possibility that phylogeny (Partridge and Harvey 1988) and predation (Martin 1995, Julliard *et al.* 1997) have influenced links between annual fecundity and other kagu life history characteristics and food supplies. Thus island birds such as the kagu, where dispersal, predation and inter-specific competition are reduced, are likely to have evolved at population densities close to the maximum level that can be supported by available food supplies (Schluter and Repasky 1991). Last, because the kagu's low annual fecundity was near the extreme even for tropical land birds, reasons for this might be easier to detect.

There are reasons to suggest that food may not be generally abundant for kagus. First, adults spent most of their active time foraging except when food supplies appeared to be superabundant (Létocart 1991, section 1.4). This was consistent with ideas that food is generally in short supply for island birds (Janzen 1980, McNab 1994a, 1994b) who seem to behave more like energy maximisers (Stamps and Buechner 1985). Long foraging hours have been reported for other tropical birds and thought to be associated with difficulty in finding prey (Marcotullio and Gill 1985). Second, kagus are flightless which is generally associated with lower basal rates and lower pectoral muscle mass, resulting in reduced energy expenditure (McNab 1994a). This, and their one-egg clutch, are invariable traits so phylogenetic constraints must be taken into account when considering kagu evolution (Partridge and Harvey 1988).

However, invariability does not exclude a trait's evolution due to ecological factors (Martin 1995). Flightlessness in island birds (McNab 1994a) and one-egg clutches in seabirds like albatrosses (*Diomedea* spp., Lack 1968) have been suggested as adaptive responses to limited food resources. The kagu's closest suggested extant relatives, Gruidae (section 1.4), with few exceptions, lay two-egg clutches (Archibald and Meine 1996) and are not flightless.

Along with low annual fecundity, other factors suggested that food might not be abundant for wild kagus when they breed. First, seasonal and annual variation in insect abundance occurs in tropical rainforests with definite wet and dry seasons, and abundance peaks in the wet season (Braby 1995 and references therein). As kagus at Parc Rivière Bleue breed in the dry season, they might be doing so outside the period of peak food abundance. Foster (1974) suggested that reduced foraging time and insect activity (especially aerial insects), but not insect abundance, associated with heavy rainfall in the wet season might be one reason some tropical insectivores breed just before or after the period of the heaviest rains. Second, captive pairs commonly produced two successful clutches per year in breeding enclosures at Parc Forestier (S. Sirgouant pers. comm.), and three successful clutches per year have been recorded there (Brégulla 1987). This showed that pairs have the ability to significantly increase their annual reproductive output from the norm of a single one-egg clutch each year observed in the wild (Létocart 1991). Third, breeding kagus can loose up to 200 g during incubation even though they generally still forage for half a day (Létocart 1991). Last, although kagu numbers at Parc Rivière Bleue have varied considerably since Létocart began studying the birds there (section 1.4), most kagu pairs he observed still produced at most one offspring per year (Létocart 1991). This suggested that factor(s) (e.g., food) limiting kagus' annual fecundity at the Parc might be doing so in a density-independent way. One pair at the Parc raised two offspring in a breeding season on two occasions (section 1.4), in 1987/1988 and again in 1995/96. This pair (mostly the male) has been occasionally hand-fed since 1992 (Y. and H. Létocart pers. comms.).

If the kagu's low and relatively invariable annual fecundity is linked to food supplies, then the food-associated factor(s) preventing larger and/or multiple clutches might also be invariable. One such factor could be highly predictable annual density-independent food limitation for kagus when they breed, and this might be evidenced in food delivery rates to chicks under different environmental conditions. Létocart (1991) presented valuable data that suggested food delivery rates to chicks might vary with weather and timing of breeding. He weighed two chicks of wild kagus at Parc Rivière Bleue from approximately one week after hatching at roughly ten day intervals. At the same time he recorded the amount of rainfall in the seven days before each chick was weighed. Both chicks were hatched in 1990, one on 9 July, and one on 6 September. At 60 days of age, the former chick weighed approximately 575 g, and the latter 475 g. Conditions were generally wetter and cooler during the 60 days the heavier chick was raised than for the lighter chick, but no data were provided on factors like parental care or habitat quality and only one chick was weighed in each period. Nevertheless, this suggested two important points: (1) if parents had difficulty feeding only one chick when food was in short supply, then they may be raising the maximum number of chicks that they can (i.e. one chick) when they usually breed (June-August); and (2) although kagus at the Parc seemed to breed outside the period of peak food supplies in the wet season, they might usually breed in the optimum period for reproduction in the dry season. Brégulla (1987) presented growth rates for two chicks raised in captivity at Parc Forestier. At 60 days of age they were approximately 600 g and 675 g. Kagus at Parc Forestier receive supplementary food but can also take prey from the environment in their enclosures.

1.6 Structure of my field research programme

I chose a study area based on four criteria: (1) a habitat different from the kagu study area at Parc Rivière Bleue; (2) sufficient kagu pairs present (*c.* 10 pairs) for a radio-tracking study to locate a different pair per day over a two week sampling routine; (3) kagus should be living under relatively undisturbed conditions where no management for kagu conservation had been undertaken; and (4) road access. The results of the kagu survey in 1991 (*Chapter 2*) clearly indicated that higher altitude habitat should be selected as many remaining birds occurred in such areas. Lower temperatures at higher altitudes on the island (*c.* 0.5°C lapse rate per 100 m, Jaffré 1980) meant that environmental conditions above 1,000 m (e.g., vegetation, Morat *et al.* 1981) were noticeably different from those in Létocart's low altitude study area (< 450 m a.s.l.). Therefore, I looked for habitat over 1,000 m where kagus lived, and found that only one higher altitude area complied with criteria 2 and 3, the forested peak of Pic Ningua (see Fig. 2-2 and Plate 3-1).

Very little was known about kagu life history characteristics or kagu food supplies at high altitude. However, based on what was known about the birds at Parc Rivière Bleue, and tropical conditions, I made four general predictions related to the hypothesis that the kagu's low annual fecundity is due to food limitation:

(1) Kagu food abundance is closely linked to climatic conditions.

(2) Kagu food supplies are relatively evenly dispersed, available year round and vary in highly predictable ways as is suggested by kagu social organisation (Emlen and Oring 1977).

(3) Kagus face annual, highly predictable density-independent food limitation for reproduction.

(4) When all factors are considered, kagus time their breeding to maximise reproductive success.

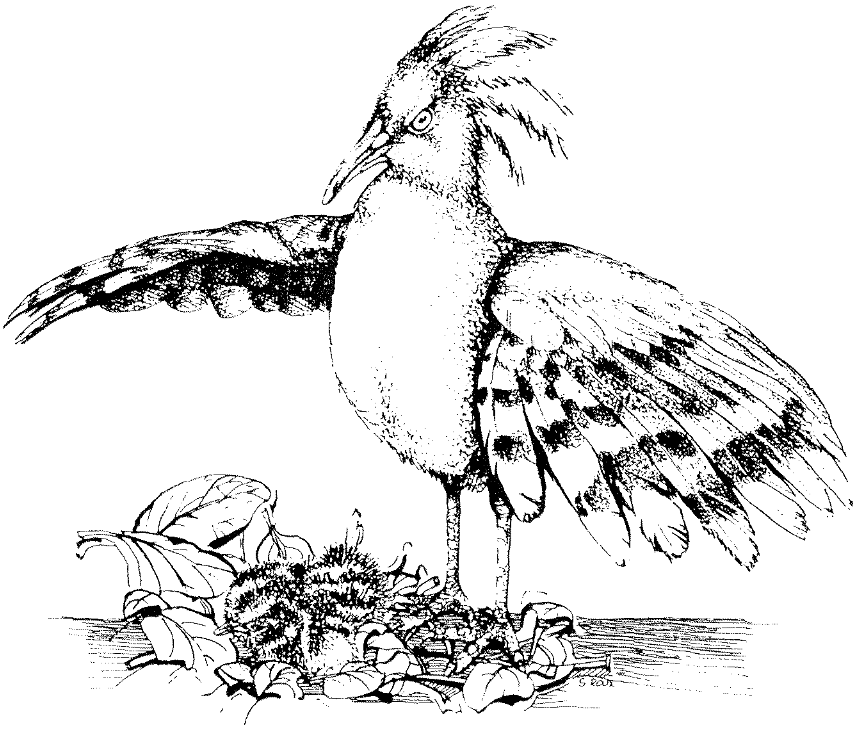
I investigated whether the kagu's low annual fecundity was due to food limitation by focusing on life history characteristics indirectly related to reproduction, rather than on more directly related ones like number of breeding attempts and food delivery rates to chicks. This was partly a consequence of dog attacks on birds at Pic Ningua which limited the amount of breeding data I could collect there (see below). First, I looked at the inter-relatedness of a range of important kagu life history characteristics (organisation of the annual cycle, the frequency and success of breeding, fat deposition, foraging and roosting behaviour, and social organisation) and environmental conditions (climate, food supply and parasites) simultaneously throughout the kagu's annual cycle at Pic Ningua. This allowed a more unifying approach to studying the kagu's reproduction through the influence of time and energy on its life history characteristics. Such an approach has been encouraged by King (1974) and more recently by theoretical workers developing life history models (McNamara and Houston 1996, Moen *et al.* 1997). Second, I compared, where possible, the relationships I found at Pic Ningua with those same ones established at Parc Rivière Bleue. Within-species comparisons between different habitats can point to reasons behind any variation in life histories (e.g., Jouventin *et al.* 1996, section 1.5). My study was descriptive and not an experimental one, therefore a cautious approach must be taken when addressing causality because an unmeasured factor(s) might be responsible for any observed correlations. Nevertheless, hypotheses of food limitation can be tested without experimentation (e.g., Schluter and Repasky 1991). I organised my data collection at Pic Ningua around a more-or-less continuous fortnightly sampling routine to try and measure variables in as much detail as possible over time, but without unnecessary over-sampling.

My study at Pic Ningua was seriously disrupted three months after I began fieldwork when many of my study birds died from dog attacks between April and August 1993 (Hunt *et al.* 1996c, *Chapter 4*). This considerably reduced the possibility of my collecting breeding data from kagus because most of the few remaining study birds were non-breeding and unpaired. I attempted to collect breeding data from birds at a second study area, on the nearby (7.5 km) peak of Mt Cindoa, from October 1993 to February 1995. I knew from my kagu survey that birds lived on the peak at altitudes above 1,000 m. Although I collected valuable data on birds there (e.g., diet, movements, roosting behaviour), I did not record any breeding activity in the almost 1.5 years that I studied them. Establishing the association between food and at least the timing of breeding for kagus was important, but I was unable to do this at my high altitude study areas. Therefore, as kagu breeding activity was well known at Parc Rivière Bleue but the association with food was not (section 1.4), I also collected data on food supplies at the Parc, from January 1994.

A life history trait is the outcome of selection on the average (phenotypic) reaction for an individual in response to its condition (McNamara and Houston 1996). Establishing individuals' average reactions is therefore essential, and requires observations on individuals over significant amounts of time (Blanckenhorn and Perner 1996). Short term, descriptive studies like mine on birds can however establish patterns which suggest what the average reaction might be (King 1974), and I attempt to do this in *Chapters 3* and *5*, along with describing kagu feeding ecology and weather-related conditions over time. In *Chapter 6* I use exploratory analyses to look for associations between the variables that I measured because this might provide clues about causality and/or indicate areas for further investigation. In *Chapter 7*, I conclude my thesis with a review of *Chapters 1-6* to see if there is support for the four predictions I made above and if food might be limiting the kagu's annual fecundity, and what the implications of my study are for kagu conservation management and kagu research in the future.

2

Environmental variables associated with kagu population patterns



2.1 Introduction

Identifying associations between environmental variables and the distribution of a threatened bird species is important. This information may help pinpoint factors responsible for shrinking distribution patterns and allow management actions for species conservation to be correctly targeted (Caughley 1994). As well, the selection of areas for new reserves may be aided by identifying environmental attributes associated with higher bird densities.

Previous surveys (Warner 1948, Béland 1975b, Jeggo 1978, Thiollay 1989) added valuable new information about the kagu population and possible factors responsible for declining kagu numbers (section 1.2), but contributed mainly qualitative data towards identifying factors associated with kagu distribution. Thiollay (1989) in his six week survey of known kagu areas from 31 listening sites measured altitude, degree of disturbance, presence of predators, and vegetation type associated with kagu presence, and identified disturbance (especially forestry activities) as being associated with low bird numbers. Thiollay suggested that certain regions where he recorded kagus should be protected, but his recommendations were based on a small data set. There was local scepticism and doubt about the seriousness of the situation facing the kagu as birds were thought to be more numerous (Cherrier 1990).

In order to obtain a larger data set and a more accurate estimate of kagu distribution and abundance, I carried out a seven month survey for kagus between June 1991 and January 1992 for the Association pour la Sauvegarde de la Nature Néo-Calédonienne (A.S.N.N.C.), the mainland provincial administrations, and the South Pacific Regional Environmental Program (S.P.R.E.P.) (Hunt 1996a, reprint in Appendix I). The expectation was that kagus would be found mainly in intact and remoter forest. This had been suggested by previous authors (e.g., Warner 1948, Jeggo 1978), and supported by Thiollay's survey.

2.2 Methods

2.2.1 Survey method

Kagu presence in an area is difficult to detect, but birds have distinctive early morning song and listening surveys are the most appropriate census method (Jeggo 1978, Létocart 1989). I carried out the survey between 11 June 1991 and 18 January

1992, which covered the main kagu breeding period for wild kagus at Parc Rivière Bleue (section 1.4). Because kagu song is sex specific and partners duet, mated pairs can be identified, although a juvenile can sometimes duet with a parent of the opposite sex when the other parent is absent (Y. Létocart pers. comm.). Kagus also sometimes sing around dusk (Jeggo 1978) so I surveyed many areas incidentally from evening campsites. Early authors commented on the considerable carrying distance of kagu song (Pouget 1875, Campbell 1904), and from preliminary observations at Parc Rivière Bleue I estimated I could hear kagu song for up to 2 km in ideal conditions.

The results of previous surveys, knowledgeable locals, and a newspaper questionnaire provided information on possible kagu areas. I also selected survey areas from aerial photographs, and after personally viewing the countryside. I did not survey Parc Rivière Bleue because the number of kagus there was known (Létocart 1992), nor the sclerophyll forests along the southwest coast because they were highly degraded and covered a small area (Bouchet *et al.* 1995, section 1.3) and there were no reports of birds living there.

Within areas to be surveyed I targeted the type of habitat (wetter forest on less steep ground) that kagus were thought to prefer at Parc Rivière Bleue (Létocart 1991). However, a broad range of vegetation types (e.g., low shrubland) was often covered incidentally from a 'listening site', where observations were made (referred to as 'site' hereafter in this chapter). I selected sites because of their acoustic attributes, preferring ridge-top clearings. I established the boundary of a 'listening area' from a site (referred to as 'area' hereafter in this chapter) taking into account weather conditions, vegetation at the site, and topography and drew it on a 1:50,000 topographical map. Overlap of areas rarely occurred. The observation period at sites was usually 45 minutes before and after sunrise to cover the known kagu singing period (Jeggo 1978, Létocart 1989).

I recorded the start and finish times of individual songs (a duet was timed as one song). I did not record juvenile kagus who may have sung with their parents, and those who may have sung alone would have been recorded as adults. I recorded duetting kagus as a pair.

I took the compass bearing of individual kagu song heard from a site, and rated its audibility as: '1' (heard occasionally); '2' (heard continuously but not clearly); '3' (heard continuously and clearly); or '4' (heard very clearly). If several pairs, or individuals, sang from the same direction at different times, I only recorded different kagus if the audibility ratings of the songs differed by more than 1 (e.g., '1' and '3'). A kagu can sing at different locations on the same morning, but most likely within its territory (Y. Létocart pers. comm.), so I recorded as different those birds who sang from distinctly different directions, regardless of song strength. The methods I used to record birds could have resulted in some being counted more than once, but I estimate this would have occurred infrequently. I plotted approximate kagu positions on the 1:50,000 maps.

Kagu numbers in most areas would have been underestimated by this census method as kagu singing frequency can vary considerably (Létocart 1989). To check the census data, I repeated observations at three sites with easy access in June and July 1992. Two were in logged forest (Mt Dzumac) where small numbers of kagus originally sang, and one in intact forest (Pic Ningua) where had I recorded 20 birds. I listened at each of the three sites for four consecutive mornings and recorded the number of kagus who sang.

2.2.2 Environmental variables

I recorded eight environmental variables at an area (continuous ones were categorised as shown below for the generalised linear modelling analyses; data in Appendix II). Létocart's (1989) data appeared to show no obvious difference in singing frequency between June and December on mornings when kagus sang, thus I did not include a 'singing season' variable.

(1) *Access* was a measure of the walking time to the site from the nearest in-use road, or (subjectively) the difficulty of public access if use of the road was restricted (those in mining areas or parks, and on private property). Distances along the restricted roads from public ones to where they came nearest the areas was at least 2 km. This variable measured 'remoteness' due to difficulty of terrain or public access which was not accounted for using actual map distances (see variables 5 and 7 below). Categories were: (1) Easy (< 2 hours walking and not restricted); (2) Moderate (2-4 hours walking or moderately restricted); (3) Difficult (> 4 hours walking or very restricted).

(2) I took the *Mean altitude* of kagu positions (to the nearest 50 m, using the lowest and highest positions only) from 1:50,000 maps. Categories were: (1) Low (0-399 m); (2) Moderate (400-799 m); (3) High (> 799 m).

(3) *Forestry history* was provided by forestry staff. Forestry consisted mainly of selective logging. I included exotic plantations as current forestry activities. Categories were: (1) Little or no activity; (2) Significant past activity (before 1987); (3) Significant recent activity (1987-1991).

(4) I obtained the *Geology* from Paris (1981). Categories for rock types were: (1) Sedimentary/Metamorphic; (2) Volcanic (non-ultrabasic); (3) Volcanic (ultrabasic).

(5) I measured the distance to the *Nearest in-use road* on the 1:50,000 maps, from the approximate centre of the area. Categories were: (1) Close (0-2.99 km); (2) Moderate (3.0-5.99 km); (3) Far (> 5.99 km).

(6) I estimated *Listening area size* by using the area of the circle (on the 1:50,000 maps) that just enclosed it. Many areas were circular in shape. Categories were: (1) Small (0-299 ha); (2) Moderate (300-599 ha); (3) Large (> 599 ha).

(7) I measured the distance to the *Nearest settlement* on the 1:50,000 maps, between the approximate centres of the settlement (virtually all were tribal villages) and the area. No distance was less than 1.5 km. Categories were: (1) Close (1.5-3.99 km); (2) Moderate (4.0-6.49 km); (3) Far (> 6.49 km).

(8) I estimated *Vegetation type* (the dominant vegetation where kagus sang from) by visual appraisal, or took it from Morat *et al.* (1981). Categories were: (1) Shrubland (the 'maquis' on the ultrabasic rocks); (2) Dry forest/Woodland; (3) Rainforest.

2.2.3 Generalised linear modelling

I fitted generalised linear models (Nicholls 1989) to the survey data to look for those environmental variables that could help explain the observed kagu distribution. I excluded areas without kagu records from the analyses for two reasons: they were not representative of those where birds did not occur because I targeted likely kagu areas (areas with kagu records probably represented those where birds occurred as the survey was comprehensive), and birds may have been present but not sung. For repeated observations in an area, I used the one where most kagus were recorded, or when numbers were identical, the first one. I excluded incomplete data recorded from one area by a local person.

I used the GLIM statistical package (NAG 1986) for the analyses. I initially included all the eight environmental variables in analyses, and 13 of the possible 28 pair-wise correlations between them were significant (Spearman correlation coefficients, $n = 83$, $p < 0.05$).

The response data (kagu numbers in areas) were counts but did not fit well a poisson (data were over dispersed; coefficient of dispersion = 5.37) or negative binomial (with zero values included; *G*-test for goodness of fit, $G = 9.48$, d.f. = 3, $n = 177$, $p < 0.05$) error distribution. I used a poisson error distribution with a log link with a scale parameter estimated from the data which accounted for the over dispersion (Crawley 1993).

As well as exploratory analyses on the main effects (analysis A), I also looked for interactions between the variables (analysis B). I present the results of both these analyses. I generally carried out model simplification by backward deletion (Crawley 1993), however some modification to this method was forced by aliasing of higher order interactions. Variables were kept in the current model if the change in deviance when they were removed was significant.

2.3 Results

2.3.1 Kagu distribution and abundance

Data from 186 morning observation periods were recorded in 177 different areas (Fig. 2-1), including three where local people recorded data for me. Repeat observations were made in nine areas, at the same sites. The estimated sizes of areas varied from 44 to 990 hectares (mean = 366 ha, $n = 83$, s.d. = 189).

Kagus mostly sung in the more remote and mountainous inland regions. They were distributed patchily throughout a large area of the island, but no birds were recorded in the northern-most parts. The northern limit for kagus was Mt Kopéto (in the southwest), and near the peak of Pouaïlatimbé (in the northeast) (Figs. 2-1 and 2-2). The southern limit was the Thy Parc (in the southwest), and along the Mamié River (in the northeast). Birds were recorded at altitudes from 100 m (along the Ouenghi River near Boulouparis) to 1,400 m (near the summit of Mé Maoya).

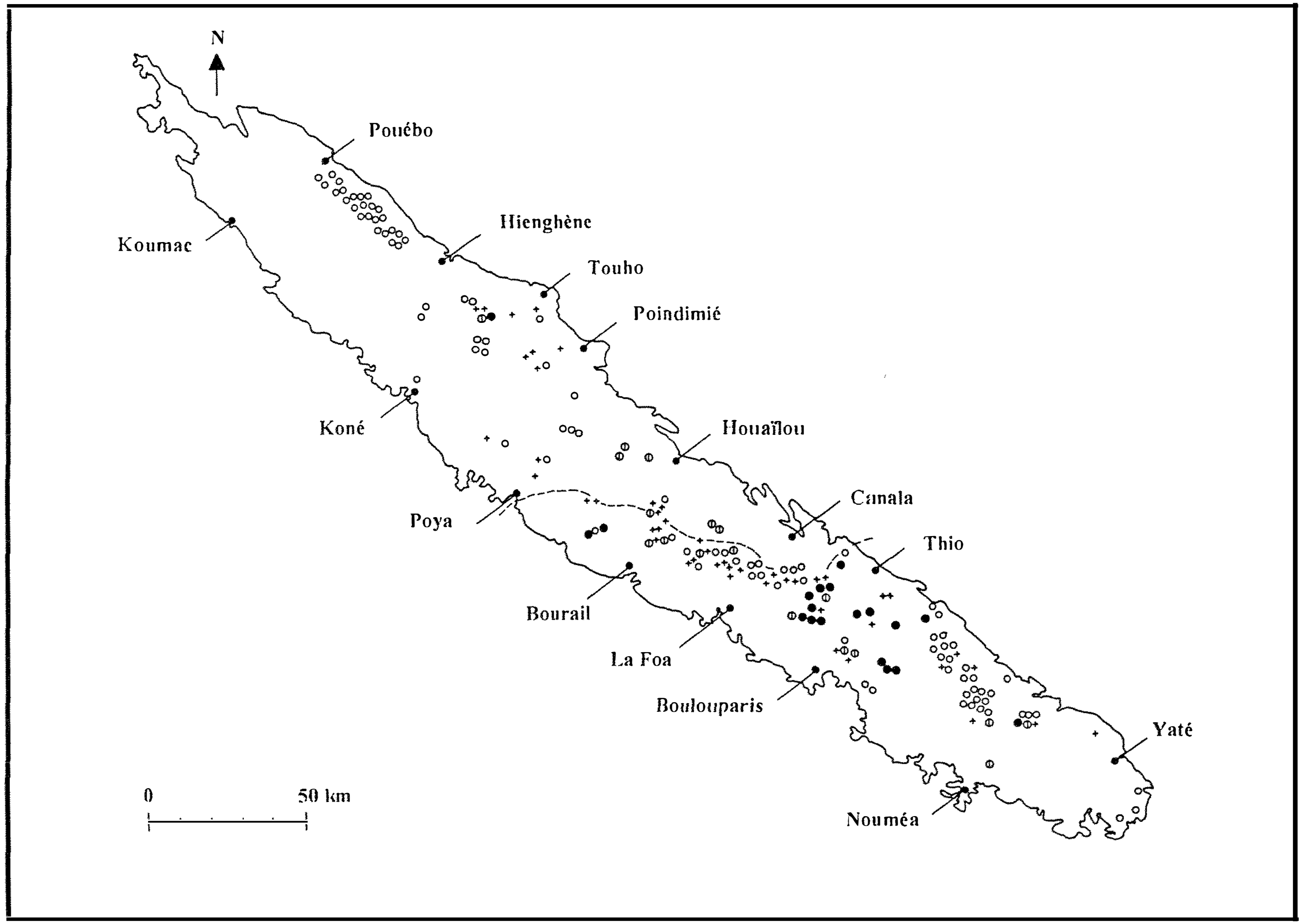


Figure 2-1. Positions of the 177 different listening areas visited on Grande Terre indicated by the number of kagus recorded in them ('o' = no kagus; '+' = 1-4 kagus; '⊕' = 5-9 kagus; '●' = > 9 kagus). The dashed line shows the position of the boundary between Province Nord and Province Sud.

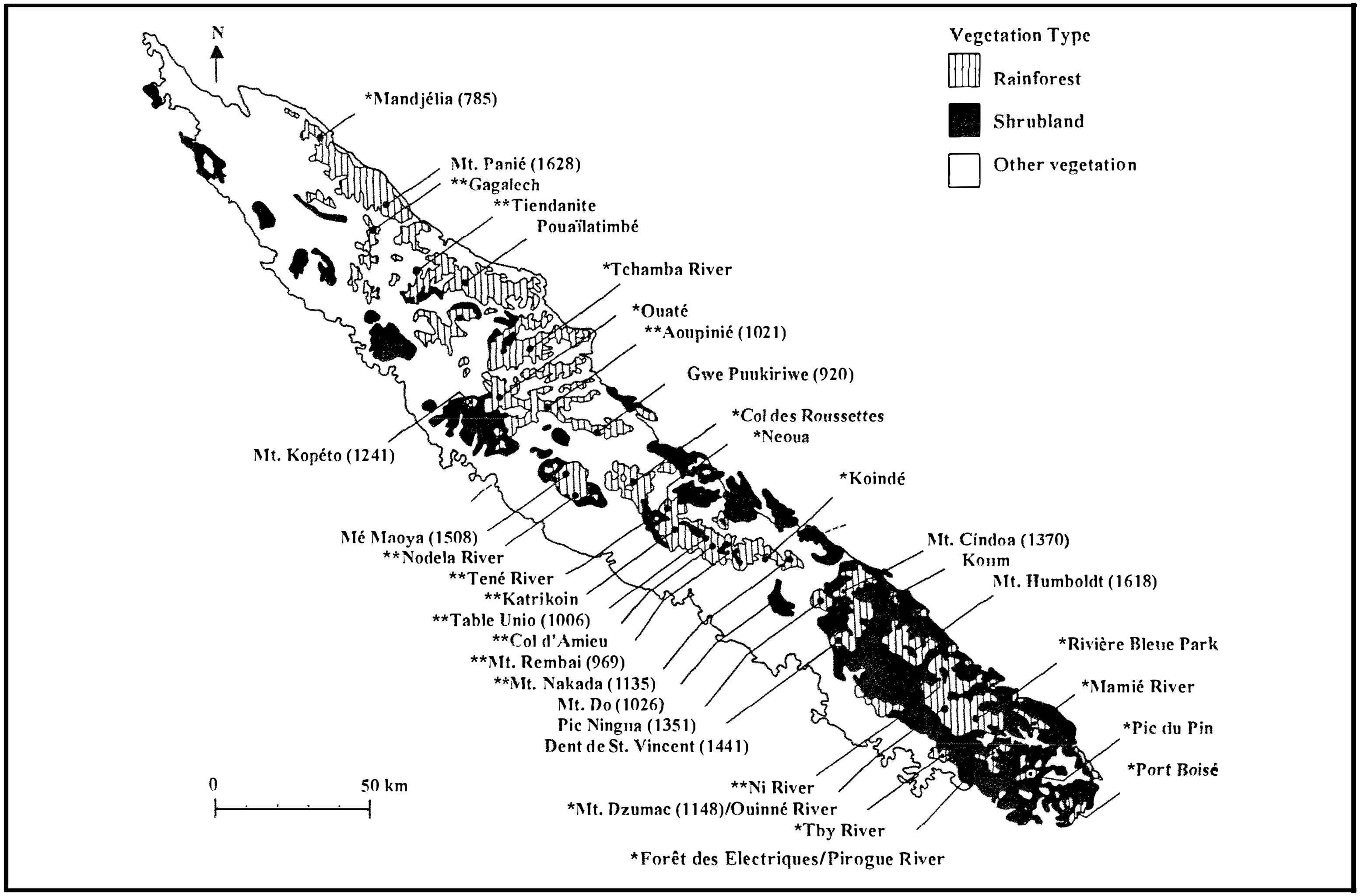


Figure 2-2. Principal vegetation types (from Paris 1981) on Grande Terre. Locations cited in the text, and those uncited where significant logging has occurred, are labelled (heights (m) of peaks are in brackets). For logged locations, '*' = logging stopped before 1987, and '**' = logging continuing or stopped between 1987-1991. Shrubland indicates the approximate distribution of ultrabasic rocks on the island. The north/south provincial boundary passes through or near the peaks of Mé Maoya, Table Unio, and Mt Nakada.

A total of 491 kagus, including 208 pairs, were recorded in 84 (47%) of the areas. Most birds (403) were in Province Sud, and those in Province Nord were in two main regions around the peaks of Pouaïlatimbé, and Gwâ Pûûkiriwé. Birds heard singing alone were predominantly males (males, n = 38; females, n = 4). The sex of 14 kagus was unknown, consisting of eight birds who made only the preliminary 'drumming' call, two heard by local people, and four seen but not heard.

In 47 (56%) of the 84 areas with kagu records, only small numbers (1-4) of birds were recorded (Fig. 2-1). More than nine kagus were recorded in each of 19 areas, accounting for 57% (n = 282) of all birds found. Eighteen of these 19 areas were in Province Sud, where 15 of them occur in the region between Boulouparis and Thio. The most kagus singing on one morning was 24, in the Nodela River valley before logging started there in August 1991.

Within areas, kagus appeared to be distributed non-randomly as they sang mainly from wetter forest on less steep terrain. They sang infrequently from tall shrubland along rivers at low altitude (e.g., on the south side of Boulinda Massif), and once from tall shrubland at high altitude (above 1,000 m a.s.l. on Mt Cindoa). No kagus sang from savanna-grassland associations, or the short open maquis on the ultrabasic rocks.

2.3.2 Calibration sites

On only one of the 12 mornings at the three calibration sites (at Pic Ningua) did the number of kagus singing approach the original number who sang (Table 2-1). I heard no birds at either site on Mt Dzumac. Thus, numbers of kagus recorded at the calibration sites were substantially less than on the original survey. Weather conditions were similar for the original and calibration visits.

Table 2-1. Numbers of kagus singing at the three calibration sites, together with the data from the original survey. Listening dates are in brackets.

	Numbers of kagus singing				
	Original	'Calibration' listenings			
Site	**listening**	**1**	**2**	**3**	**4**
Pic Ningua	20 (23/8/91)	0	5 (13-16/6/92)	0	15
Mt Dzumac (site 1)	6 (27/12/91)	0	0 (22-25/6/92)	0	0
Mt Dzumac (site 2)	4 (25/12/91)	0	0 (30/6/92-3/7/92)	0	0

2.3.3 Environmental variables associated with kagu numbers

The majority of areas with ten or more kagus were at least 400 m a.s.l., on volcanic rocks, in habitat difficult of access, 6.5 km or more from settlements, closer than 3 km to in-use roads, and small to moderate in size. No areas with ten or more kagus occurred in shrubland or in habitat with a history of significant forestry activities.

Generalised linear modelling analysis with only the main effects (analysis A) retained two variables, Access and Geology, in a minimal adequate model (Tables 2-2 and 2-3), indicating that kagus were in larger numbers in remoter habitat, and on volcanic rock types (Fig. 2-3). In analysis B, only two two-way ones were retained in a minimal adequate model: Access x Listening area size, and Access x Nearest settlement (Tables 2-2 and 2-3).

Table 2-2. Goodness-of-fit statistics for the null, minimal adequate, and maximal models for analyses A and B carried out on the data set with kagu records. I calculated the scale parameter manually to adjust for over dispersion in the response data (section 2.2.3, Crawley 1993).

Model	**Deviance**	**Cumulative change in deviance**	**d.f.**	**Scale parameter**
Analysis A: Main effects only				
Null model	117.98	-	82	3.22
Minimal model AC+GE	89.94	28.04	78	3.22
Maximal model AC+AL+FO+GE+ LS+RO+SE+VE	69.24	48.74	66	3.22
Analysis B: Main and two-way interaction effects				
Null model	117.98	-	82	3.22
Minimal model AC+GE+LS+SE+ ACxLS+ACxSE	72.25	40.73	73	3.22
Maximal model Main effects and two-way interactions	8.86	109.13	12	3.22

AC = Access; AL = Mean altitude; FO = Forestry history; GE = Geology; RO = Nearest in-use road; LS = Listening area size; SE = Nearest settlement; VE = Vegetation type.

Table 2-3. Parameter estimates and their standard errors for the two minimal adequate models (in Table 2-2) of environmental variables fitted to the numbers of kagus recorded in listening areas. Parameters for Geology, Listening area size, and Nearest settlement in analysis B were combined without a significant increase in the deviance. The Parameter estimate / Standard error (s.e.) ratio (Column 4) is a rough guide as to the significance of parameters (ratio < 2 = usually not significant; ratio > 3 = usually significant) (Crawley 1993).

Parameter	**Parameter estimate**	**Standard error**	**Parameter estimate / s.e.**
Analysis A: Main effects only minimal adequate model			
Constant	0.872	0.478	3.649
Access			
Moderate	0.707	0.210	3.373
Difficult	0.296	0.235	1.407
Geology			
Volcanic (non-ultrabasic)	0.580	0.239	2.431
Volcanic (ultrabasic)	0.921	0.237	3.879
Analysis B: Main and two-way interaction effects minimal adequate model			
Constant	0.786	0.521	1.509
Access			
Moderate	0.707	0.639	1.108
Difficult	-0.705	0.907	0.780
Geology (volcanic)	0.495	0.191	2.590
Listening area size (moderate/large)	0.235	0.461	0.509
Nearest settlement (moderate/far)	-0.067	0.430	0.155
Access (moderate) x Listening area size	-0.758	0.531	1.426
Access (difficult) x Listening area size	0.432	0.526	0.821
Access (moderate) x Nearest settlement	0.378	0.583	0.648
Access (difficult) x Nearest settlement	1.412	0.864	1.635

Figure 2-3. Frequencies of listening areas by the numbers of kagus recorded in them for each category of the eight environmental variables initially entered in the maximal models (Table 2-2). Key to classes for kagu numbers is in the Access graph. Categories for the variables are described in section 2.2.2.

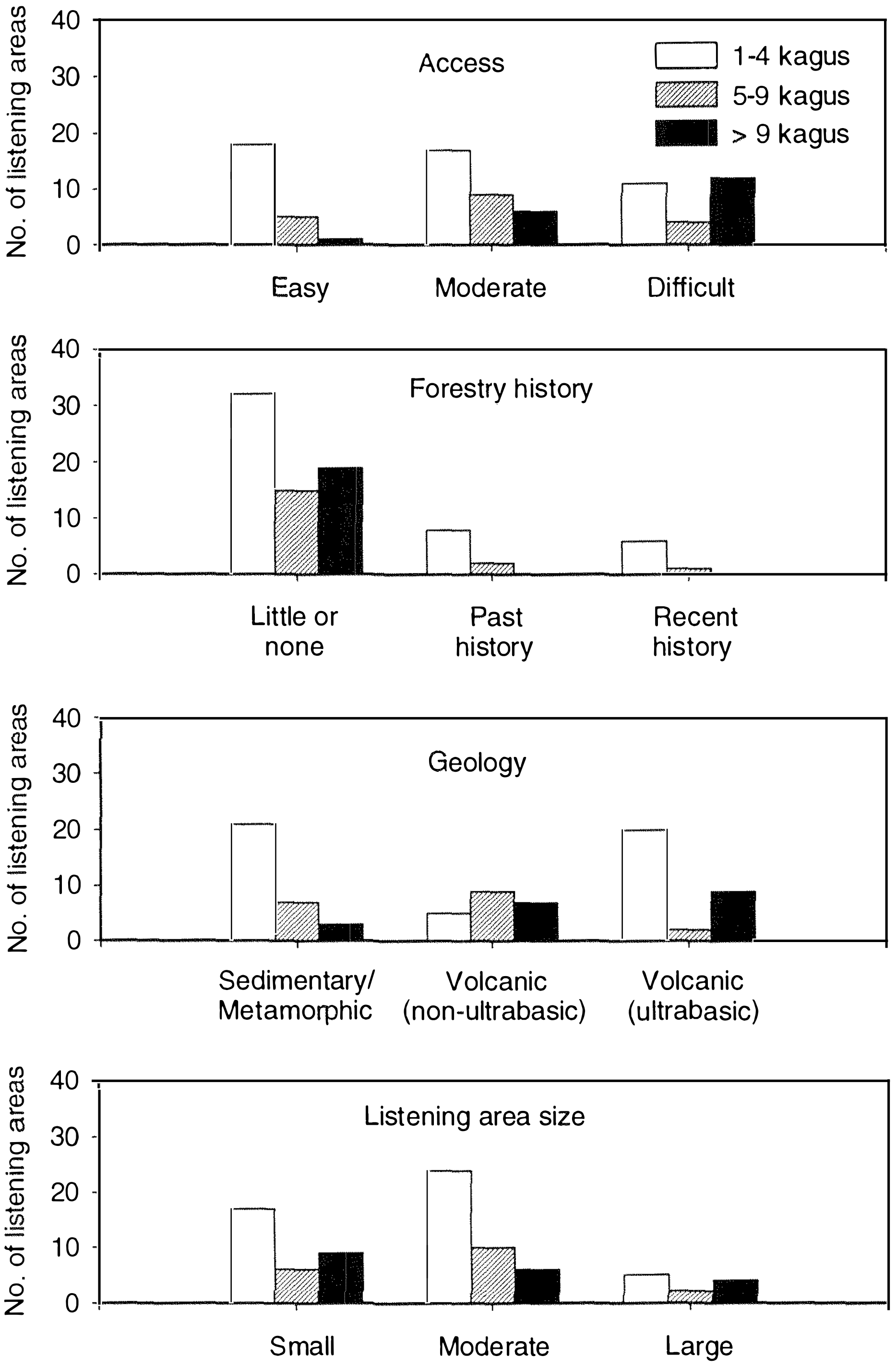
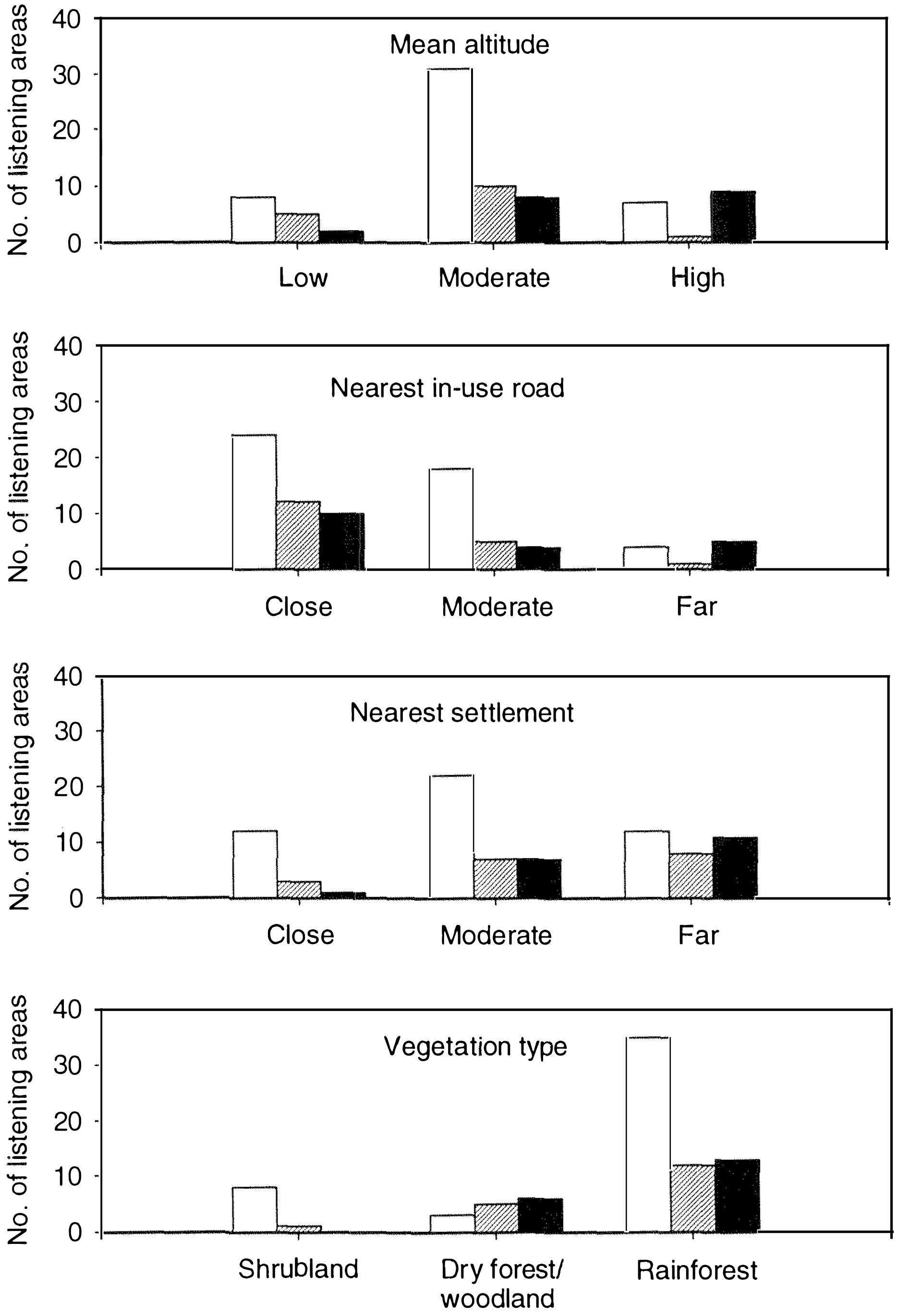


Figure 2-3 continued next page.

Figure 2-3 continued.



2.4 Discussion

The 491 adult kagus recorded on the survey, plus the 163 birds (including juveniles) counted at Parc Rivière Bleue (Létocart 1992), brought the known kagu population on the island to 654 in early 1992. The survey total was only a minimum estimate for three reasons: all birds in an area were unlikely to sing on any morning (Létocart 1989), birds may have been in areas with no kagu records, and not all potential kagu habitat was surveyed. However, there may not be substantially more than 491 kagus. First, when birds sang at Parc Rivière Bleue in the same season as this survey, on average about 50% present did so (Létocart 1989). Second, it is reasonable to assume that kagus were absent from at least some of the 93 (53%) areas with no kagu records, for example Panié Massif where no kagus were recorded. Last, the survey covered most of the likely-to-be-important kagu regions on the island.

Comparison of the calibration and survey data showed kagu singing behaviour can vary considerably, assuming a similar number of birds were present in both visits to each of the three areas. However, if the variation in the percentages of kagus singing in areas was relatively uniform over the survey then the generalised linear modelling analyses should still provide meaningful results in identifying environmental variables associated with kagu numbers because it is based on a relatively large data set. A good fit of the response data supported this, there were no large (> -2.0) negative residuals (where more kagus were predicted than recorded) and only three large (> 2.0) positive ones for the minimal adequate model for analysis B.

The fragmented kagu distribution is due in part to a patchy forest cover (Fig. 2-2), especially on the ultrabasic rocks that cover approximately 6,000 km^2 in mostly the southern third of Grande Terre. Mainland forests are not extensive (section 1.3), and are even less so on the ultrabasic rocks (*c.* 750 km^2; 12.5% of their surface area) (Schmid 1981). Forest on these rocks tends to be restricted to higher altitude and along water systems, but more widespread on other geology. Just over 39% (n = 192) of the kagus recorded were on ultrabasic rocks where only a small percentage (22%) of remaining rainforests occur. Annual dry season fires are largely responsible for reducing the island's once extensive forests (Mittermeier *et al.* 1996), and habitat loss is an increasingly important threat to kagus.

The Access variable seems an important measure of remoteness of areas from human activity as it was significantly positively correlated with Nearest in-use road and Nearest settlement, and negatively correlated with Forestry history. Thus the minimal adequate model for analysis A appears to suggest that kagus away from human activity (in areas difficult of access) will more likely be in greater numbers. This is also consistent with greater numbers recorded on the generally more rugged volcanic rocks. Analysis B identifies the nearness of settlements to kagus as an important human-related factor associated with lower bird numbers. An obvious anomaly is the apparent disappearance of kagus from forests on the rugged and remote Panié Massif, but this might be related to a possibly greater dog *Canis familiaris* presence in northern regions (Seitre and Seitre 1990, *Chapter 4*).

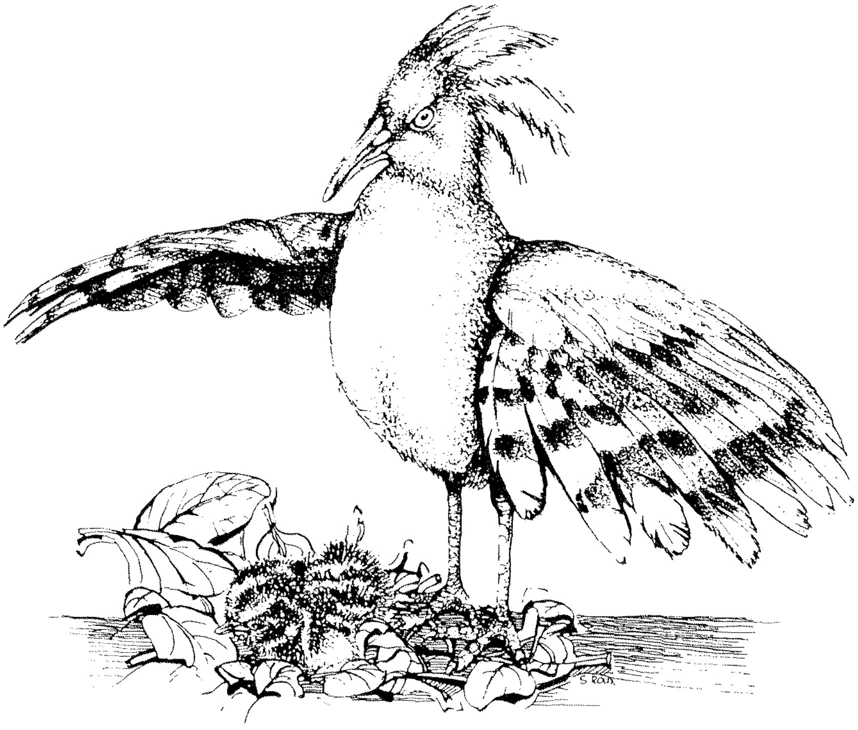
Forestry history did not explain well the variation of kagu numbers in areas as it was absent from both minimal adequate models, perhaps because small numbers of kagus were also recorded in intact forest. However, the lack of kagus in logged forest strongly suggests that factors associated with forestry activities have an important long-term adverse impact on birds as exploited forest remains unsuitable to support their numbers at pre-logging levels. Local people informed me that in logged areas where kagus were recorded (e.g., Thy River valley, Mt Dzumac, Col des Roussettes) greater numbers of birds were present before logging began.

Nearest in-use road was also not selected in either minimal adequate model, possibly because 59% of the areas with over four kagu records were close to in-use roads. Thus any 'presence' effect of these roads on kagu numbers occurs at less than 3 km from birds. The type of road use could be an important factor effecting kagu numbers and is partly taken into account by the Access variable. For example, restricted-use roads were sometimes very close to areas with many kagus (e.g., northeast of Mt Do), but unrestricted ones into or near logged forest, often used by hunters and their dogs, were always associated with low bird numbers.

A real danger for the kagu population is that small numbers of birds restricted to higher altitudes or remoter areas will become increasingly isolated from each other. This is happening on the southern ultrabasics where kagus are becoming confined to mountain peaks (e.g., Pic Ningua, Dent de St. Vincent, Mt Cindoa) or remote river valleys (e.g., Koum). This may have repercussions for the maintenance of genetic diversity and long term kagu persistence if migration of birds between 'patches' cannot occur (Soulé 1980). Therefore kagu numbers even in intact and less disturbed habitat may be in a slow state of decline (Thiollay 1989), which is not uncommon for similar long-lived threatened species (Goodman 1981).

3

Bodyweights, breeding, movements, moult, roosting behaviour, and social organisation of kagus on the forested peaks of Mt Cindoa and Pic Ningua, and the effects of dog predation on surviving birds at Pic Ningua



3.1 Introduction

It was difficult to predict what the life history characteristics (breeding behaviour, timing of moult, roosting behaviour and social organisation) of kagus might be at high altitude from knowledge of birds at Parc Rivière Bleue (bodyweight variation and length of primary moult were not well known at the Parc; section 1.4) because environmental conditions there were different compared to the Parc (section 1.6). Increase in altitude might lead to stronger seasonality and/or different weather which could influence food supplies and annual cycles and result in aspects of kagu life history differing compared to low altitudes. In west Cameroon for example, some bird species bred in montane areas in the dry season and in lowland areas in the wet season, even on the same mountain (Tye 1991). One reason suggested for this was that the high rainfall and associated lower temperatures and mist at high altitude might make conditions unsuitable for breeding in the wet season (Serle 1981), possibly because of deleterious factors like reduced foraging time, lower insect activity, and nest damage by heavy rainfall (Tye 1991). Heavy rainfall can also break down chicks insulation (Török and Tóth 1988). Weather maps indicated that Parc Rivière Bleue should have a higher annual rainfall than Pic Ningua, but rainfall would be highest at Mt Cindoa (Pesin and Thomas 1993).

One important energetic aspect of a bird's annual cycle is moult, and its timing and duration are generally assumed to be adaptive (King 1974). The timing, frequency and duration of primary moult in bird species shows considerable variation even at one location (e.g., Chapman 1995), but there are some general trends. Moult and breeding activity are commonly partitioned in the annual cycle where the former generally follows closely after the latter (Murton and Westwood 1977), and duration of moult tends to increase with decreasing latitude in some species (Welty and Baptista 1988, Bensch *et al.* 1991). In their study of palaearctic migrants in west Africa, Bensch *et al.* (1991) found that birds moulted almost as fast as some rapidly moulting birds in temperate zones. From their results they predicted that slow moult should occur in the tropics in a prolonged and predictable wet season, but should be rapid or partial in a wet season that is short and preceded by a predictable dry season because food supplies during the dry season may not be sufficient for moult. High rates of moult (e.g., less than 125 days) associated with strong seasonality can occur within tropical latitudes (e.g., Bensch *et al.* 1991, Tidemann and Woinarski 1994).

Létocart (in litt.) only observed moult in kagus at Parc Rivière Bleue from January to May over the relatively short wet season (section 1.4), therefore providing support for the latter prediction. Snow (1976) noted that the moult period tended to be far more predictable that the breeding period, coinciding with predictably high food supplies.

Fat deposition in birds may have fitness benefits related to survival in the non-breeding period (Rogers and Smith 1993, Grubb and Pravosudov 1994), and energetic demands of breeding (Drent and Daan 1980, Merkle and Barclay 1996). Bodyweight variation in birds mostly reflects changing fat or energy reserves obtained from food (Meijer *et al.* 1994), although the mass of other body components like protein reserves for reproduction (Fogden and Fogden 1979) and flight (Ward 1969) may also vary. Temperature and photoperiod are thought to be the two most important influences on bodyweight variation (Blem 1990, Meijer *et al.* 1996). Most research on this subject has involved small passerines in northern hemisphere temperate climates (e.g., Haftorn 1989, Rogers and Smith 1993), and has focused on the 'winter fattening model' (Lehikoinen 1987). This attempts to explain mid-winter peaks in fat deposition in some temperate birds as a mechanism to cope with unpredictable conditions in winter. Thus variation in fat reserves is predicted to be negatively associated with predictability and level of food supplies (Lima 1986). Studies show that the bodyweights of ground-foraging passerines where snowfall is common peaked in mid winter (data in Meijer *et al.* 1996), and Witter and Swaddle (1997) recently showed experimentally that fat reserves increased in periodically food-deprived starlings *Sturnus vulgaris*. Species living in milder climates or foraging above the ground where food supplies are less affected by snowfall showed little or no winter fattening (Rogers and Smith 1993, Graedel and Loveland 1995). A similar life history trade-off in fat deposition can occur in relation to social status in which socially subordinate birds show a greater tendency to fatten in winter than social dominants whose food supply is more predictable (Grubb and Pravosudov 1994, Pilastro *et al.* 1995).

Few data have been published on annual bodyweight variation in tropical forest birds (Meijer *et al.* 1996). Seasonal changes in bodyweights were only slight for two non-forest equatorial species, yellow-vented bulbuls *Pycnonotus goiavier* (Ward 1969) and grey-backed camaroptera *Camaroptera brevicaudata* (Fogden and Fogden 1979) at locations where rainfall and air temperatures also varied little. Bodyweight variation in rainforest passerines in Sarawak showed clear seasonality (Fodgen 1972). Weights peaked early in the breeding season around February/March at the end of the months of heaviest rainfall, then declined until increasing again as monthly rainfall began increasing in October. Davies (1977) found no obvious relationship between bodyweight variation and temperature in wild granivorous subtropical zebra finches *Taeniopygia castanotis* over three years in Western Australia. A recent study on captive zebra finches *T. guttata* in Germany showed that annual variation in their bodyweights was opposite to the winter fattening model as bodyweights peaked in summer (Meijer *et al.* 1996). The authors reported a positive association between bodyweights and length of photoperiod for the breeding birds. This appeared to be the main association rather than temperature since the birds were living in an indoor aviary at relatively constant temperatures. The bodyweight variation of zebra finches living in ambient temperatures in an outdoor aviary appeared to have a closer relationship with temperature than length of photoperiod, but data on annual variation in temperatures were not presented nor the relationship between them and bodyweights examined.

Due to the lack of data it is much less clear that energy storage strategies are important for resident tropical birds. However, dry season food scarcity is not uncommon for tropical land birds (e.g., Lack 1950, Ward 1969, Fogden 1972, Fogden and Fogden 1979, Snow 1976, Sinclair 1978, Dittami and Gwinner 1985) and can cause significant mortality in some island species (Catterall 1985, Grant and Grant 1996). As well, poor body condition is thought to cause higher mortality in green woodhoopoes *Phoeniculus purpureus* because this reduces their ability to survive night-time temperatures (Du Plessis and Williams 1994). Therefore fat deposition may be an important trait under selection for many tropical birds as well as temperate ones. In tropical forests where food supplies are thought to vary predictably and be available year round, birds should not exhibit winter or lean season fattening but instead have a positive relationship with food supplies.

A range of other factors may influence bodyweight variation in birds in addition to annual climate-related patterns as they attempt to meet the energetic demands for phases of their annual cycle, such as parasites (see *Chapter 5*), predation risk while foraging (Stephens and Krebs 1986, Lima 1986) and roosting in winter (Walsberg and King 1980), social reasons like rank (Ekman and Lilliendahl 1993, Pilastro *et al.*

1995), inter-specific and/or intra-specific competition and reproductive activity. Birds' bodyweights tend to be high or in an increasing phase just before they breed (Perrins 1970, Murton and Westwood 1977), and they may lay down fat in this period as a strategy to meet the energetic demands (e.g., incubation) of their young (Merkle and Barclay 1996).

The lapse rate in New Caledonia (section 1.6) meant that temperatures in forest over 1,000 m a.s.l. at Pic Ningua might be at least several degrees lower than those where Létocart studied kagus at Parc Rivière Bleue. Therefore the energy cost of night-time thermoregulation in cold periods might be an important constraint for kagus at high altitude. Observations have shown that bird species in temperate climates switch to more favourable roosting microclimates in colder weather where avoidance of cold temperatures seemed the obvious explanation (e.g., Berger 1961, Elkins 1983). For example, many gallinaceous birds burrow in snow to reach warmer ambient temperatures than occur at the surface. Seasonal change in roosting behaviour is known in communal roosting birds like American crows *Corvus brachyrhynchos* (Gorenzel and Salmon 1995), jackdaws *Corvus monedula* (Gyllin *et al.* 1977), bald eagles *Haliaeetus leucocephalus* (Stalmaster and Gessaman 1984, Buehler *et al.* 1991), starlings *S. vulgaris* (Kelty and Lustick 1977, Yom-Tov 1977), black vultures *Coragyps atratus,* turkey vultures *Cathartes aura* (Thompson *et al.* 1990) and American robins *Turdus migratorius* (Walsberg and King 1980). Studies on the behaviour of solitary roosters in the wild that vary their roost positions are relatively few. Walsberg (1986) showed that roosts of phainopepla *Phainopepla nitens* in winter provided considerable thermal benefits because of shelter from wind. Webb and Rogers (1988) also found the winter roosts of dark-eyed juncos *Junco hyemalis* provided shelter from wind, but suggested that this was relatively unimportant for small birds compared to fasting time. A thermal advantage of winter roost sites has been found or assumed for many of the above species, but other factors like protection from predation might also be important in influencing selection of winter roost sites (Gyllin *et al.* 1977, Yom-Tov 1977). However, this reason at least may not apply to kagus because adults have no known native non-human predators (*Chapter 4*).

The only tropical bird species that I know of other than the kagu whose roosting behaviour has received considerable attention is the green woodhoopoe which roosts in cavities year-round (Ligon *et al.* 1988, Du Plessis and Williams 1994). Permanent use of such obviously sheltered sites makes it extremely difficult to detect what the historic reasons for cavity roosting might have been. Du Plessis and Williams (1994) suggested though, that cavity roosting did have fitness benefits for green woodhoopoes because of reduced energy expenditure in colder conditions. If food was scarce for kagus in cooler dry season months at high altitude, then birds might exhibit roosting behaviour that reduced overnight energy costs at those times.

I also had the opportunity to record the behaviour of kagus at Pic Ningua following a large reduction in their numbers because of dog *Canis familiaris* predation (Hunt *et al.* 1996c, *Chapter 4*). This allowed me to collect information on the movements of birds after they lost their partners and/or neighbours, look at the process of pair formation, observe what factors might be behind fixed territory (an area of exclusive use that is defended; Davies and Houston 1984) holding behaviour by kagus and observe how bodyweights varied when intra-specific competition for food was negligible or absent. The latter was important in investigating if food supply for kagus might be density-independent. In *Chapter 4*, I describe in more detail the events surrounding the deaths of kagus on the peak and the evidence for dog predation.

My specific objectives at Pic Ningua and Mt Cindoa were to describe (1) kagu bodyweight variation over time; (2) the timing and frequency of breeding; (3) the timing and frequency of primary moult; (4) roosting behaviour; (5) social organisation and establish if breeding pairs lived in long-term relationships on relatively fixed territories, and lived in families; (6) morphological characteristics of kagus; and (7) meteorological conditions (rainfall and temperature). At Pic Ningua, I also described the behaviour of kagus after they lost their partners and/or neighbours because of dog predation.

This chapter is substantial and covers the range of data that I collected other than that on kagu diet, food supplies, parasites and possible competition from feral pigs *Sus scrofa* (presented in *Chapter 5*). In sections 3.3.1 to 3.3.4, I describe weather conditions at my two study areas and present data on kagus (morphometric measurements, timing of primary moult) that were probably little affected by the dog attacks. In sections 3.3.5 to 3.3.9, I mainly describe home range use and movements of kagus before, during and after the dog attacks at Pic Ningua. I describe the home range use and movements of kagus at Mt Cindoa in section 3.3.10. Lastly, in sections 3.3.11 to 3.3.13, I describe kagu breeding activity, and variation in birds' bodyweights and roosting behaviour over time at both study areas, aspects which might have been influenced by the dog attacks.

3.2 Methods

3.2.1 Study sites

Pic Ningua

Pic Ningua is an ultrabasic (see section 1.3), cone-shaped peak (1,351 m a.s.l.; 21°44'47" S and 166°8'16" E) situated in the central mountain chain of Grande Terre (Fig. 2-2), and slightly closer to the wetter northeast than the drier southwest coast. It was mostly separated from surrounding mountains by river valleys, but low saddles in the southeast connected Pic Ningua with mountains to the southwest and northeast (including the Mt Cindoa area). Its southeast slopes formed part of the sides of a large basin area (Camp des Sapins) draining into the Hwa Kwédé River. The northwest slopes descended to below 100 m and the Kuenthio River. The southwestern and northeastern slopes descended mostly below 500 m to the Koua and Nakaré Rivers (Fig. 3-1), respectively, which drained into the Kuenthio River.

Extensive nickel mining operations and associated roads have scarred the lower slopes below the forest around the peak (Plate 3-1). Mining was still continuing in the Camp des Sapins region and the mining access road ran around the north-facing slopes and part of the south-facing slopes of the mountain (Figs. 3-1 and 4-1). The road passed the forest at 950-1,100 m on the north-facing slopes (Plate 3-1), and was used mainly between 0300 and 1900 hrs for mostly light vehicle transport.

Over 500 ha of primary forest occurred on the peak and its slopes, mostly above 950 m (Fig. 4-1), and much of this (350 ha) was inside the Pic Ningua Botanical reserve established in 1983. The distinction between the various vegetation types (from montane rainforest to a range of 'maquis' or shrubland; indicated in Plate 3-1) was often not clear. Canopy height varied considerably but remained lower than the tallest rainforest at lower altitudes at Parc Rivière Bleue. Areas of low bracken-type ferns were also present, resulting from disturbance or past mining exploration (Fig. 3-

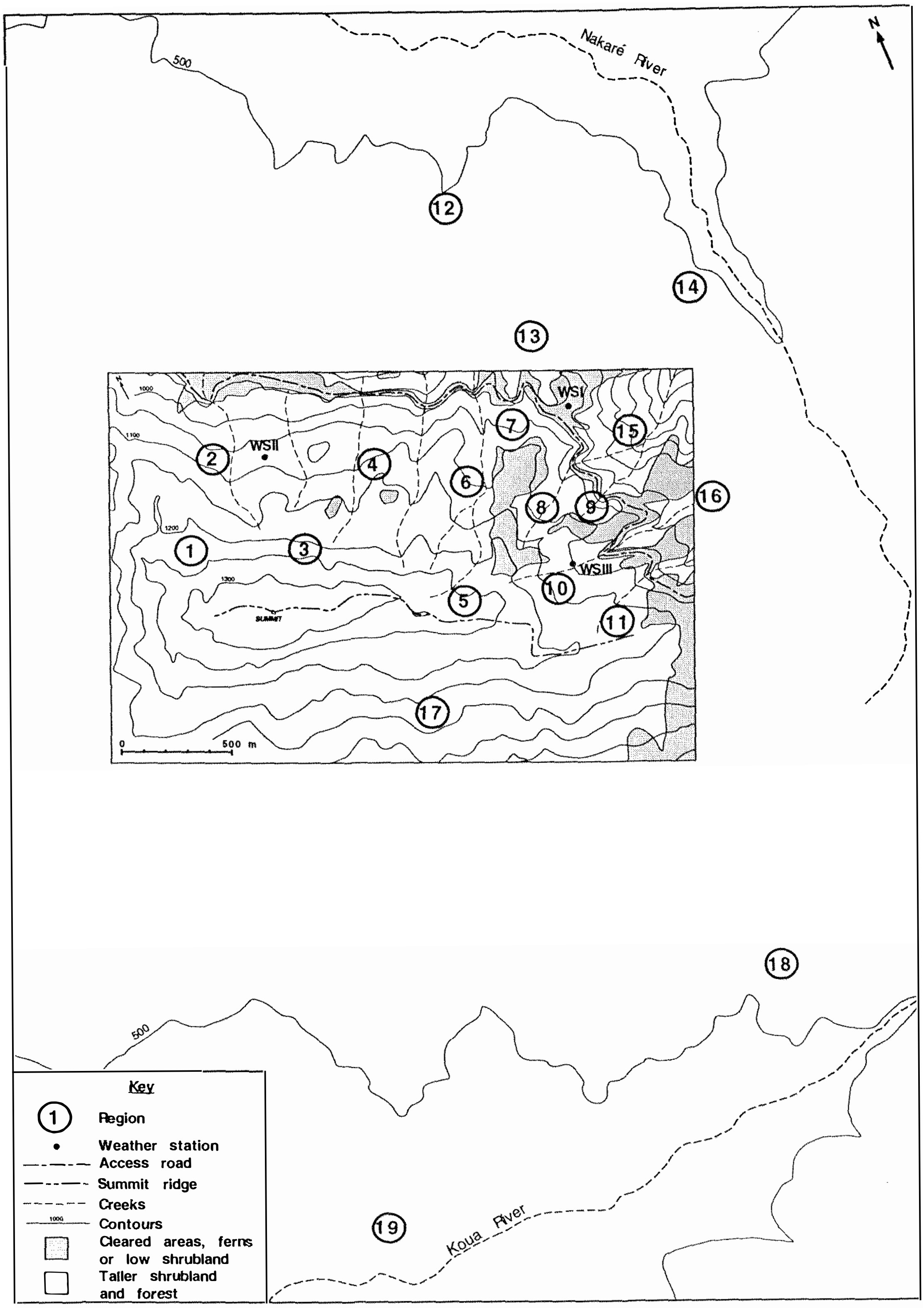


Figure 3-1. Map of Pic Ningua where I followed kagus for over two years. A smaller area (boxed in) is shown in more detail as I mostly followed kagus there. Shown within the boxed-in area are 50 m contours, the scale, direction of north, and the positions (black dots) of the three weather stations (WSI, WSII and WSIII) (see Key to map). The nineteen numbered regions (1-19, within circles) were used in describing kagu positions or their movements in the text. The 500 m contour is shown outside the detailed area. The map was drawn from a 1:10,000 map supplied by the Service Topographique du Territoire, Nouméa.

Plate 3-1. The north-facing slopes of Pic Ningua. Interesting features are the access road running around the slopes, the nickel mining damage particularly at far right, the gallery forests in valleys below the access road that descend to the Nakaré River, the contrast between forest and 'maquis' (shrubland) and the sometimes patchy forest cover above the road. The summit is 1,351 m a.s.l..

1). Descending the slopes from the main area of forest higher on the peak to lower altitudes were occasional gallery forests along steep-sided creek valleys (Plate 3-1). No logging had occurred on the peak, but from the abrupt forest/non-forest boundary and its patterning on the south-facing slopes, forest loss by fire had obviously occurred there. Because much of the shrubland on the ultrabasic rocks on Grande Terre was probably a consequence of ancient forest destruction by human-associated fires (Morat *et al.* 1986), most of the shrubland at my study areas had also probably replaced forest.

The forest understorey from 950-1,300 m was mostly open or not too difficult to negotiate, but tangled vines (mostly *Freycinetia longispica*), above-ground tree roots and low, thick vegetation dominated above this altitude near the summit. Forest at around 950 m appeared similar to rainforest at lower altitudes where mosses, for example, were lacking, but quickly changed into cloud-type forest above this level where tree ferns and mosses were common (see Schmid 1981 for a general description of the flora). In this damper forest, and in montane tropical forests in general (Leigh 1975), roots were more common above the soil, and leaves were generally smaller than at lower altitudes. Roots sometimes formed a raised forest floor, and on sloping terrain this created an abundance of sheltered sites under root/rock formed structures. Throughout the forest rock outcrops were common, often associated with ridges and steeper terrain and they sometimes formed rock faces. Creeks descended through the forest (Fig. 3-1) but were dry except when tropical cyclones or depressions in the wet season brought very heavy rain, and even at these times many of the creeks still did not visibly flow.

A summit ridge roughly divided the south- and north-facing slopes (Fig. 3-1). I initially followed kagus on only the north-facing slopes because many birds lived there and it had better road access, but as a consequence of the dog attacks I also later followed birds on the south-facing slopes as well. I had many kilometres of marked (coloured plastic tape tied to trees) walking tracks in forest on both sides of the peak.

Mt Cindoa

Mt Cindoa (1,370 m a.s.l.; Fig. 2-2) was approximately 7.5 km (between summits) east-northeast of Pic Ningua and formed the northern side of the Camp des Sapins river basin. Being closer to the northeast coast it had a wetter climate than Pic Ningua

(Pesin and Thomas 1993), and was often under cloud when skies at Pic Ningua were clear. Forest was less extensive there than at Pic Ningua, and at higher average altitudes. The terrain was also generally rockier than at Pic Ningua, especially on the northerly windward-facing slopes. Soils appeared to be less well established in many areas within the forest, and the humus layer was often thick with leaves and little decomposed, features which are associated with cooler and wetter climates in tropical forests (Olson 1994). Perhaps as a consequence, shrubland vegetation was more common, as well as sedge species outside the forest proper. Access to the forest where kagus lived was by an old mining exploration road to 1,000 m about 1 km from the forest, then by my marked walking tracks (Fig. 3-2).

3.2.2 Data sampling intervals

Much of my data collection was based around fortnightly sampling intervals (referred to as intervals hereafter) (see section 1.6). I collected data at Pic Ningua in 56 intervals, beginning 25/1/93 and ending 19/3/95 (Appendix III), and at Mt Cindoa in 37 intervals from 4/10/93. In addition, I recorded some observations on kagus at Pic Ningua in 1992, and three roosts after 19/3/95 when I removed transmitters from birds. I located two of these roosts on 21/3/95 and included them in interval 56 for data analyses as I had no other roost records in that interval. I did not include the third roost (located on 9/4/95) in interval 56, but used it when describing kagu movements or analysing total numbers of roost records.

3.2.3 Meteorological data and length of photoperiod

To obtain an indication of what the rainfall was at Pic Ningua and Mt Cindoa in 1992 (the year before I started fieldwork) and during my study (1993-94) relative to long-term average rainfall on the peaks, I used rainfall data at Thio (on the northeast coast 16.5 km from Pic Ningua; Figs. 2-1 and 2-2) (Anon. 1993, 1994, 1995). I graphed the mean rainfall at Thio for the period 1961-1990, as well as that for 1992-1994, with rainfall data I collected at Pic Ningua.

I installed rain- and air temperature gauges at Pic Ningua and Mt Cindoa. I had three weather stations (WSI, WSII and WSIII; each with a rain- and temperature gauge) at Pic Ningua (Fig. 3-1): two in forest (1,090 m and 1,100 m a.s.l.) and one just outside forest (1,010 m). The tops of the raingauges were 1.2 m above the ground

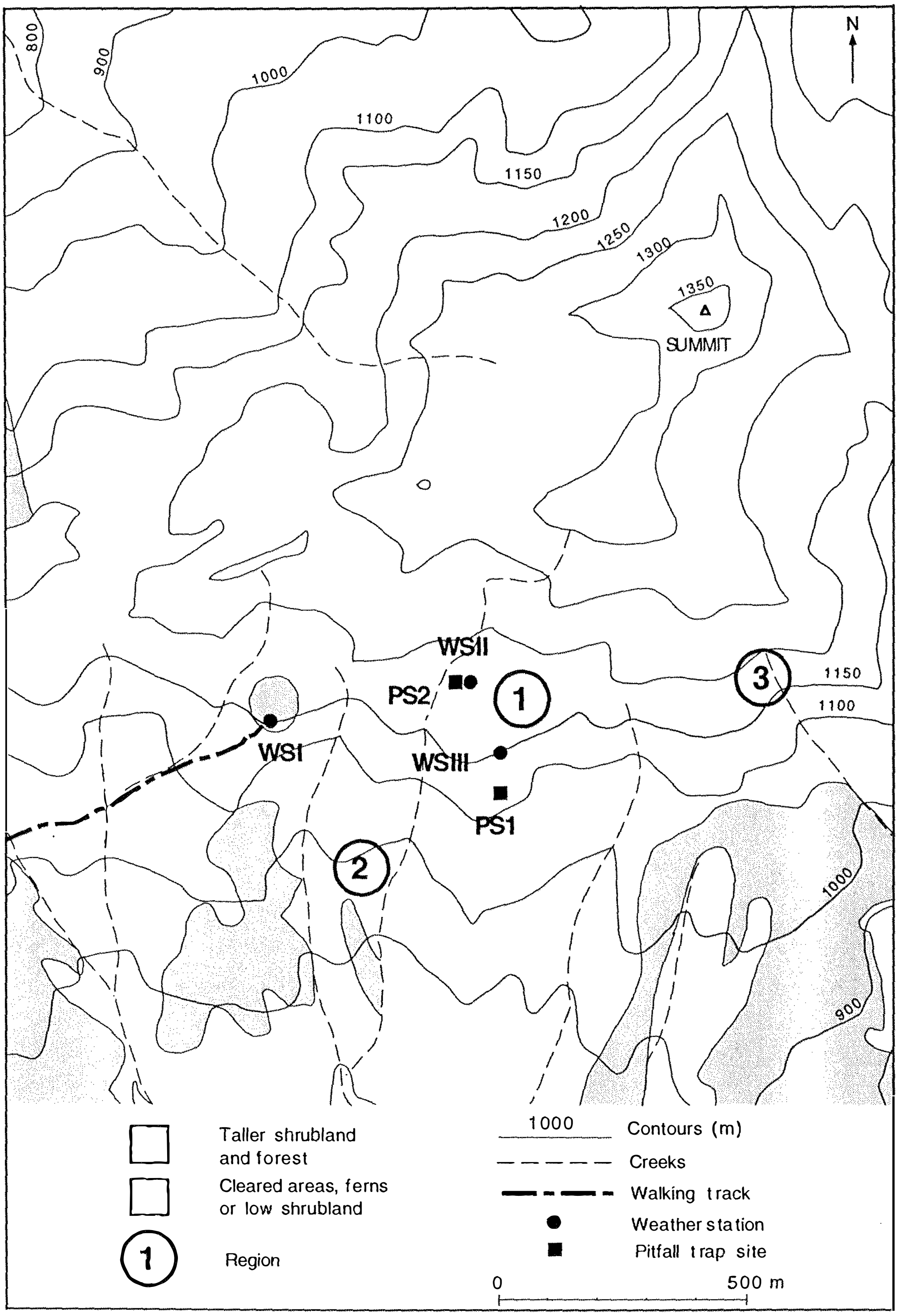


Figure 3-2. Map of the Mt Cindoa summit area mainly above 900 m a.s.l.. Positions (black dots) of the three weather stations (WSI, WSII and WSIII), the two pitfall trap sites (black squares, PS1 and PS2), and the three numbered regions (see Key) used in describing kagu movements in the text are shown. The map was drawn from a 1:25,000 map supplied by the Service Topographique du Territoire, Nouméa.

and the gauges were attached to free-standing stakes. The temperature gauges were shaded under small shelters and 1.5 m above the ground. I recorded the minimum and maximum air temperatures and rainfall at WSI daily when I was in the field, and at the forest stations when I passed them in the course of my research work (at least once a week). To reduce any evaporation of rainwater in raingauges, I glued a plastic funnel into the top of each (circular) gauge.

I initially had two weather stations (WSI and WSII at 1,110 m and 1,160 m a.s.l. respectively) at Mt Cindoa (Fig. 3-2) from interval 19; both had raingauges but only WSI had a temperature gauge. I installed a raingauge just outside forest (WSIII at 1,150 m) from interval 30, and recorded data at all stations once each fortnight when I visited the area up to 5/3/95. The temperature gauge was installed as per the Pic Ningua gauges, but because of the high rainfall at Mt Cindoa I used 5-litre plastic containers (with 92 mm diameter collection funnels) placed on the ground to collect rainwater.

For my study I divided New Caledonian climate into two seasons: the wet season (December to March) and the dry season (April to November). I also distinguished the early from the late dry season (after Frith and Frith 1985). The early dry season was April to August when temperatures are declining and conditions are cool and damp, and the late dry season from September to November when temperatures are rising and conditions are generally much drier, especially in September and October.

To obtain the average number of daylight hours per day (from sunrise to sunset) at Pic Ningua in an interval, I calculated the mean number of daylight hours from the first and last days of each interval. I obtained the times for sunrise and sunset from the Carter Observatory, Wellington, New Zealand, for the co-ordinates of the summit of Pic Ningua at 1,000 m a.s.l..

3.2.4 Catching kagus

Radio-tracking is essential for a close study of kagu behaviour because birds are generally difficult to find during the day unless they are surprised or they approach an observer. Individual birds also have many roosts on their home ranges, making it almost impossible to find birds at night (Létocart 1991).

Létocart (1991) used three methods to catch birds to fit them with radio-transmitters. The first involved playing back kagu song to bring a bird(s) into a net set out in a 'V'-shaped design in the forest. Birds probably approached a speaker because they actively defended territories (and/or partners) against intruding kagus (Létocart 1991). This method was most effective when more than one person was used to close the 'V' on the bird. Second, if a kagu could not be captured with the net method, then playbacks could be used at dusk to bring the bird close by in the hope that it would roost there and could be found in a night search. Last, birds not fitted with radio-transmitters were often caught when they roosted with birds fitted with transmitters; shared roosts on the same night were not uncommon, especially during the breeding season (Létocart 1991).

I captured 37 kagus at my two study areas using a variety of methods (Table 3-1, the method used to capture each individual bird is in Appendix IV). The technique that led to the capture of 18 birds involved the use of a wooden, painted kagu model (Plate 3-2). When attempting to capture kagus, I set up the model in a likely kagu area and placed around it small sheets of plastic mesh fitted with foot snares made from nylon fishing line (C.J. Veltman pers. comm.). I chose level sites on which to stand the model, taking into account the need for me (and an assistant if present) to remain concealed. I used playback of kagu song (a duetting pair taped at Parc Rivière Bleue by Y. Létocart) to bring a bird(s) to the model. The duet was played through a custom-made amplifier and Toa 10 watt horn speaker. The speaker was placed near the model with an extension cord leading back to a concealed position up to 15 m from it, depending on where the most suitable position was. At the model, birds often adopted a defence display (Pouget 1875, Campbell 1904) in which they circled closely around the model (Plate 3-2) thus providing the opportunity for them to become snared. For birds who were reluctant to closely approach the model, I often tied approximately 1 m high lengths of nylon fishing net to trees in a semi-circle around the model at a distance of one to several metres from it. This was the first time that the model/snare method had been used to capture kagus, and provided a successful field technique that one person could operate. The model/snare method led indirectly to the capture of many more birds that I later caught roosting with those already fitted with transmitters.

Plate 3-2. Male 105 defending his territory against the wooden kagu model at Pic Ningua. His display is also the same one used by both partners in courtship. Green plastic mesh is pegged around the model on which foot snares (on the down-facing side in this instance) were tied to catch birds while they were at the model. Kagus paraded around and close to the model as they displayed to it, in both directions.

Plate 3-3. Male 105 attacking the kagu model from behind (see legend to Plate 3-2 above for further details).

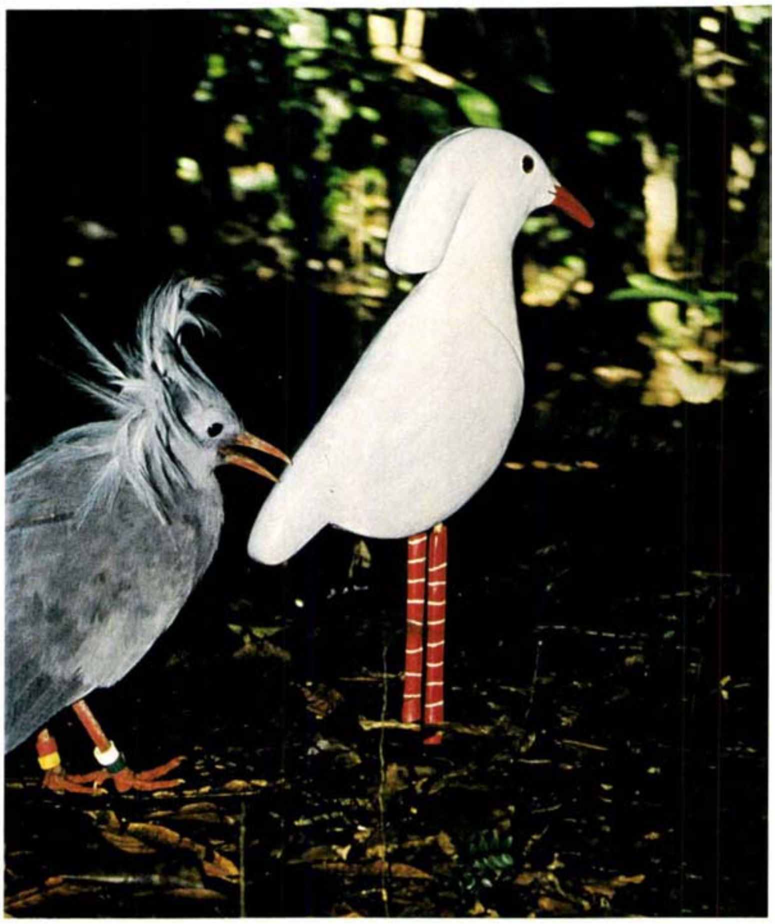


Table 3-1. Frequencies of the different methods used to capture different kagus for the first time at Pic Ningua and Mt Cindoa.

Method of capture	Females	Males	Sex unknown	Row totals
Model / foot snare	3	1	7	11
Model / fishing net	2	2	3	7
Playbacks / fishing net	1	-	-	1
Roosting with a bird wearing a transmitter	2	4	8	14
Alone on a known roost	-	1	-	1
Playbacks / night search	1	-	-	1
On a perch by chance	-	1	1	2
Column totals	9	9	19	37

3.2.5 Banding, measuring and weighing kagus, and recording primary moult

When possible, I banded, measured and weighed all birds when I first captured them. I fitted most birds I banded with combinations of coloured plastic bird bands (mostly 2 on each leg) to individually identify them. I 'super-glued' each band to the appropriate diameter (Y. Létocart pers. comm.) once it was on the leg. I also gave each kagu that I knew individually a unique 3-digit identification number. ID numbers at Pic Ningua began with '1' and those at Mt Cindoa with '2'. For example, bird 109 was bird No. 9 at Pic Ningua, and bird 203 was bird No. 3 at Mt Cindoa.

I took seven measurements (bill length, width and depth, tarsus length, foot length, mid toe length, and mid claw length) on kagus (to the nearest 0.01 mm) using manually-read vernier callipers, and measured wing length to the nearest 1.0 mm using a plastic t-square-like ruler. I always took bill and wing length and leg measures on the left side of the body. I took the eight measurements as follows:

Bill length:	From the point where the proximal (to the bill tip) edge of the nasal flap (section 1.4) joins the bill to the tip of the bill.
Bill width:	At the position where I took bill length (the point where the edge of the nasal flap joined the bill).
Bill depth:	At the same position on the bill as for bill width.
Tarsus length:	From the notch on the straightened leg to the edge of the bent-back foot.

Foot length:	On the flattened, opened out foot from the claw tip of the mid toe to the outside edge of the bent-back claw on the hind toe.
Mid toe length:	From the claw tip on the mid toe to the edge of the bent-back foot.
Mid toe claw length:	From the claw tip to the start of the skin on the foot.
Wing length:	The cord of the folded wing from the carpal joint to the tip of the longest wing feather (primary or secondary as feathers were often badly damaged).

I weighed birds using a 1.5 kg Pesola spring balance. Birds were either weighed in a non-transparent synthetic bag or upside down by string tied around their legs. I weighed individual birds at approximately monthly intervals, depending on whether I could find and/or capture birds (see Appendix VIII). I weighed most birds at least once every two months.

Whenever I captured a bird I noted if it was moulting its primary wing feathers, and the stage of moult. I collected too few data to establish if birds replaced their primary feathers in a descending moult from primary 1 to primary 10, as is common in birds (Welty and Baptista 1988). Thus I could not calculate the rate of moult, and only give data on the present or absence of primary moult.

I also collected one plucked breast feather from each bird that I captured.

3.2.6 Sexing and ageing kagus

Kagus are not obviously sexually dimorphic in the usual body measurements (Brégulla 1987). The banded and striped patterning on their primary wing feathers (see Plate 4-1) might provide a simple method of determining the sex of birds in certain areas (Hunt 1996b, my unpublished data), but this requires further investigation. I sexed kagus by song (Pouget 1875) at Pic Ningua, but could sex only a small number of birds with certainty (Appendix IV) as this requires viewing individuals singing or reliable knowledge of the identity of unseen birds who sang. I was unable to sex any birds at Mt Cindoa.

Distinct plumage differences exist between adults and young juveniles (Brégulla 1987, Létocart 1991); juveniles have browner patterning on their wing coverts than adults that disappears slowly over time. The stage at which juveniles obtain full adult plumage remains unclear because remnants of juvenile coloration may persist for many years (Y. Létocart pers. comm.). I could identify young juveniles (< 1 year old) because they had distinct juvenile plumage in conjunction with smaller body measurements (e.g., beak length), indicating they were from the last breeding season. All other birds (> 1 year old) I classed as adult or subadult/adult.

3.2.7 Radio-tracking kagus

After Létocart (1991), I fitted birds with two-stage radio-transmitters (*c*. 33 g) positioned on their backs by nylon securing cords looped around the base of each wing. I incorporated a safety release system (a cotton thread) into the securing harness in case of transmitter or battery failure. I detected no cases of injury to birds from wearing transmitters, and no evidence that they irritated the birds or changed their behaviour. I used a Telonics TR-4 receiver with a yagi directional antenna to locate the radio signals.

To investigate kagu movements and establish their home ranges, I initially located the roost site and daytime position of each radio-tracked bird in a 24 hour period, once in each interval. I sometimes recorded more than one roost position per bird in an interval, and used all roost records to establish an individual's home range.

I found the approximate daytime position of a bird (usually between 1000 and 1400 hrs) by approaching it (unseen) to within a distance of about 50-100 metres, but not closer to avoid my disturbing it and possibly influencing its choice of roost site that night. If a bird was disturbed, it was difficult to tell if it was moving naturally in the forest or to avoid me. I used the negative relationship between signal strength and distance from the transmitter (Létocart 1991) to roughly estimate my distance from a bird. I measured the signal strength by noting the position of the volume dial when I could not hear the radio signal beeps from the receiver when the speaker area on the receiver was placed up to my right ear. From approaching birds at night I knew that the receiver signal strength was a reliable indicator of my distance from a bird when quite close to it. To obtain some relative idea of the dial position in ideal conditions when I was 50 and 100 m from the transmitter, I carried out tests with the receiver and a transmitter outside the forest in open, flat terrain. I did not carry out tests in the forest because I was not attempting to determine actual distances, and it would have been extremely difficult to cover the range of variability in signal strengths between any two positions (myself and a bird) in forest on the peak. When I had approached to within 50-100 metres of a bird in the daytime, I recorded my position on a 1:10,000 contour map (using a Thommen TX 6,000 m altimeter to record altitude) and the compass direction of the signal.

I took a cautious approach when using the daytime telemetry locations to determine home ranges because my methods meant that the estimated positions of birds were probably highly inaccurate at times due to, for example, signal bounce off the mountainous terrain. I assumed all birds were 50 m from my final position in the compass direction taken, and only used the positions to establish home range boundaries (by fitting minimum convex polygons) when they ‘pushed out’ (when I was within a bird’s home range and locating a signal) rather than ‘pulled out’ (when I was outside a bird’s home range and locating a signal within it) boundaries. This resulted in a conservative estimate of home range size. I measured the map area of forest and tall shrubland within a pair’s home range by counting the number of 1 mm squares (on grid paper placed over the range) covering that vegetation (drawn to a scale of 1 cm = 100 m).

I located the roost of an individual bird the night after I estimated its daytime position. I usually did this between midnight and first light (when kagus left their roosts) so there would be sufficient faecal material available for diet analysis (*Chapter 5*). At the roost site, I described the roost (section 3.2.8) and plotted its position (using an altimeter to record altitude) on either a 1:10,000 (Pic Ningua) or 1:25,000 (Mt Cindoa) contour map.

I mostly used data on daytime locations at Pic Ningua to help establish the home ranges of pairs before one or both pair members were attacked by dogs. After the last recorded dog attacks in August 1993, I mainly took telemetry fixes on birds from roads around the mountain to establish their general positions as most birds travelled widely on the peak and therefore it was less important to establish their locations with greater accuracy. However, I continued to try and locate them at their roosts in each interval. I did not record daytime locations at Mt Cindoa as I usually visited there in the evenings for only one night in each interval.

To enable a bird’s movements to be described at Pic Ningua from telemetry fixes taken from roads around the peak, I divided the peak into 19 regions (Fig. 3-1). I established the regions based on what I considered was my ability (from knowledge of the terrain and the behaviour of birds) to reliably determine the position of a kagu from telemetry fixes. The south-facing slopes above about 800 m in altitude covered only one region (region 17). This was because I had difficulty in estimating a bird's position within this area as radio signals were often very weak from the roads on that side of the peak and road access there was limited.

3.2.8 Kagu roosting behaviour

Kagus were generally reluctant to move from their roosts before I saw them, but if they had I often located the roost by finding fresh faecal material at the site. For all roost sites, I noted if they had been used previously by either recording re-use by a bird during my study (I marked the positions of most roosts with plastic flagging tape on nearby trees, or I knew them individually) or finding old kagu faeces at the roost site. If two birds roosted together at a previously used roost, I recorded it as a single re-use. I recorded the diameter of a perch at the location on the perch where the bird roosted and also the vertical height of this location above the ground. Early in my study I noticed that kagus at Pic Ningua and Mt Cindoa often used ground-roosts in apparently sheltered positions. To investigate if environmental conditions were associated with a bird's choice of roost position, I classified each roost as either a sheltered or an unsheltered one. A sheltered position was on the ground under or next to some type of physical structure (e.g., rock, tree roots). An unsheltered position was on the ground or on a perch not up against or under a structure other than the forest canopy. Finally, I recorded the type of sheltered (e.g., a rock-formed shelter) or unsheltered (e.g., a perch on a branch) roost position that a bird used.

3.2.9 Analyses

I used the SAS statistical software (Release 6.11 for Windows) for all the statistical analyses carried out by computer in remaining chapters in this thesis.

I used rainfall and air temperature data from the forest sites at Pic Ningua and Mt Cindoa for all analyses. Because I did not record air temperature in the forest every day at Pic Ningua, measurements there were more biased towards extreme values compared with those outside forest (at WSI) where I recorded temperatures more often. However, mean maximum and minimum air temperatures in and outside forest were highly correlated (Spearman correlation coefficients: $r = 0.88$ and $r = 0.96$, $p < 0.0001$, $n = 54$, respectively). Although the forest data were more biased, I used them for all analyses because they probably still better represented temperature conditions where kagus lived than those at WSI. For example, on sunny days following cold nights, daytime temperatures outside forest quickly warmed up, whereas those in forest did so to a lesser extent probably because the understorey was insulated by the forest canopy. An indication that this occurred was the lower correlation coefficient for the test comparing maximum temperatures than the one comparing minimum temperatures. Also, in cold conditions in interval 17 maximum temperature increased by around 6^{o}C outside forest, but only by about 3^{o}C in forest. Rainfall in intervals in forest covaried similarly to that recorded outside forest (Spearman correlation coefficient: $r = 0.95$, $p < 0.0001$, $n = 56$), therefore I used the former data as the raingauges were located where kagus lived and where the pitfall traps (*Chapter 5*) were located.

To compare weather data between Pic Ningua and Mt Cindoa, I collated them into the same intervals. This meant that the data at the two areas were compared over slightly different time periods because I usually visited Mt Cindoa on the first day (Monday) of a new interval (e.g., No. 45), but recorded the data in the previous interval (No. 44).

I use univariate *t*-tests (SAS TTEST procedure) and nested ANOVA's (SAS GLM procedure) to compare kagu morphometric data, as well as multivariate analysis of variance (SAS GLM procedure) to look for linear combinations of the body measurements (except wing length because variation in measurements were also dependent on damage to primary feathers) that could best summarize the differences between the sexes. I confirmed that the morphometric data were approximately normal with SAS Univariate procedure. I did not attempt to obtain a reliable discriminant function to try and sex birds because of the small number of males and females whose sex I knew.

As sample sizes for the number of individual birds weighed in each interval were very small, I drew a mean kagu bodyweight curve through mostly 8-weekly means. I used this time period because I weighed most individual birds every two months. To include all the data at Mt Cindoa, the period between the last two means there was nine weeks. Also, the first mean at Pic Ningua was out of sequence with the other means because I had weighed most birds there in interval 1 when I first captured them, and did not start to weigh birds again until around interval 9. I used weight records of all adult birds (except bird 205 as it was unusually thin; section 3.3.11) when calculating the '8-weekly' means, but only one record per individual bird to calculate each mean. When there was more than one weight record per bird in each period, I calculated its average weight then used that to calculate the 8-weekly mean.

Because the 8-weekly means for bodyweight data were time series, normal ANOVA tests were probably inappropriate because of the likelihood of correlated errors which would violate a key assumption for use of these tests. As well, my data were often repeated measurements on individuals therefore not independent. I used repeated measures ANOVA (SAS GLM procedure) to test for within and between area differences in 8-weekly means. For these tests, I could only use birds on whom I had repeatedly weighed over the longer term. At Pic Ningua there were five such birds (106, 109, 111, 119 and 120; data for 11 8-weekly means), and three at Mt Cindoa (201, 202 and 203; data for eight 8-weekly means). I compared the 8-weekly means ($n = 8$) between the two study areas over approximately the same time period. For within-subject effects and interactions, I used the more conservative Huynh-Feldt adjusted-F probability values in case the assumption of a Type-H covariance was not met (SAS Institute 1990).

Unless stated, I only used one roost record (the first one I found in chronological order) from an individual bird in each interval when presenting and analysing roosting data. I also excluded roost records of birds < 1 year old and those of adults when they incubated chicks on the ground. I hand calculated χ^2 tests when making comparisons to expected ratios, and did the same for *G*-tests when analysing 2 x 2 contingency table data.

3.3 Results

3.3.1 Rainfall and temperature at the study areas, and length of photoperiod

Distinct seasonal patterns existed in rainfall at Pic Ningua and Mt Cindoa during my study. Most rain fell during the wet season in association with tropical cyclones or depressions (Figs. 3-3 and 3-4), with a smaller peak in both years in July/August. As expected, rainfall was lowest in the late dry season, but considerable rain fell in

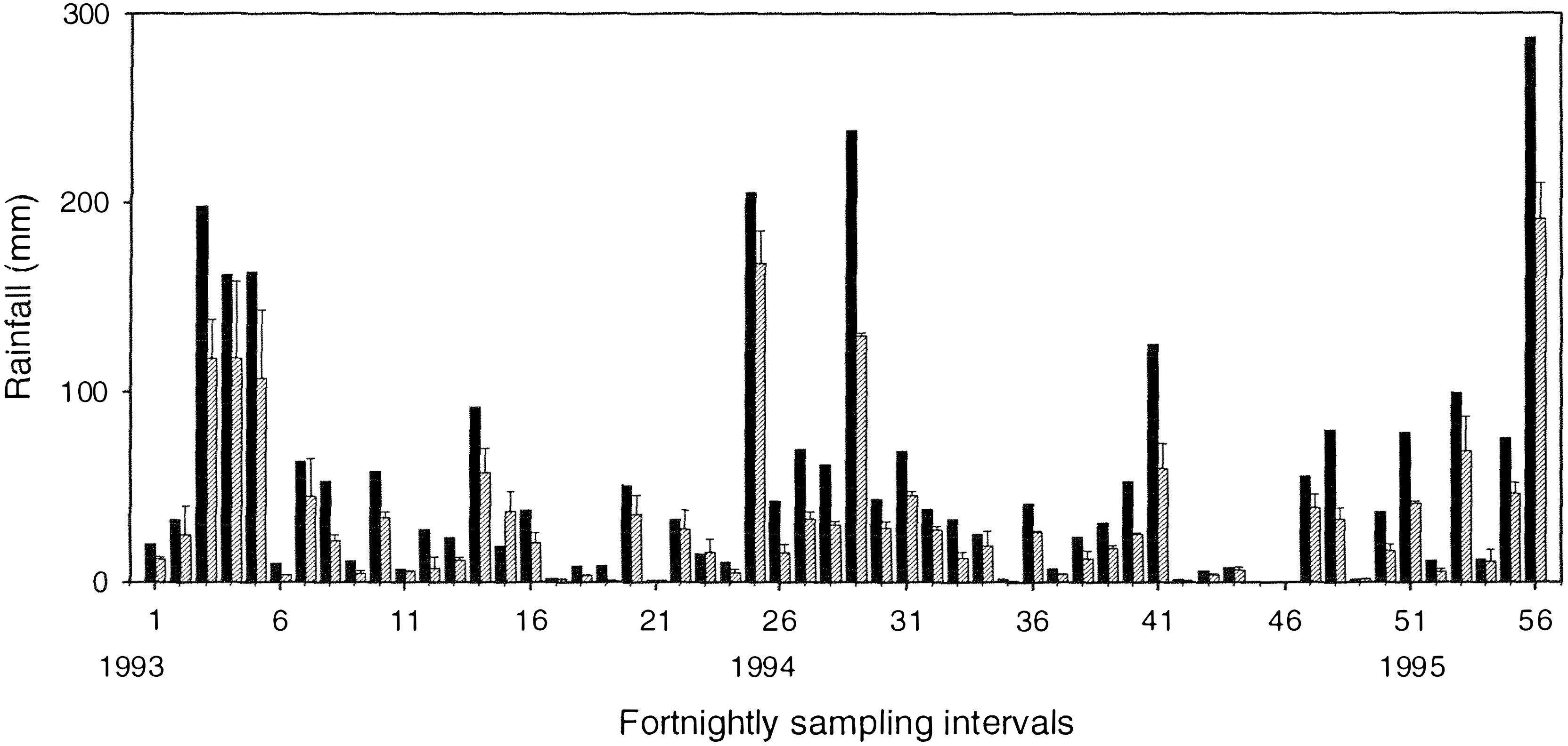


Figure 3-3. Rainfall at Pic Ningua outside forest (WSI, black bars) and in forest (hatched bars, mean rainfall at WSII and WSIII, error bars = 1 s.e., n = 2 for all intervals). Substantial rainfall in intervals 3-5, 25, 29 and 56 was associated with tropical cyclones or depressions.

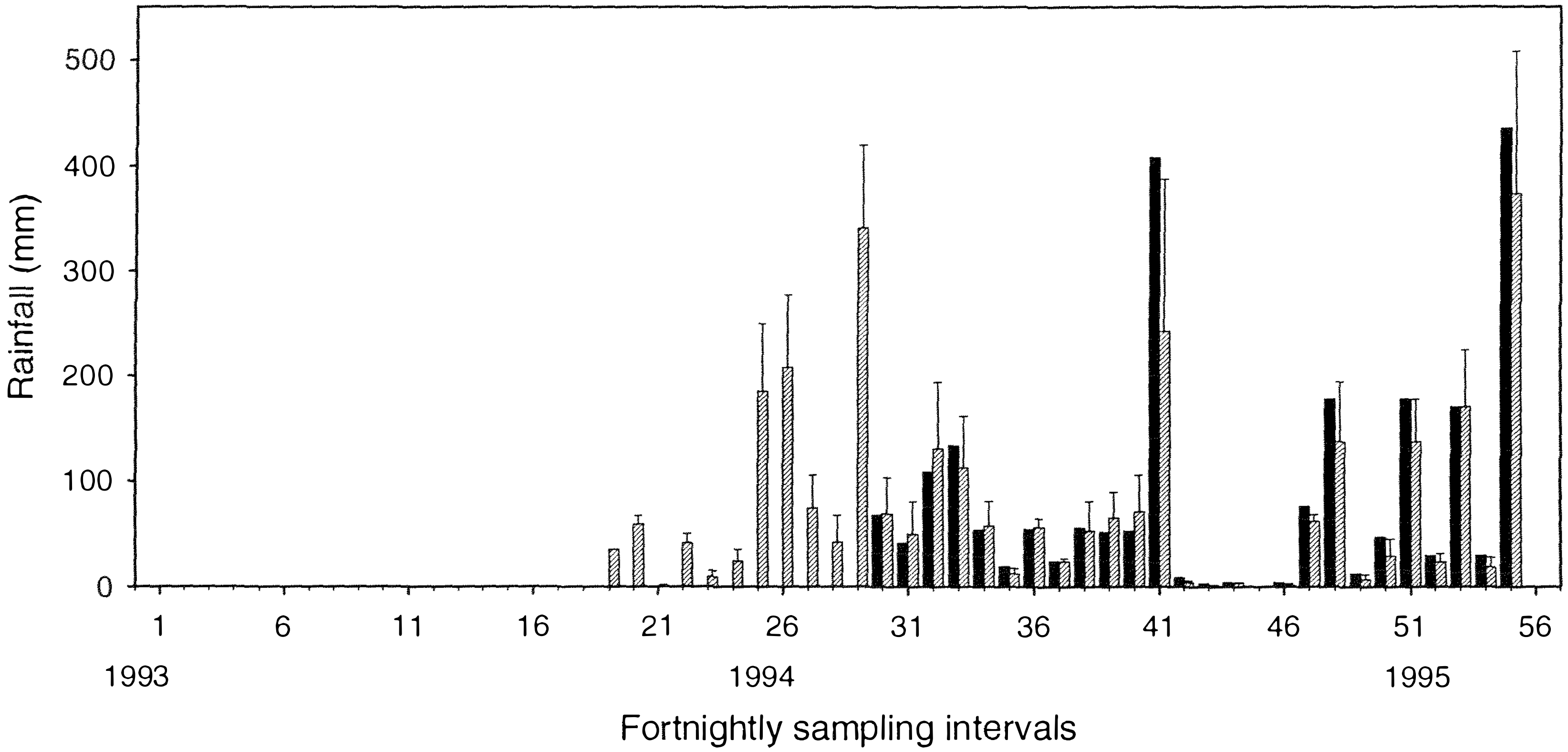


Figure 3-4. Rainfall at Mt Cindoa outside forest (WSI, black bars, intervals 30-55) and in forest (hatched bars, mean rainfall at WSII and WSIII, intervals 19-55, error bars = 1 s.e., n = 2 for all intervals except interval 19 when I only recorded rainfall at WSIII). Because the raingauge overflowed, I estimated rainfall at WSII in interval 25 from the amount measured in WSIII. Rain associated with tropical cyclones or depressions fell in intervals 25, 29 and 55.

November of both years. There was a particularly long dry spell in 1994 when only 15 mm fell at Pic Ningua in intervals 42-46 (22/8/94-30/10/94). Pic Ningua had a much drier climate than Mt Cindoa; total rainfall measured outside forest over the 12 month period that I was able to compare the two sites (intervals 30-55) was 961 mm and 2,249 mm, respectively. Total rainfall at Pic Ningua between years (intervals 1-25 and 26-52) was 1,313.5 mm and 1,187.0 mm, respectively. Drier than average conditions were experienced at Thio from late 1990 (Pesin and Thomas 1993). The annual rainfall deficit there grew increasingly from 1992 (13%) through to 1994 (44%) (Fig. 3-5), suggesting that Pic Ningua and Mt Cindoa also probably experienced drier weather in these years.

Both study areas also experienced distinct seasonal changes in air temperatures (Figs. 3-6 and 3-7). Outside the forest at Pic Ningua, mean maximum temperatures were usually between 25 and 30°C in summer, dropping to below 20°C in the coldest months of July and August. Mean minimum temperatures dropped below 10°C in both 1993 and 1994, between July and September. Mean minimum temperatures in forest at Pic Ningua were several degrees below those outside forest, and mean maximum temperatures were generally around 5°C lower in forest (Fig. 3-8). Absolute minimum and maximum air temperatures in intervals in forest were similar at both study areas (Fig. 3-7). Mean monthly air temperatures at Thio in 1993 and 1994 varied little from those calculated over a 30 year period from 1961-1990 (Fig. 3-9). Air temperatures at Thio tended to be colder than average in the 1994 dry season, which was consistent with unusually cold air temperatures at Parc Rivière Bleue then also (section 5.3.1).

The average number of daylight hours per day in an interval at Pic Ningua ranged from 10.98 to 13.63 (Fig. 3-6), giving an annual variation in photoperiod on the peak at 1,000 m a.s.l. of approximately 2.65 hours.

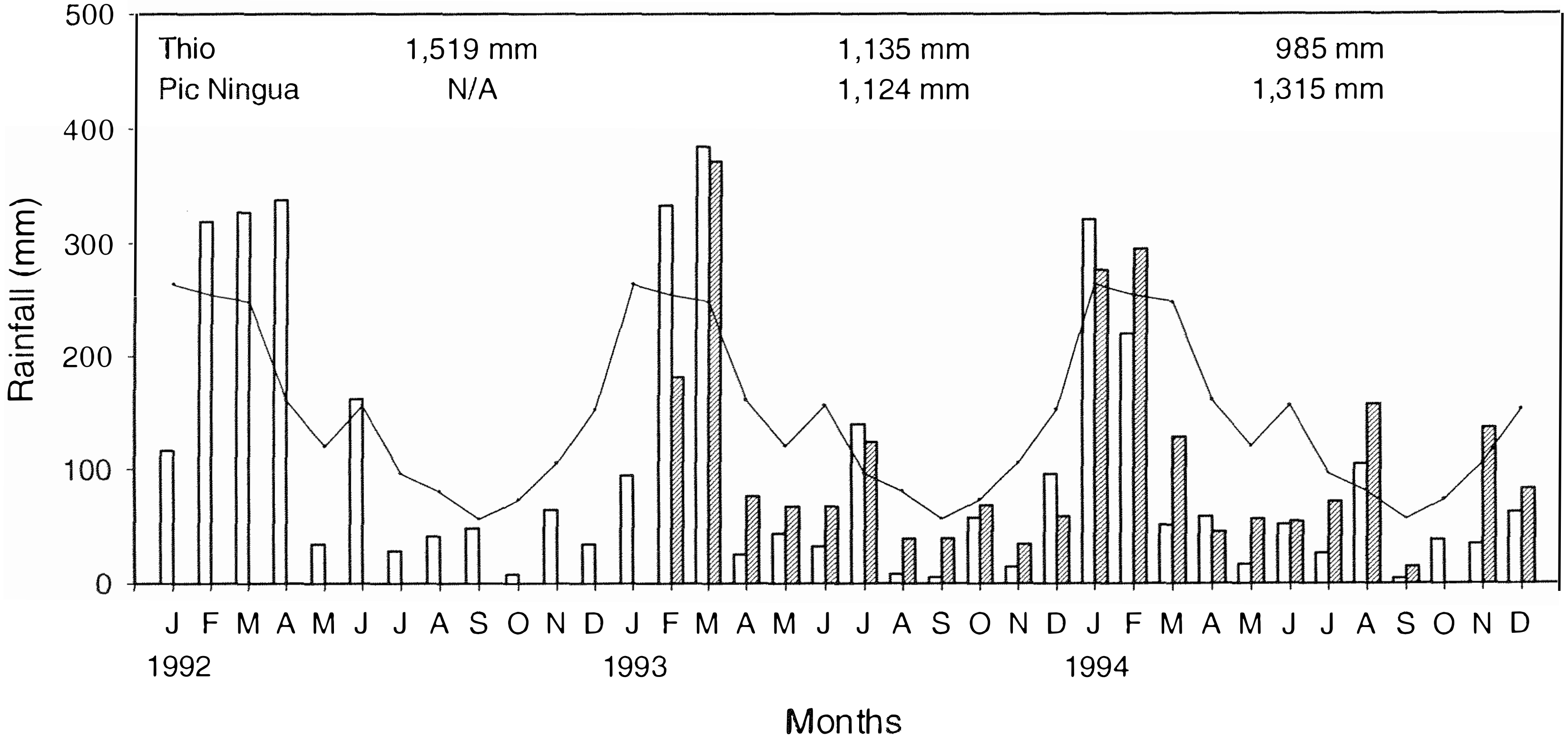


Figure 3-5. Comparison of monthly rainfall at Thio (on the coast 16.5 km north-northeast of Pic Ningua) (unfilled bars, 1992 to 1994) and Pic Ningua (hatched bars, February 1993 to December 1994). The line shows the mean monthly rainfall at Thio for the period 1961-1990 (annual mean for the period = 1,749 mm). Annual rainfall figures for Pic Ningua (1993-1994) and Thio (1992-1994) are along the top of the graph (the figures for 1993 exclude rainfall falling in January to allow a comparison between the two areas). Rainfall data for Thio were taken from Anon. (1993, 1994, 1995).

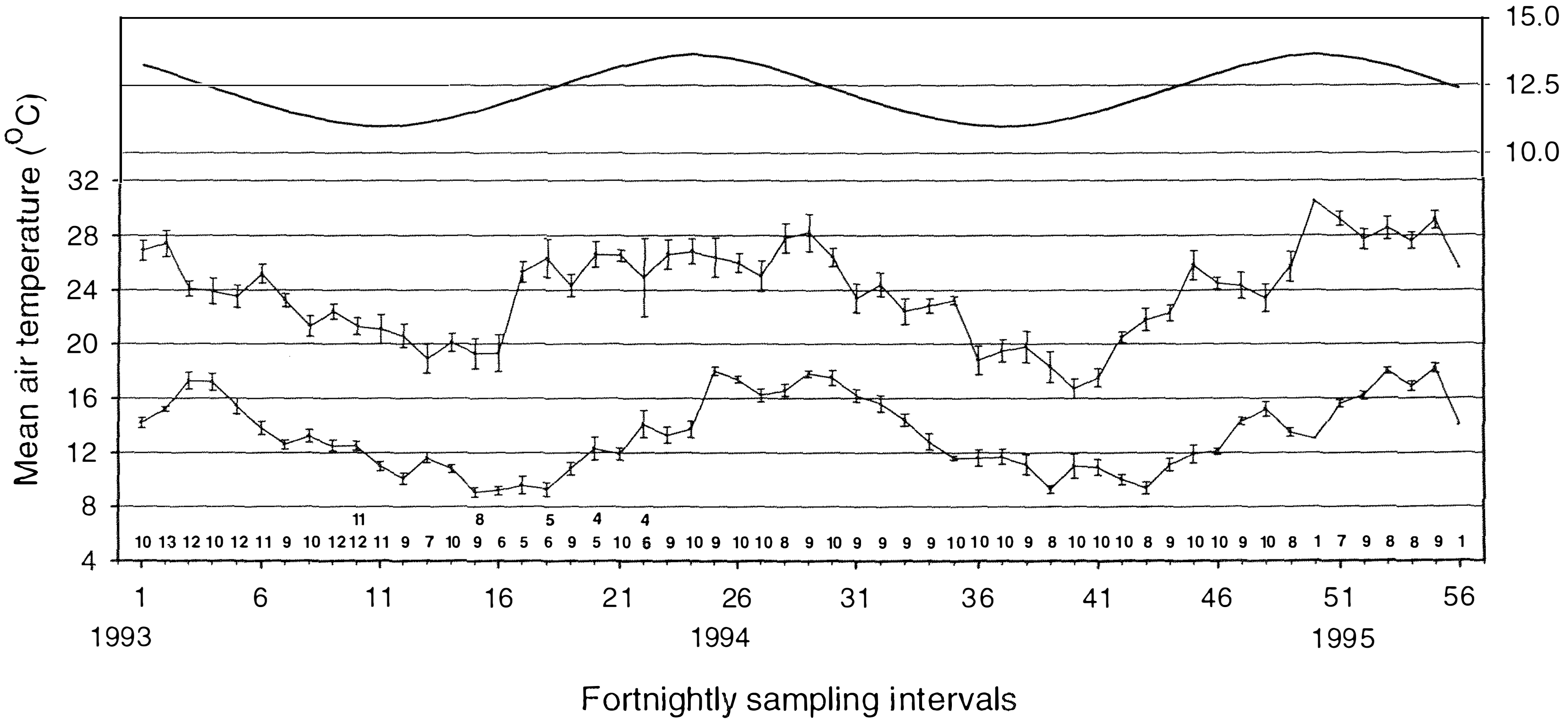


Figure 3-6. Mean maximum and minimum air temperature at Pic Ningua outside forest (WSI), and length of photoperiod (top line) on the peak at 1,000 m a.s.l.. Sample sizes (daily records) for mean minimum (bottom row) and maximum (top row only when different from bottom row) temperature in each interval are along the bottom of the graph (error bars ± 1 s.e.).

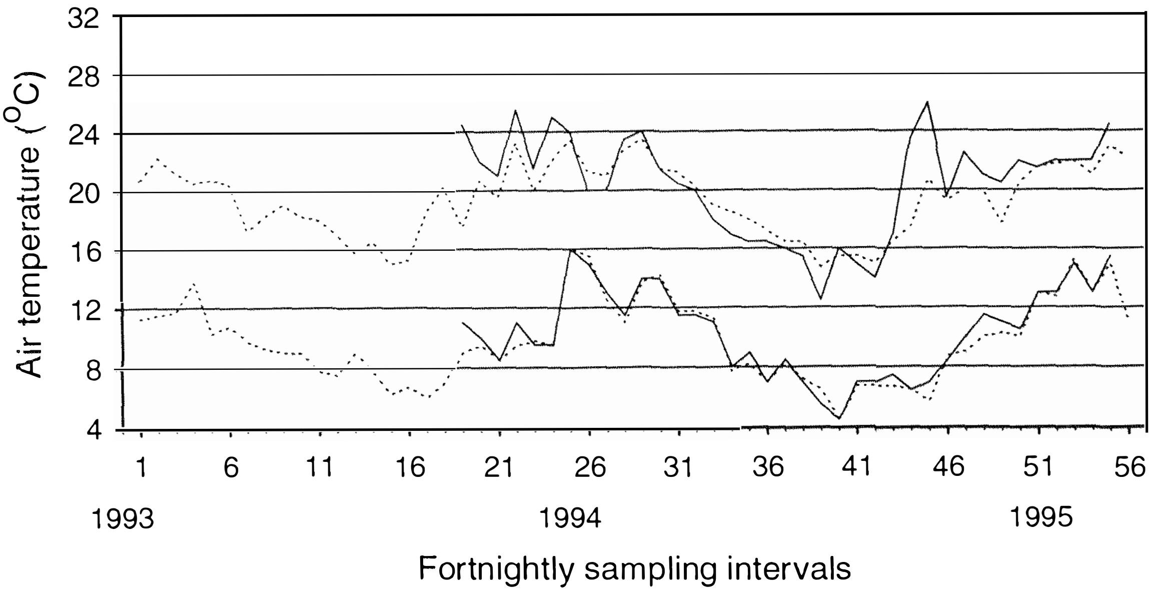


Figure 3-7. Comparison of fortnightly absolute maximum and minimum air temperatures in forest between Pic Ningua (dotted line, intervals 1-56) and Mt Cindoa (solid line, intervals 19-55). Pic Ningua data are means at the two forest weather stations (WSII and WSIII).

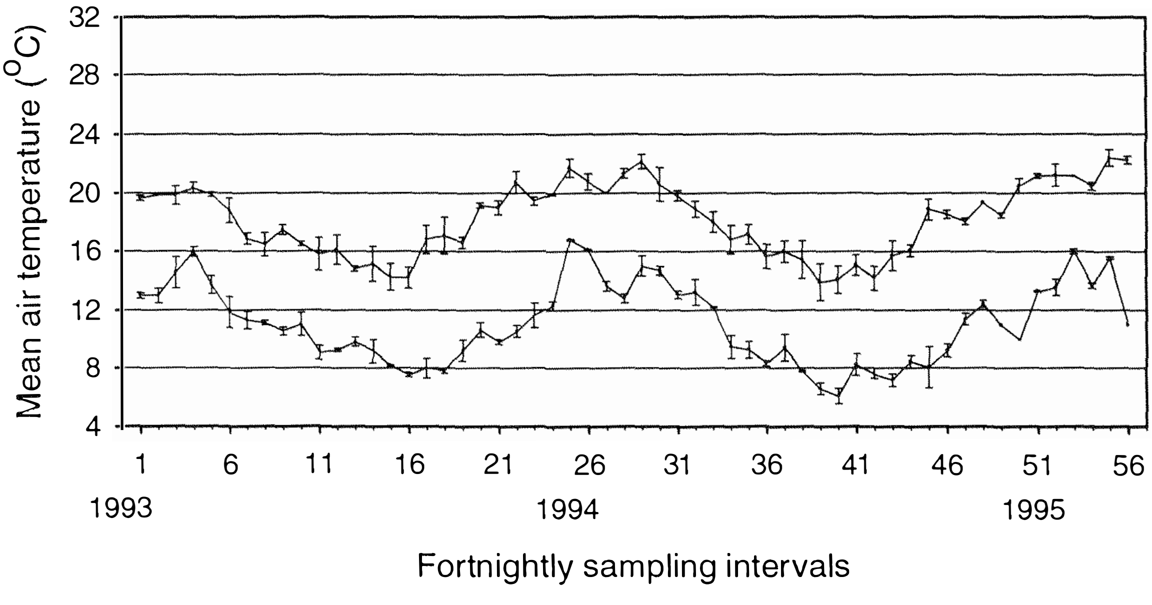


Figure 3-8. Mean maximum and minimum air temperature at Pic Ningua in forest at WSII and WSIII. I averaged data in each interval at each station (n = 1 at each site for intervals 50 and 56) before calculating the means at the two stations (error bars ± 1 s.e., n = 2 for all intervals). Data points without error bars indicate when mean temperature at each site was identical.

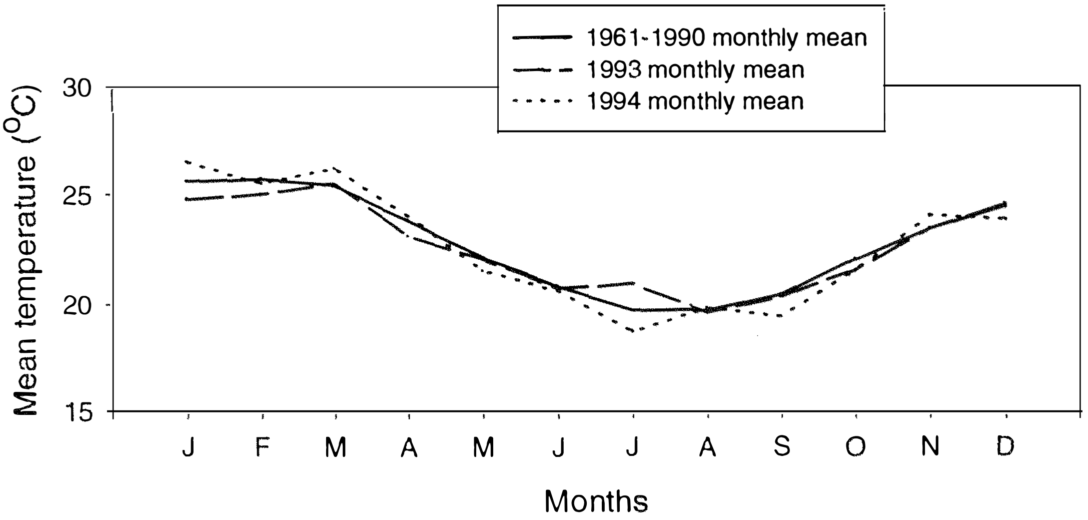


Figure 3-9. Comparison of mean monthly air temperatures at Thio in 1993 and 1994 with the monthly means there for the period 1961-1990.

3.3.2 Number of study birds at Pic Ningua and Mt Cindoa

I captured (n = 31), saw (n = 1) or found dead (n = 4) 36 different kagus at Pic Ningua, and captured six at Mt Cindoa (Appendix IV). Most of these birds (n = 32) wore a radio-transmitter at some stage of the study (Fig. 3-10), but many of them subsequently died as a result of being attacked by dogs. I began fitting kagus with radio-transmitters on 19/1/93 and had a maximum of 16 birds wearing them (all at Pic Ningua) in February 1993. From August 1993, when I recorded the last dog attacks on kagus, I had either five or six birds wearing transmitters at Pic Ningua until I began removing them at the end of my study (Appendix V). I began fitting kagus with transmitters at Mt Cindoa on 1/10/93, and had either three or four birds wearing them until I stopped following kagus there in February 1995. The transmitter on bird 124 may have failed because I could not locate its signal after 2/2/94 despite attempts to do so for several months after that date. At the completion of my study I had removed all other transmitters from birds.

I banded all birds captured at Pic Ningua except individual 125 (birds 132 and 134 whose remains I found could also have been banded) (Appendix IV), and three of the

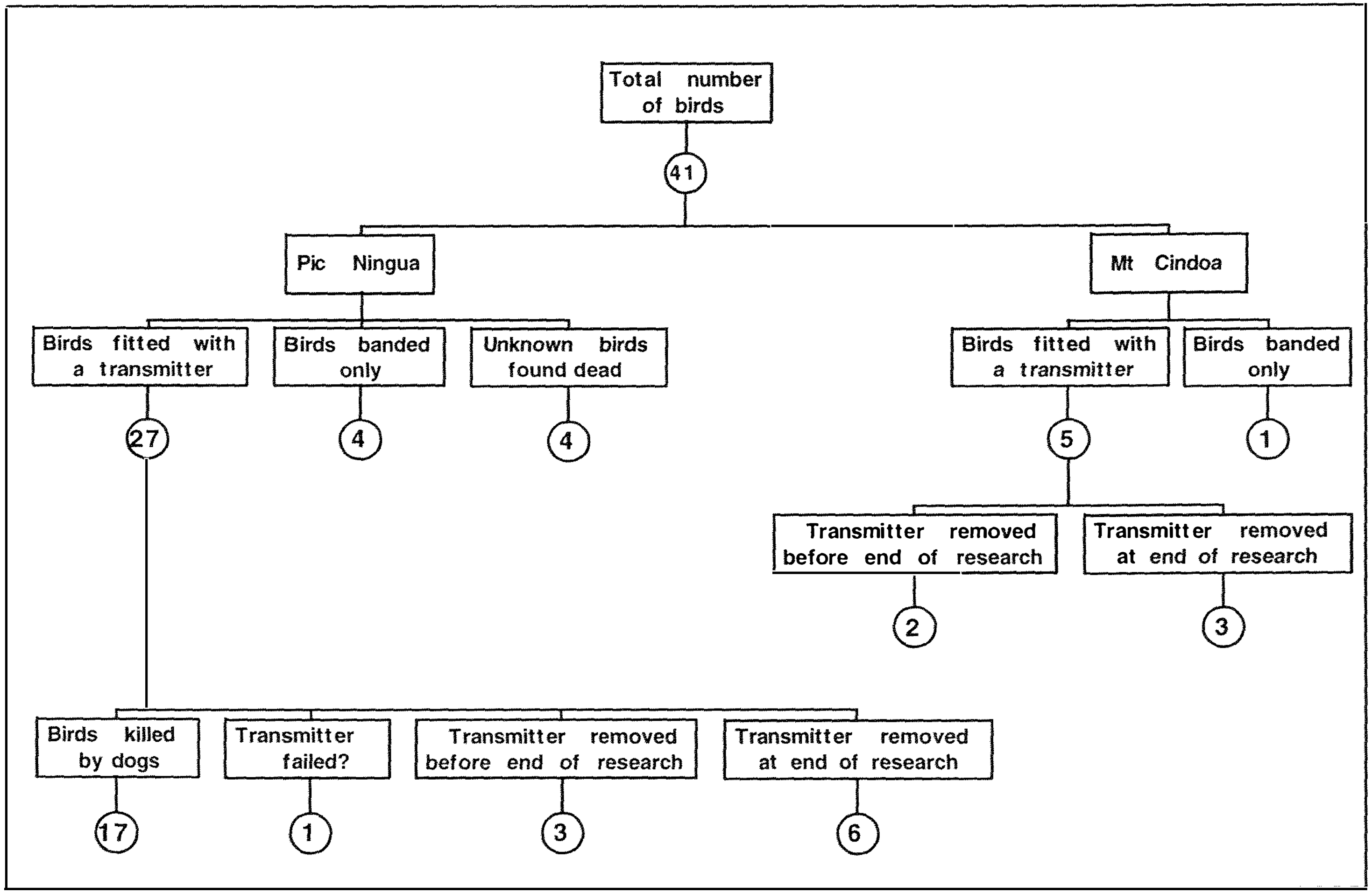


Figure 3-10. Path diagram showing the ways (e.g., radio-tracking, banded only) that I collected data from kagus at Pic Ningua and Mt Cindoa, and how radio-transmitters were eventually removed from radio-tracked birds.

six birds captured at Mt Cindoa. I did not remove the leg bands at the completion of my study.

Of the 31 birds captured at Pic Ningua (Fig. 3-11), two were young chicks from the 1992 (bird 130) and 1994 (bird 135) breeding seasons and, from their plumage, two (birds 122 and 123, first captured on 27/4/93 and 7/6/93, respectively) were less than one year old from the 1992 breeding season. Most of the remaining 31 birds were adults, and some were probably subadults who had yet to pair and breed. This was likely the case for three birds (either bird 112 or 128 captured with female 111, bird 129 captured with pair 103 and 104, and bird 136 observed with pair 113 and 114). I estimated that two of the four unknown birds whose carcasses I found (birds 131 and 133) were adults, but I could not estimate the age of the other two (birds 132 and 134) whose remains were incomplete. The birds captured at Mt Cindoa were adults and possibly subadults (bird 206).

I established the sex of 16 birds by song at Pic Ningua, but none at Mt Cindoa (Appendix IV). These 16 consisted of six pairs, three unpaired or widowed adults or new birds I found with widowed birds, and a juvenile (female 123).

3.3.3 Kagu morphometric data

I captured 37 different birds at Pic Ningua (n = 31) and Mt Cindoa (n = 6) (weight and morphological data for these individuals are in Appendices IV and VI, respectively). Seven of the eight (bill width was the same) morphological measurements were slightly larger for birds at Pic Ningua than at Mt Cindoa, but the differences were not significant (Table 3-2). Annual kagu bodyweight variation was considerable at the two study areas (section 3.3.11), therefore long-term weight records or those recorded in the same time period were necessary for meaningful comparisons between areas and/or individuals. I compared kagu bodyweights between the two study areas using only birds from who I had collected long-term records (Pic Ningua: birds 106, 109, 111, 119, 120 and 125; Mt Cindoa: birds 201, 202 and 203). First, to check if body size might have been a confounding variable (Clutton-Brock and Harvey 1979), I correlated the mean bodyweight for each of these nine birds with their tarsus and beak lengths. Mean bodyweight was not significantly correlated with either tarsus or beak length (Spearman correlation coefficients: $r = 0.10$ and $r = -0.12$, $n = 9$, ns, respectively). Mean kagu bodyweight was not

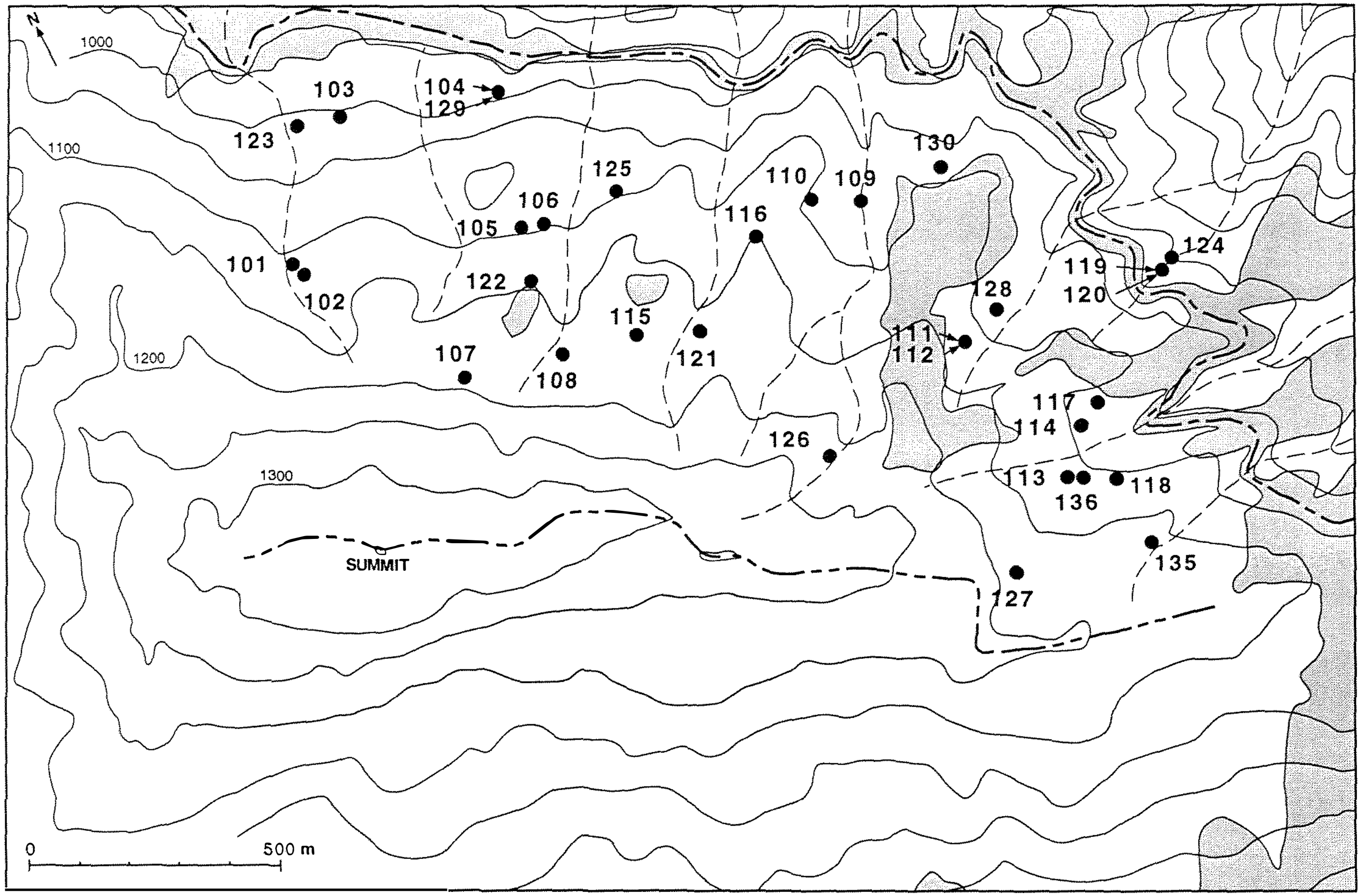


Figure 3-11. Pic Ningua summit area (Key in Fig. 3-1) showing the positions (black dots) where individual kagus (indicated by their ID Nos, see Appendix IV) were first captured (n = 31) or seen (bird 136). Arrows indicate where I captured two kagus at the same position at the same time.

significantly different between Pic Ningua and Mt Cindoa after accounting for variation between birds at each area (Nested ANOVA, $F_{[1,7]} = 1.947$, ns). It was also not different between the two areas when I compared bodyweight over roughly the same time period (October 1993 to the end of my study) (Nested ANOVA, $F_{[1,7]} = 2.03$, ns).

I also compared morphological measurements between males and females for the 15 adults or sub-adults whose sex I knew. Male birds tended to be larger in five measures (all beak measures, tarsus length and mid claw length), and females in two (mid toe and wing length), but these measurements were not significantly different between the sexes (Table 3-3). The lack of long-term data on male bodyweights (only obtained for bird 120) meant that an unbiased comparison was not possible between males and females, therefore I did not compare bodyweight between the sexes.

Table 3-2. Means and standard errors for the eight morphological measurements (cm) taken on kagus at Pic Ningua and Mt Cindoa (Appendix VI). I calculated mean kagu bodyweight (g) (means calculated after weight records for individuals were averaged; means for individuals in Appendix IV) using only birds for who I had long-term weight records (Pic Ningua: birds 106, 109, 111, 119, 120 and 125; Mt Cindoa: birds 201, 202 and 203). *T*-tests comparing all eight morphological measurements between study areas were not significant, nor were ANOVA tests comparing mean bodyweight (see text). Full description of the measurements is in section 3.2.5.

Measurement	**Pic Ningua**			**Mt Cindoa**		
	Mean	**S.E.**	**N**	**Mean**	**S.E.**	**N**
Bill length	4.28	0.041	28	4.14	0.069	6
Bill width	1.09	0.011	28	1.09	0.037	6
Bill depth	1.86	0.016	28	1.80	0.023	6
Tarsus length	11.12	0.101	28	10.71	0.129	6
Foot length	9.04	0.082	28	8.99	0.151	6
Mid toe length	7.04	0.071	28	6.99	0.125	6
Mid claw length	1.16	0.017	28	1.11	0.036	6
Wing length	29.67	0.356	27	28.00	1.225	4
Bodyweight	899.85	24.336	6	850.32	15.508	3

A multivariate analysis of variance (MANOVA) also did not detect a significant difference between males and females (Table 3-3) using seven of the eight morphological measurements (I excluded wing length) (Multivariate statistics, F = 1.49, d.f. = 7, ns). There was also no significant difference when I used only the three bill measurements (Multivariate statistics, F = 1.11, d.f. = 3, ns).

Table 3-3. Means and standard errors for the eight morphological measurements (cm) from eight male (104, 105, 107, 110, 116, 120, 121 and 124) and seven female (103, 106, 108, 109, 111, 115 and 119) adult/subadult kagus at Pic Ningua. *T*-tests comparing all the morphological measurements between females and males were not significant. Full description of the measurements is in section 3.2.5.

Measurement	**Females**			**Males**		
	Mean	**S.E.**	**N**	**Mean**	**S.E.**	**N**
Bill length	4.28	0.092	7	4.41	0.076	8
Bill width	1.07	0.024	7	1.13	0.019	8
Bill depth	1.86	0.037	7	1.90	0.023	8
Tarsus length	11.14	0.280	7	11.12	0.183	8
Foot length	9.02	0.181	7	9.03	0.164	8
Mid toe length	7.07	0.198	7	6.96	0.116	8
Mid claw length	1.12	0.035	7	1.20	0.035	8
Wing length	29.86	0.595	7	29.75	0.648	8

3.3.4 Timing and duration of primary feather moult

I detected primary moult in kagus at Pic Ningua and Mt Cindoa mostly between January and May (Table 3-4). The earliest moulting record was for bird 204 on 28/12/93, and the latest for bird 116 on 23/5/93, although birds may have still been undergoing moult before and after these dates, respectively. There was evidence that kagus undertook primary moult annually, for example bird 106 moulted in all three years (1993-1995), and birds 109, 111 and 125 in 1994 and 1995. I did not detect moult for many birds in 1993 probably as I had not inspected them during the moult period, nor in 1995 as I may have removed transmitters before moult began (birds 119, 120, 201, 202 and 203). Pair 119 and 120 had not started moult on 21/3/95, but it may have been delayed because they were raising a chick then (section 3.3.12).

Moult records in 1994 for seven birds (106, 109, 111, 119, 120, 202 and 203) gave a rough indication of the duration of their primary moult because I could roughly estimate the start and finish dates for each bird. I did this by calculating the mean date (rounded upwards) between the after and before dates for both the moult start and finish columns in Table 3-4. This method could have under or overestimated the length of primary moult for individuals. The length of moult ranged from approximately 71 to 161 days (Table 3-4) (mean = 117.43, s.d. = 36.19, n = 7).

Table 3-4. Approximate times when primary moult occurred (presence or absence) in adult or subadult kagus at Pic Ningua and Mt Cindoa based on examination of birds. A '?' indicates no record. One line of data gives an annual moult record. Thus records for birds 106, 109, 111, 119, 120, 125, 201, 202 and 203 cover observations for 2-3 years. A '(?)' with a date indicates that moult probably took place that year, but there was a lack of data over the likely moulting period. Column 6 gives a rough approximation of the length of moult when records were complete (see text for method of calculation).

Bird	**Primary moult started**		**Primary moult finished**		**Length (days)**
	after	**before**	**after**	**before**	
Pic Ningua					
101	?	28/1/93	?	?	
102	?	3/2/93	?	?	
103	19/1/93(?)	?	?	?	
104	11/2/93(?)	?	?	?	
105	19/1/93(?)	?	?	?	
106	?	3/2/93	?	12/5/94	
	17/1/94	23/2/94	23/3/94	12/5/94	71
	4/1/95	14/2/95	?	?	
107	20/1/93(?)	?	?	?	
108	?	8/2/93	?	?	
109	21/1/93(?)	?	?	16/6/93(?)	
	4/12/94	5/1/94	14/3/94	5/5/94	110
	7/12/94	4/1/95	14/2/95	?	
110	18/3/93(?)	?	?	29/6/93(?)	
111	24/1/93(?)	?	?	3/6/93(?)	
	8/12/93	13/1/94	16/3/94	13/4/94	89
	30/12/94	31/1/95	?	?	
112	?	24/1/93	?	?	
113	23/1/93(?)	?	?	?	

Table 3-4 continued next page.

Table 3-4 continued.

114	?	1/2/93	?	?	
115	20/1/93(?)	?	?	1/6/93(?)	
116	?	19/2/93	23/5/93	?	
119	13/12/93	10/1/94	5/5/94	15/6/94	150
	21/3/95(?)	?	?	?	
120	22/12/93	10/1/94	18/5/94	15/6/94	151
	21/3/95(?)	?	?	?	
124	27/11/93	13/1/94	?	?	
125	?	12/4/94	?	9/5/94	
	11/1/95	14/2/95	?	?	
126	21/1/93	5/3/93	?	?	
127	23/1/93(?)	?	?	?	
128	23/1/93(?)	?	?	?	
129	12/2/93(?)	?	?	?	
Mt Cindoa					
201	11/1/94	8/2/94	?	22/3/94	
	21/2/95(?)	?	?	?	
202	15/12/93	11/1/94	8/3/94	19/4/94	90
	21/2/95(?)	?	?	?	
203	29/11/93	11/1/94	17/5/94	14/6/94	161
	7/2/95(?)	?	?	?	
205	15/11/93	28/12/93	?	?	
206	?	24/1/95	?	?	

3.3.5 Birds known at Pic Ningua before the first dog attacks

I captured (20 adults and subadults, 1 young juvenile and 1 chick; all banded) or saw only (bird 136), at least 23 different kagus on the north-facing slopes above the road just before recording the first dog attacks there in late April 1993 (*Chapter 4*). The 20 adults and subadults included seven pairs (101 and 102, 103 and 104, 105 and 106, 107 and 108, 109 and 110, 113 and 114 and 115 and 116) and one female (bird 111 who I captured perching with birds 112 and 128; Fig. 3-11) who lived on well defined home ranges and all wore radio-transmitters. From her subsequent behaviour, bird 111 had a good knowledge of her home range (e.g., she had many roosts there that were well used; section 3.3.6), thus was probably paired with bird 112 or 128. After fitting female 111 with a transmitter I failed to find birds 112 or 128 again, or any other bird with 111 by the time I recorded the first dog attacks on 26/4/93. I assumed that 111 became widowed on 26/4/93, although she probably lost her partner earlier. I had no transmitters on other birds, but had removed them from three kagus (birds 126, 127 and 128) because I had sufficient study animals (roost locations of 126 and 127 are in Fig. 3-20). The other adults or subadults were birds 112 and 129 (captured roosting with pair 103 and 104; Fig. 3-11).

The two remaining birds that I had banded were juvenile 122 who I had captured perching on the home range of pair 105 and 106 (Fig. 3-11), and may have been their offspring (I had heard a third bird at the time I captured 106), and the chick (bird 130) of pair 109 and 110. I saw bird 136 on two occasions with pair 113 and 114 when I was attempting to capture them. I knew from hearing kagu song that other birds lived in forest just below the road (region 15; Fig. 3-1) and at lower altitudes close to the Nakaré River (region 12). Also, on 11/2/93 I saw a bird who appeared to be a juvenile (from its shortish crest and whitish/brown leg coloration) on the home range of pair 115 and 116.

3.3.6 Kagu social structure in a relatively undisturbed population on Pic Ningua

Data I collected before I recorded the first dog attacks on birds at Pic Ningua suggested that pairs there held territories as their home ranges were relatively fixed and overlapped little with those of neighbouring pairs (Fig. 3-12). Home range boundaries, though, were based on only very small numbers of positions collected over several months and mainly determined by roost positions (Fig. 3-13). The area used by pair 109 and 110 overlapped considerably with that of pair 115 and 116 (Fig. 3-12), but this was due to only one roost and daytime location in mid June 1993 by male 110 after male 116 had been killed in May. When I removed these two data points, pair 109 and 110's boundary only just overlapped that of pair 115 and 116's. Bird 111 also kept to a well defined area up until I recorded the first attacked kagu on 26/4/93.

Evidence also suggested that kagus lived in families (a pair with one or more unpaired offspring) on the peak. I observed more than two subadult or adult kagus together at Pic Ningua on four occasions. First, in June 1992 four birds had responded to playback of kagu duet song at the approximate position where I captured bird 128 (Fig. 3-11). All the birds approached to within 2-3 m of me at the same time which suggested that they were often in eachother's company. Second, on 24/1/93 I captured 111, 112 and 128 together on the same perch. Third, on two

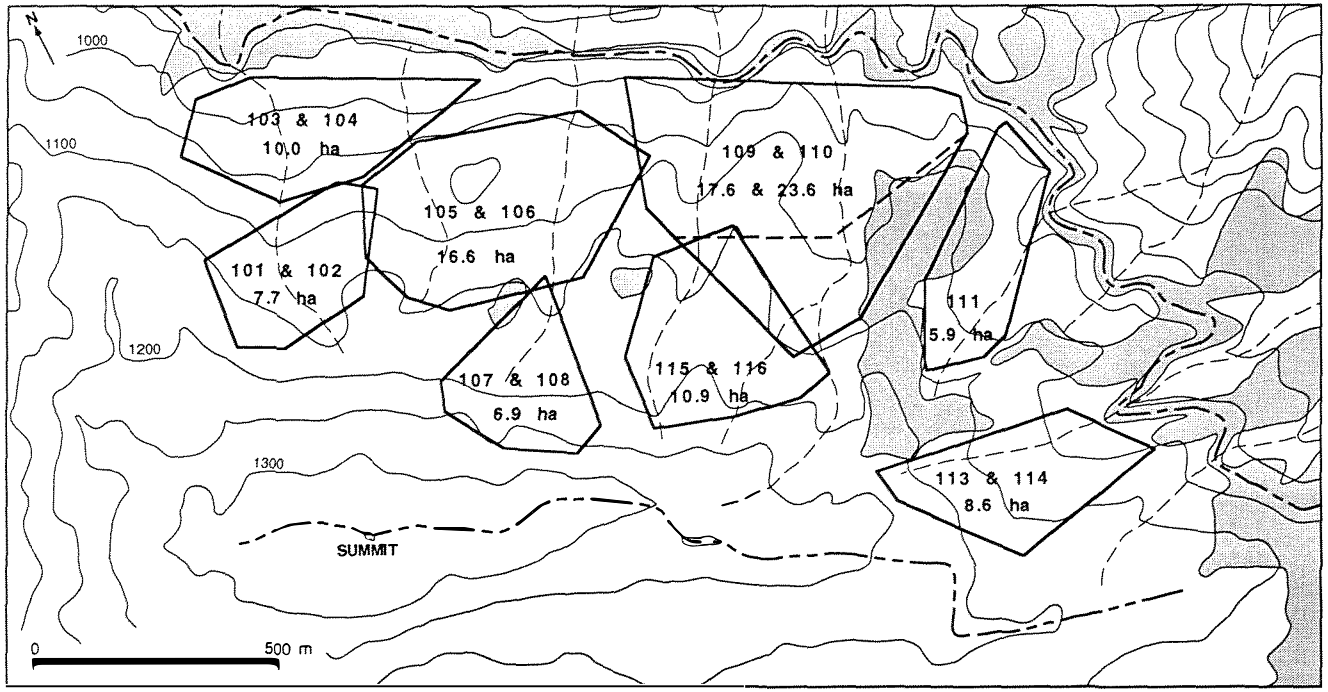
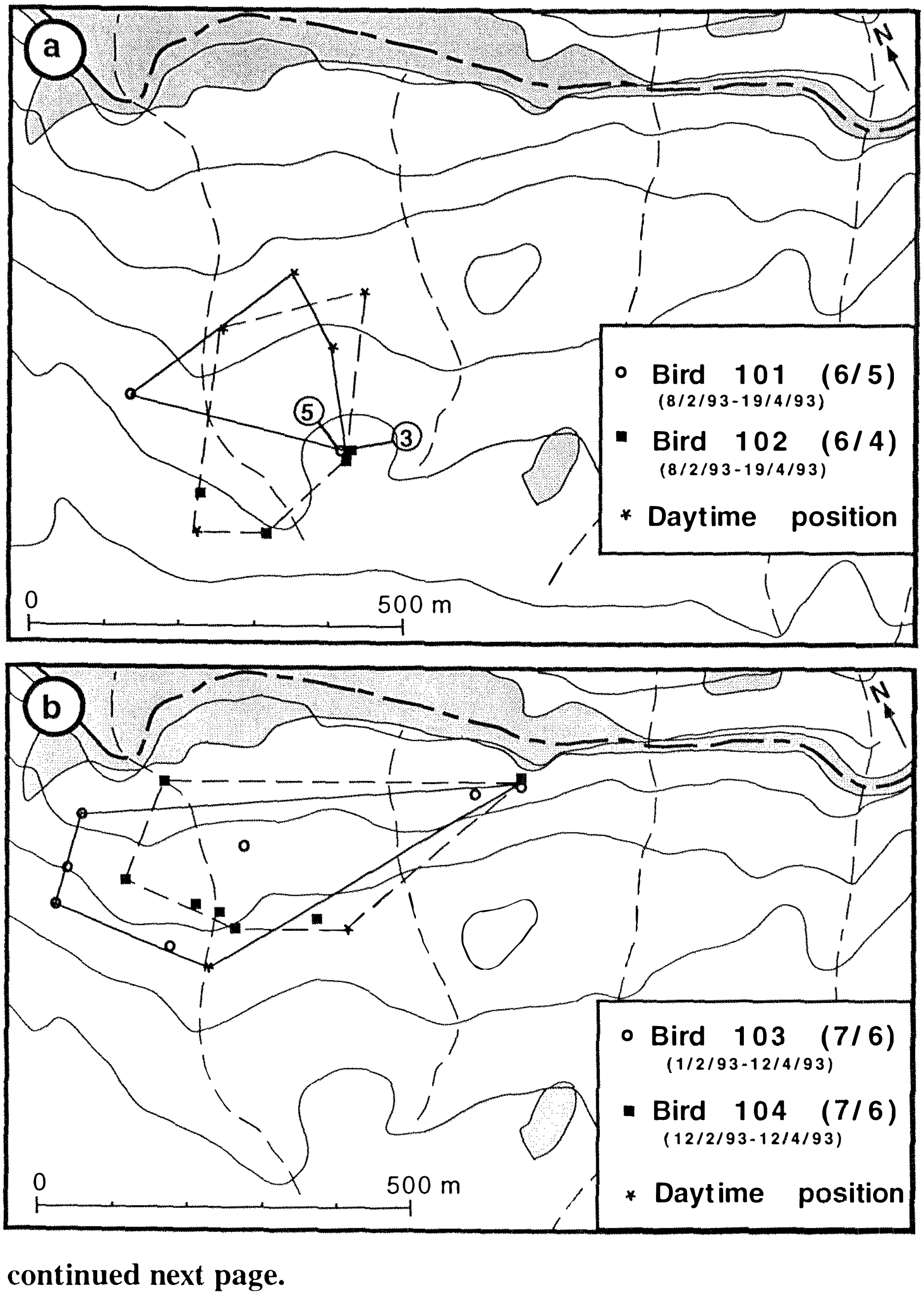


Figure 3-12. Home ranges of seven kagu pairs and bird 111 at Pic Ningua from late January 1993 up until one or both partners were attacked by dogs (see Fig. 3-13 for dates when data collection ceased). I established boundaries by fitting minimum convex polygons around roost positions and daytime locations (Fig. 3-13). ID Nos of partners and the areas (ha) of their combined home ranges are given within respective home range boundaries. The home range boundary for pair 109 and 110 extended to the south because of an intrusion by male 110 into female 115's home range after 116 was killed (section 3.3.6, Fig. 3-13e). The dashed line within 109 and 110's home range represents the southern borders of the smaller home range (17.6 ha) used by the pair excluding 110's visit to 115's territory. Bird 111's home range was the area she used up to 25/4/93. Key to map details in Figure 3-1.

Figure 3-13. Home ranges of individual members of seven kagu pairs (a, 101 and 102; b, 103 and 104; c, 105 and 106; d, 107 and 108; e, 109 and 110; g, 113 and 114; and h, 115 and 116) and bird 111 (f) at Pic Ningua (see Fig. 3-12) before they or their partners were attacked by dogs. I established the home range boundaries by fitting minimum convex polygons around roost positions (I could not find one roost of bird 107, but I knew its location to within 10 m) and daytime locations. I used all roost records (when a roost was used more than once, the number of times is indicated within circles) of individuals to establish their home ranges, including when either pair 109 or 110 roosted on the ground with their young chick. I did not use records when a bird's choice of roost may have been influenced by playbacks in the evening. Only the daytime locations that helped to position the boundaries are shown. A smaller and a larger home range is drawn for bird 110 (e) (see Fig. 3-12, section 3.3.6). The total number of roost positions and daytime locations for individuals are in brackets, respectively, in the Keys on the same line as the respective ID Nos. The period over which data were collected for each bird is in brackets underneath each ID No. Maps (a) to (h) are enlarged sections of the detailed inset in Figure 3-1, and using map features can be 'positioned' on Figure 3-12 where only the boundaries of the combined home ranges of pairs are drawn. Key to map details is in Figure 3-1.



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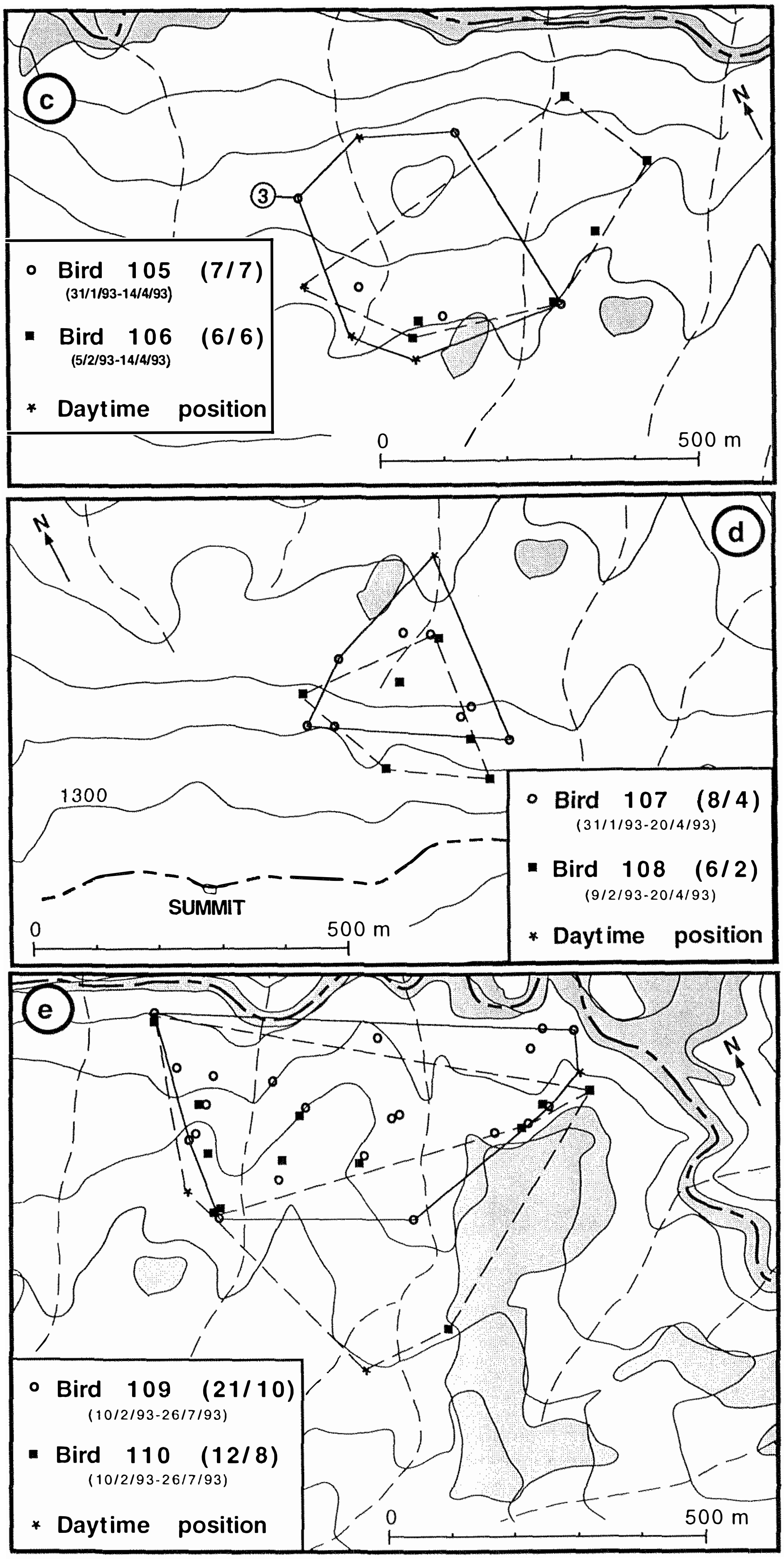

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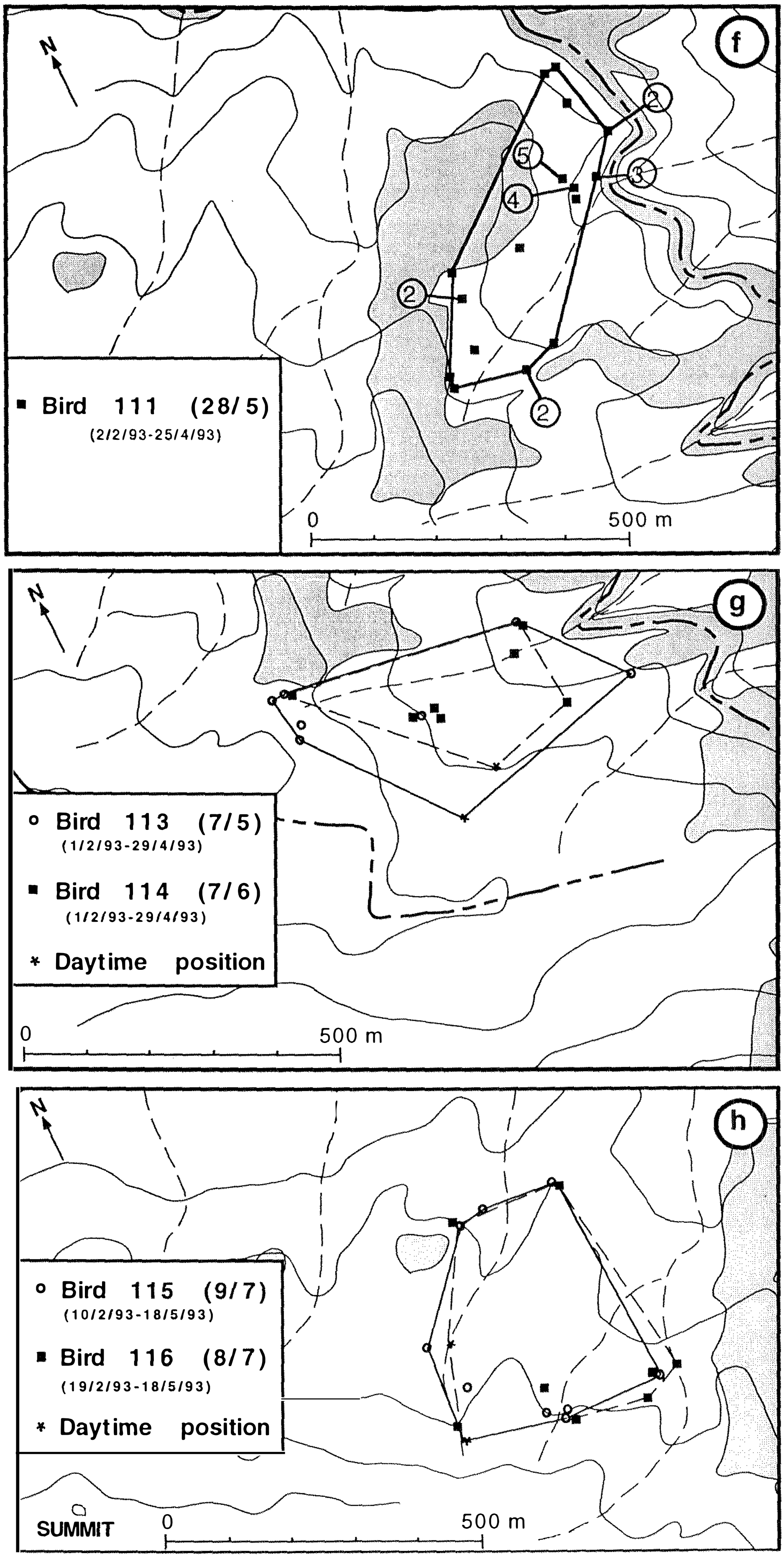


occasions in January 1993 I observed a third bird (possibly 136 both times) with pair 113 and 114, and all three birds exhibited defence behaviour in response to playbacks and the kagu model. Last, I captured bird 129 roosting with pair 103 and 104. Birds 112, 128 and 129 were more than one year old, and although I could not estimate the age of 136 its behaviour indicated it was also raised before 1992. Thus, it was possible that at least three pairs I knew of (103 and 104, 111 and partner, and 113 and 114) at Pic Ningua shared their combined home ranges with older offspring, but I had no evidence of the genetic relationships between birds.

Although data were few, they suggested that the home ranges of partners of some pairs did not overlap completely (Fig. 3-13). The home ranges of partners differed little for pair 115 and 116, moderately for pairs 113 and 114, 103 and 104, 107 and 108, 109 and 110 (excluding 110's incursion into 115's home range), and considerably for pairs 101 and 102, and 105 and 106.

Direct evidence suggesting kagu pairs held territories year round was that birds reacted to playbacks and defended against the kagu model in colder (June, October) and warmer (November, January, February) months of the year (Appendix IV). Both females and males approached and displayed to, or came near the model (Table 3-1). On two occasions I caught a kagu pair at the same time when using the model. Pair 119 and 120 were snared at the model and captured in fishing net nearby, respectively, and birds 201 and 202 were both snared at the model. Because I was usually hidden from the model while controlling the playback equipment and waiting for a bird to become snared, I did not observe whether both birds of each pair displayed to the model at the same time or whether one may have approached closer to aid the other when it was captured (a kagu has been reported to go to the assistance of another bird being attacked by a dog; Pouget 1875). After male 105 was captured, I used playbacks and the model to observe his behaviour on two further occasions. On both times he displayed around the model for approximately 40 minutes until I removed it. During his time at the model he sometimes tried to attack it (Plate 3-3) by mostly biting the legs from behind (behaviour also described by Campbell 1905), indicating his display to the model was defence behaviour and not courtship.

Birds were often highly agitated when hearing kagu duet song I played, and moved quickly around the area where the speaker was situated in an attempt to locate the duetting pair. Many birds also sang in response to the playbacks, on their own (both males and females did this) or duetted with their partners. Some duets could have been between birds who were not partners, for example between a parent and its offspring (section 2.2.1). At times, close neighbours also commenced duetting. One pair that I observed duetting in response to the playbacks had positioned themselves on the same perch about 1 m above the ground and were changing directions as they sang, perhaps to broadcast their song to as wide an area as possible.

The mean size of the home ranges of the seven kagu pairs (Fig. 3-12, excluding 111's, and using the smaller home range area for pair 109 and 110) was 11.2 ha (s.d. = 4.27, n = 7). Bird 111's home range was 5.9 ha, and pair 109 and 110's was 23.6 ha when based on the larger home range of male 110.

3.3.7 Home ranges of kagus at Pic Ningua after they or their partners were attacked by dogs, and those of new birds found after the first recorded dog attacks

Twelve of the 15 birds wearing radio-transmitters just before I discovered the first kagus attacked on 26/4/93 were killed or died later from attack wounds (Appendices IV and V), leaving only three (birds 106, 109, 111) surviving after the last recorded attacks in early August 1993. I captured eight new birds (117, 118, 119, 120, 121, 123, 124, and 125) after 26/4/93, found four unidentified birds dead (131, 132, 133, and 134), and saw one new bird (137) (capture, discovery or sighting dates in Appendix IV). I fitted all the eight new birds I captured with radio-transmitters, as well as the previously banded juvenile 122. Five (117, 118, 121, 122 and 123) of these nine birds were subsequently killed, the transmitter on bird 124 apparently failed (section 3.3.2), and pair 119 and 120 remained unharmed.

I collected data on the home ranges of females 106 and 109 from the time they lost their partners until 1995, of female 111 from 26/4/93 (she was unpaired at least from that date) to 1995, of female 115 after her partner 116 was killed until she died from attack wounds in August 1993, of new pair 117 and 118 from early June 1993 until they were killed, of new pair 119 and 120 from mid June to 1995, and of unpaired bird 125 from 12/4/94 to 1995. I collected limited roost and/or movement data on two juveniles (birds 122 and 123, both killed) and on birds who interacted (male 124) or may have paired (birds 121 and 137) with widowed females.

Widowed females 106 (Fig. 3-14), 109 (Fig. 3-15) and 111 (Fig. 3-16) greatly extended their home ranges after losing their partners, travelling widely over the peak

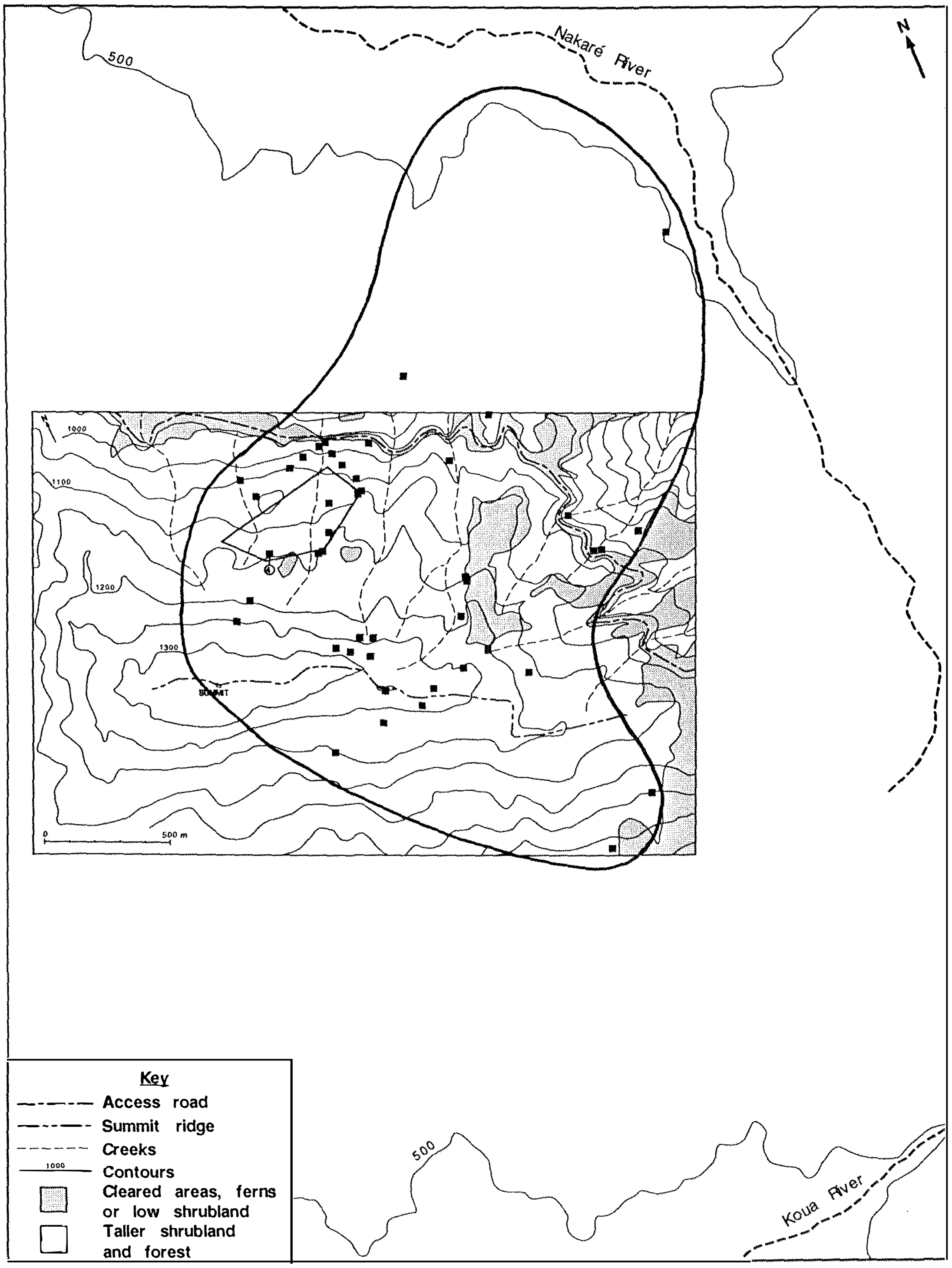


Figure 3-14. Roost positions (black squares, n = 48, from 26/4/93- 1/3/95) for bird 106 on Pic Ningua after her partner was killed by dogs in late April 1993. Two roosts are outside the detailed map section. When a roost was used more than once, the number of times is indicated within a circle. The home range used by 106 before 26/4/93 (Fig. 3-13c) is also shown (enclosed within the unbroken boundary). An indication of the home range of 106 from 26/4/93 to 1/3/95 is shown by the area enclosed within the hand-drawn line around the roost positions, taking into account movements determined from telemetry fixes (methods in 3.2.7).

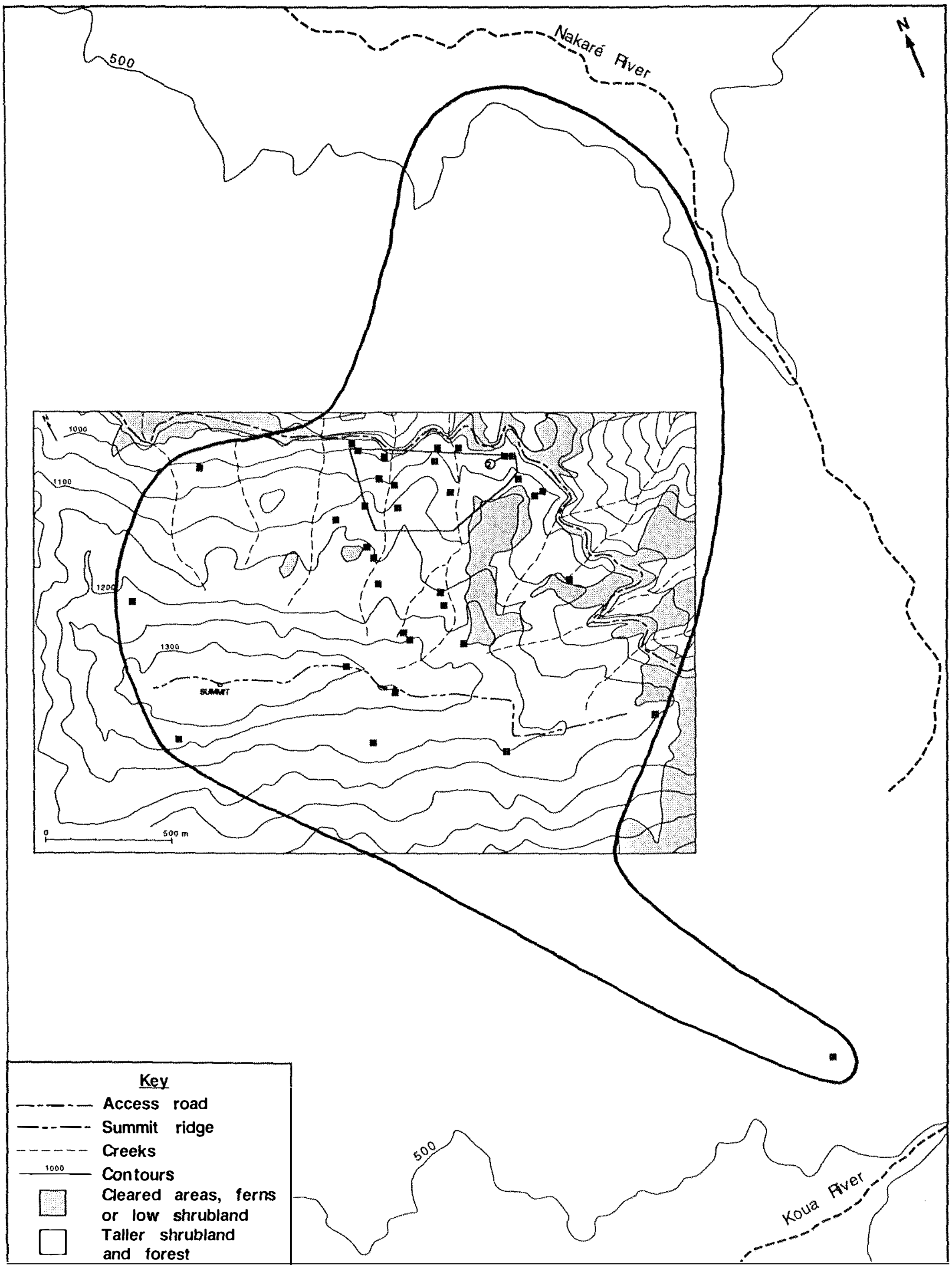


Figure 3-15. Roost positions (black squares, n = 36, from 12/8/93-14/2/95) for bird 109 on Pic Ningua after her partner was killed by dogs in early August 1993. One roost is outside the detailed map section. When a roost was used more than once, the number of times is indicated within a circle. The home range used by 109 before August 1993 (Fig. 3-13e) is also shown (enclosed within the unbroken boundary). An indication of the home range of 109 from 12/8/93 to 14/2/95 is shown by the area enclosed within the hand-drawn line around the roost positions, taking into account movements determined from telemetry fixes (methods in 3.2.7).

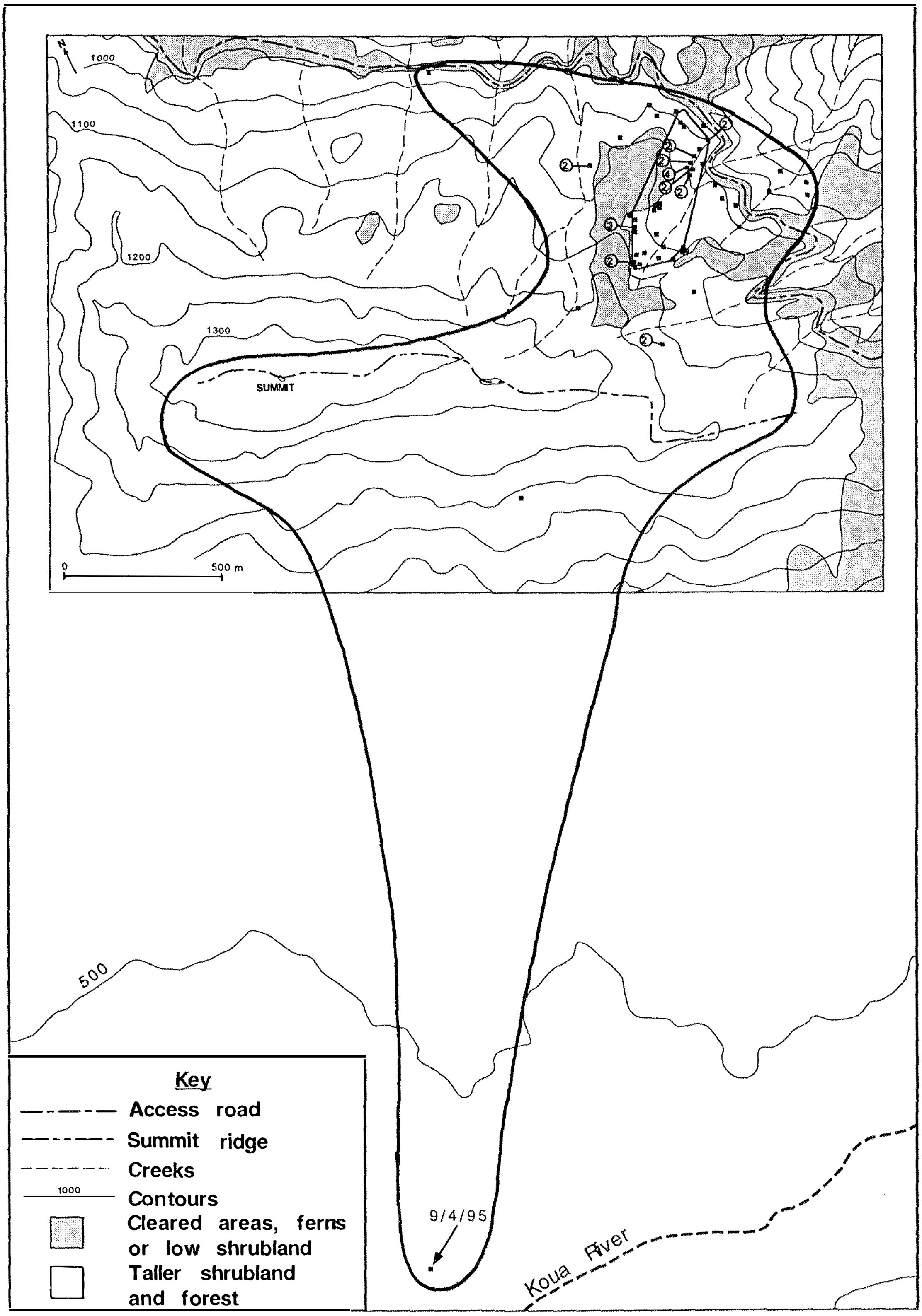


Figure 3-16. Roost positions (black squares, n = 63, from 26/4/93-9/4/95) for bird 111 on Pic Ningua. One roost is outside the detailed map section. When a roost was used more than once, the number of times is indicated within a circle. The home range used by 111 before 26/4/93 (Fig. 3-13f) is also shown (enclosed within the unbroken boundary). An indication of the home range of 111 from 27/4/93 to 9/4/95 is shown by the area enclosed within the hand-drawn line around the roost positions, taking into account movements determined from telemetry fixes (methods in 3.2.7).

and down to lower altitudes in the river valleys around the peak. The home range of female 109 was the most extensive as she descended to both the Nakaré and Koua River valleys. Female 106 descended to the Nakaré River, and female 111 to the Koua River where I found her roosting with bird 137 on 9/4/95. Bird 125's home range was more similar to 106's (Fig. 3-17).

After her partner 116 was killed, female 115 apparently extended her home range slightly further west (Fig. 3-18a) where she roosted with another bird, possibly 121. Pair 117 and 118's home range (Fig. 3-18b) covered almost the same area as pair 113 and 114's (Fig. 3-12) who had been killed earlier.

The home range used by pair 119 and 120 extended from below the road to the south-facing slopes (Fig. 3-19). Both birds visited similar areas except that 119 briefly (probably at most several days) went below the road around region 12 in September 1994. The movements of the two birds within their home ranges were however less similar (section 3.3.9).

I recorded only small numbers of roosts for birds 122 (n = 2), 123 (n = 4) and 124 (n = 6) (Fig. 3-20) over the short time periods that I followed them and knew little about their home ranges.

3.3.8 Kagu movements and interactions before the first recorded dog attacks

Before the dog attacks, I only observed bird movements within well defined home ranges. As Létocart (1991) observed at Parc Rivière Bleue, birds at Pic Ningua could be on one side of their home range in the morning and roost hundreds of metres away on the other side that night. I knew little about the social organisation of birds who shared the same home ranges, and had no evidence of social interactions other than what appeared to be between family members.

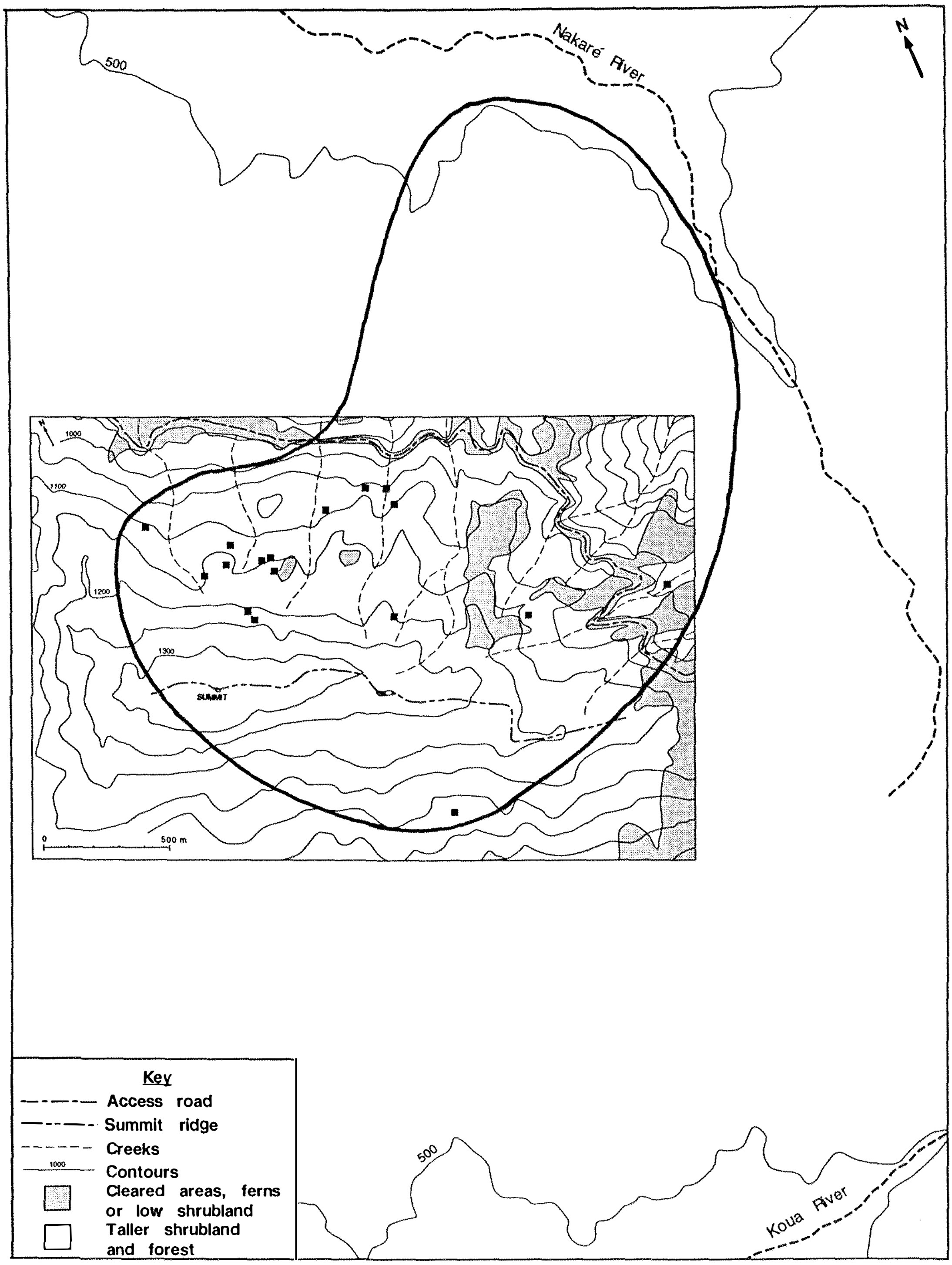
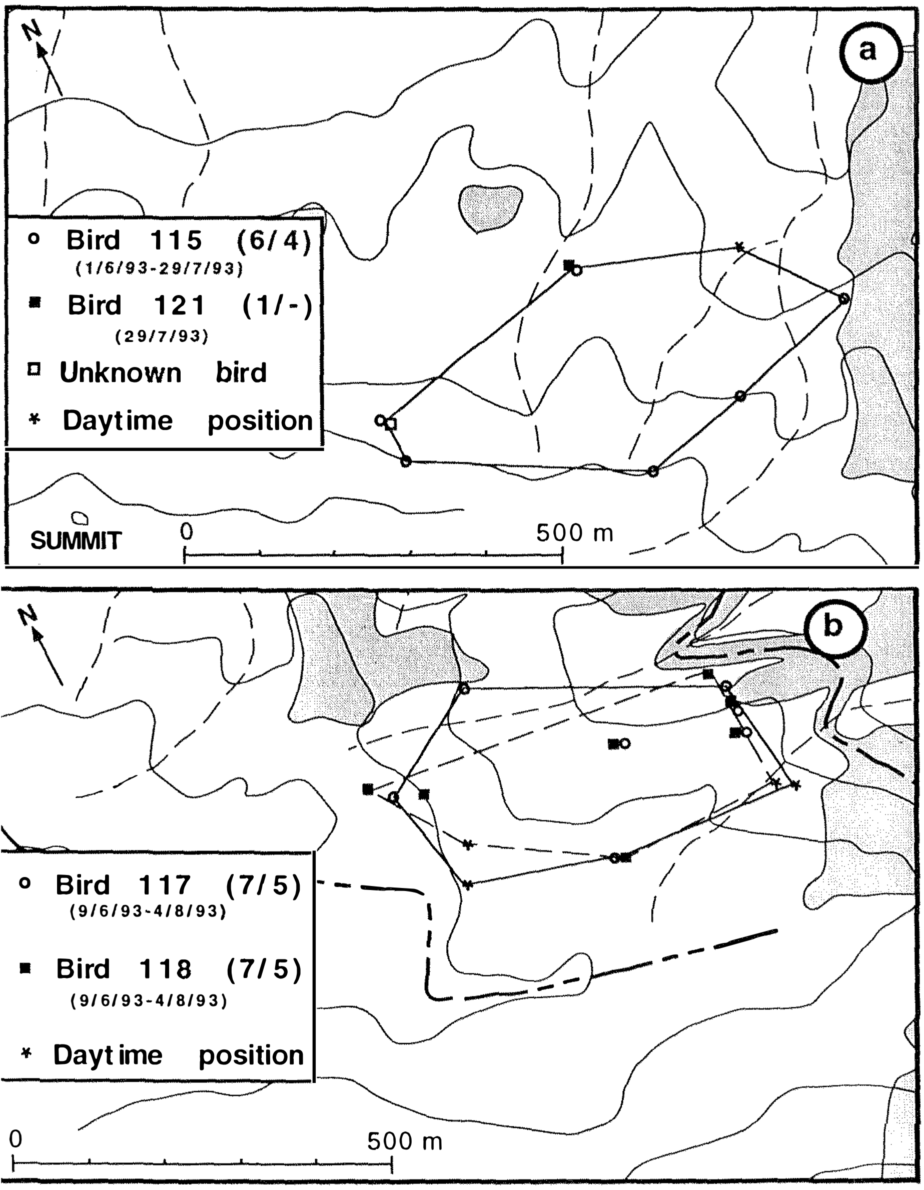


Figure 3-17. Roost positions (black squares, n = 17) for bird 125 on Pic Ningua from its capture on 12/4/94 to 14/2/95. No roosts were outside the detailed map section. An indication of the home range used by bird 125 from 12/4/94 to 14/2/95 is shown by the area enclosed within the hand-drawn line around the roost positions, taking into account movements determined from telemetry fixes (methods in 3.2.7).

Figure 3-18. (a) Home range of female 115 at Pic Ningua after her partner was killed by dogs. The roost of male 121 who perched with 115 on 29/7/93, and that of an unknown bird (possibly bird 121) who roosted a few metres from 115 on 27/7/93 are also shown. (b) The home ranges of birds 117 and 118 covered much the same region as the home range of killed pair 113 and 114 (Fig. 3-12). I established the home range boundaries by fitting minimum convex polygons around roost positions and daytime locations. All roosts of the individual birds were used to establish their home ranges. Only the daytime locations that positioned boundaries are shown. The total number of roost positions and daytime locations for individuals are in brackets, respectively, in the Keys on the same line as the respective ID Nos. The period over which data were collected for each bird is in brackets underneath each ID No. Maps (a) and (b) are enlarged sections of the detailed inset in Figure 3-1, and using map features can be 'positioned' on Figures 3-12 and 3-19 for comparison with the home ranges of other kagus. Key to map details is in Figure 3-1.



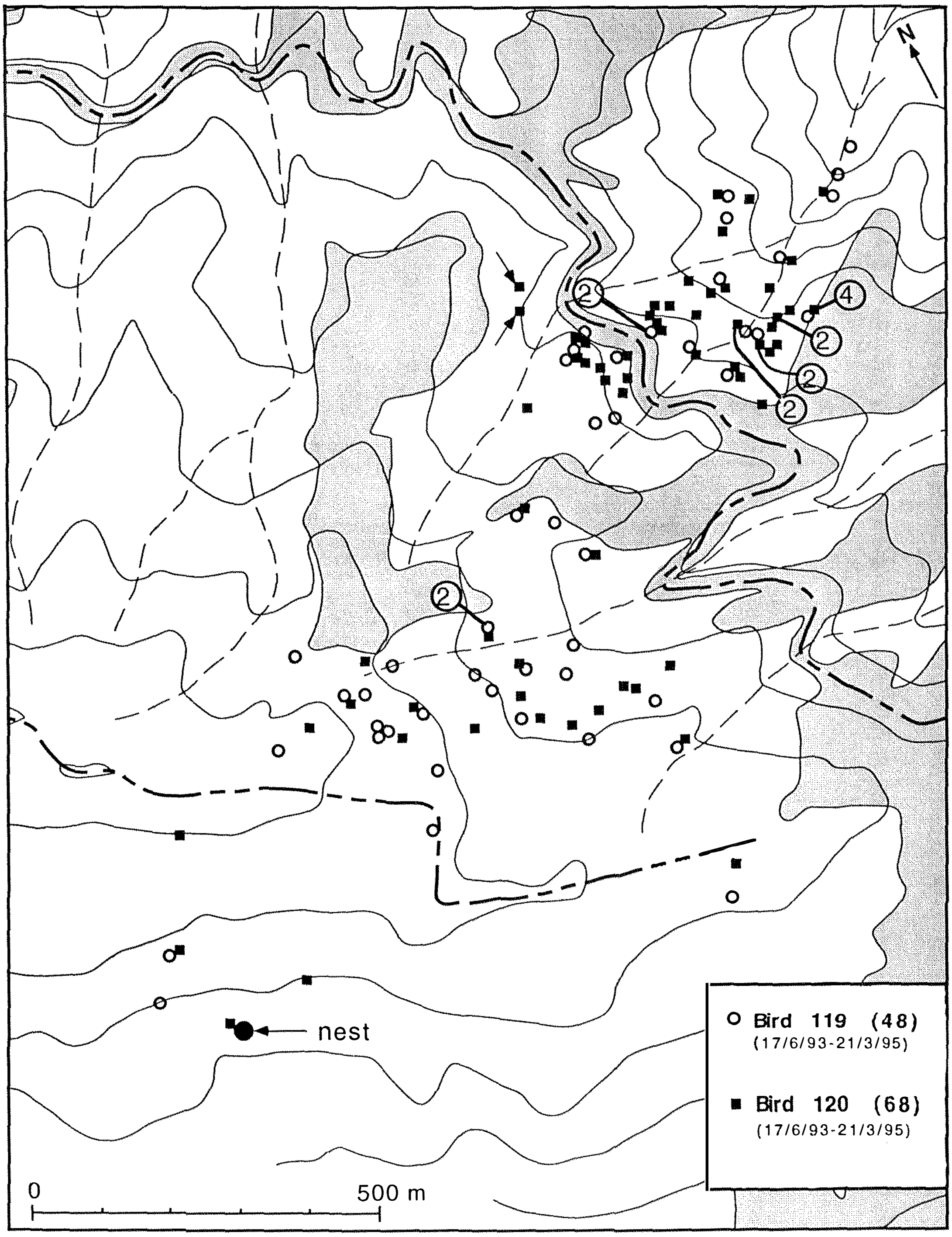


Figure 3-19. Roost positions of pair 119 and 120 on Pic Ningua from the time they were captured on 17/6/93 until 21/3/95. When a roost was used more than once, the number of times is indicated within a circle. The location of the pair's nest (large black dot) in late 1994/95 is indicated. All roost positions (numbers in brackets in the Key) are shown (excluding when on the nest), including when either parent incubated the young chick on the ground away from the nest. Roost positions of bird 120 indicate accurately his known home range use, but 119 probably travelled further west along the south-facing slopes and I also detected her once in region 12 (see Fig. 3-25, section 3.3.7). The two roosts of female 111 that 120 used in October 1994 are arrowed. Key to map details is in Figure 3-1.

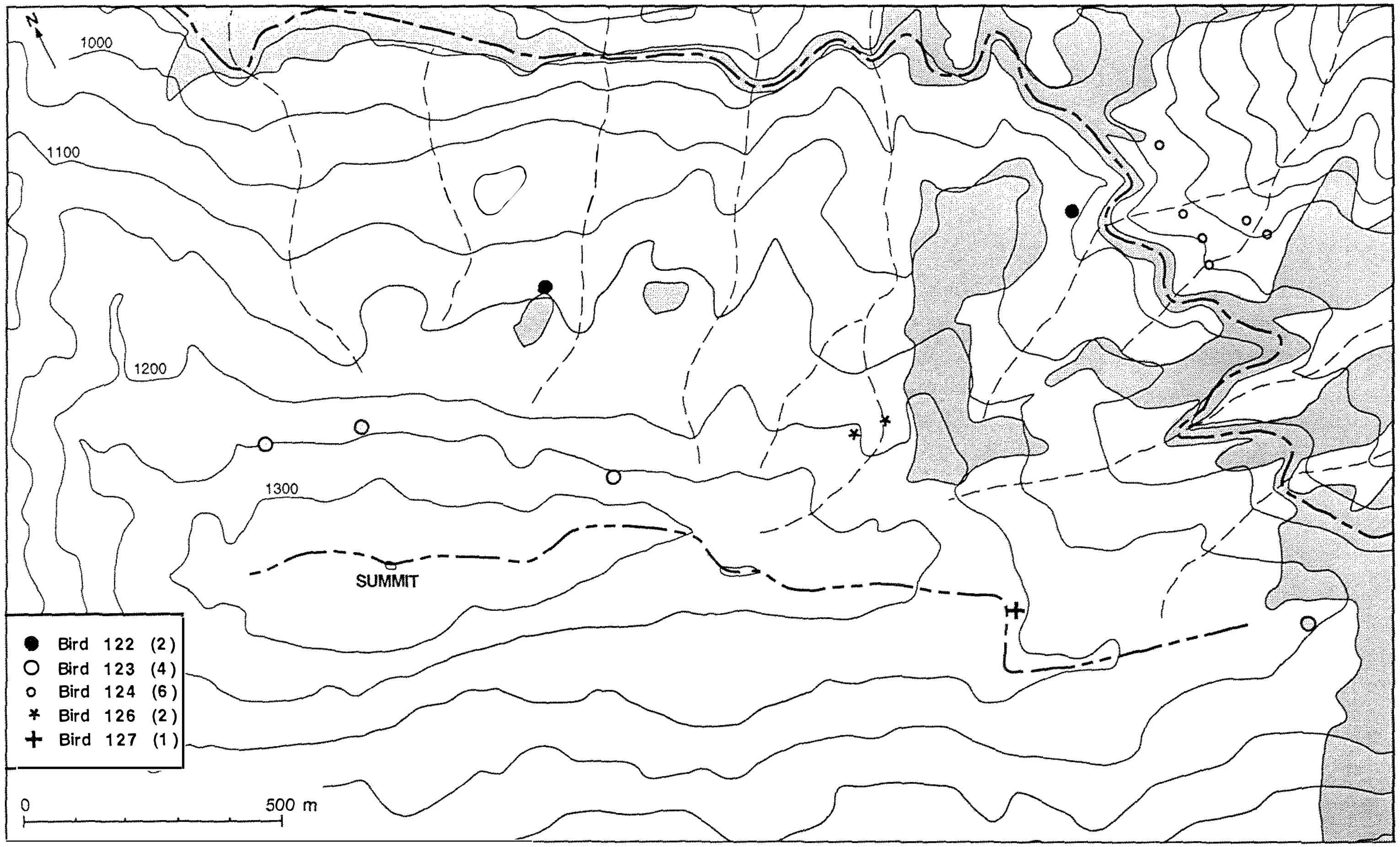


Figure 3-20. Roost positions of five kagus (birds 122, 123, 124, 126 and 127) on Pic Ningua who I knew only briefly (summary data on individual birds are in Appendices IV and VII). I included roosts of birds 126 and 127 here to reduce map use, although they were located before I recorded the first dog attacks. Numbers of roosts for individual birds are in brackets in the Key. Key to map details is in Figure 3-1.

3.3.9 Kagu movements and interactions by wounded and widowed birds at Pic Ningua and those that became known after the first recorded dog attacks

This section describes the movements and interactions of birds during much of 1993, and 1994/95. Few data are available for some birds (122, 123, 124, 115, 121, 117 and 118) as I only knew them briefly. I drew path diagrams (Appendix VIII) of kagu movements between regions (Fig. 3-1) to describe the way that birds 106, 109, 111, 119, 120 and 125 (from who I had collected long-term data) travelled on the peak. I presented the data in each diagram in the text as a bar graph, and a map showing the relative frequency of movements between regions.

Birds 122, 123 and 124

I first captured (and banded) bird 122 on 7/4/93 (Fig. 3-11) on pair 105 and 106's home range. I subsequently came across 122 again by chance on 27/4/93 roosting on the ground at a sheltered site previously used by female 111 (Fig. 3-20), the morning I found male 105 dead. After I fitted bird 122 with a transmitter it spent time in region 6 close to where I found its remains on 9/5/93 (Fig. 4-1).

Female 123 (< 1 year old) travelled widely along the summit ridge between the date (7/6/93) I fitted her with a transmitter on pair 103 and 104's home range (Fig. 3-11) and 10/8/93 when I found her dead (Fig. 3-20). After I captured her she mostly foraged high up on the north-facing slopes around region 3, but also visited region 4. I found her second roost on the south-facing slopes (close to where I found her dead; Fig. 4-1), before she returned to region 3.

I captured male 124 in region 15 roosting with female 111 (see *Bird 111* below) on 27/11/93, on a perch previously used by female 119. Male 124 stayed below the road (Fig. 3-20) until I lost his transmitter signal (last heard on 2/2/94). During the time I radio-tracked 124 in region 15, female 111 visited the area more than once and from my knowledge of birds and their positions in that region she appeared to duet with male 124. I never recorded 124 above the road, even though 111 crossed it. Male 124 may have come from the Nakaré River area as he spent time lower down in the valley. If his transmitter failed, it was strange that I never heard him sing in the area again. I had no evidence that a bird had been accidentally killed on the road in that area but I knew from vehicle tracks and human and kagu footprints on the road that someone had tried to catch a kagu at the same location (where pair 119 and 120 crossed the road between regions 9 and 15) previously.

Birds 115 and 121

Male 110 visited female 115's home range in mid June 1993 after 115 lost her partner five weeks earlier in May (Fig. 3-13), but I had no evidence that both birds interacted with each other. Just before female 115 was attacked by dogs, she roosted further west of the range she had held with 116 (Figs. 3-13h and 3-18a). One of her two roosts I located there was about 2 m from another roosting bird (from excrement at the site), possibly 121 (an adult male) who I found perching with 115 on 29/7/93 on the home range she had shared with male 116.

Birds 117 and 118

I radio-tracked birds 117 and 118 for approximately eight weeks from early June until they were killed. Pair 117 and 118 had very similar home ranges and duetted together, and may have been a pair.

Bird 106

After male 105 was killed by dogs in late April 1993, his partner 106 remained in the area of their combined home range (region 4) until I recorded her in region 5 on 11/8/93 (Appendix VIII). From that time she mostly stayed outside region 4, returning only for short periods or seeming to 'pass through' to other areas (Figs. 3-21 and 3-22). The longest time she stayed was approximately four weeks in October 1993. The last time I recorded her in region 4 was on 3/7/94 for about two days. She travelled widely on the peak, especially onto the south-facing slopes and around region 5 near the summit ridge. Between 21/9/93 and 5/11/94 she descended seven times below the road to near the Nakaré River, staying longest there (at least 5 weeks) in November/December 1994. She, as well as female 109 and bird 125 (see below), appeared to descend to the river via forest corridors along creeks. The birds may have been attracted to this area by kagus who regularly sang there in the mornings, and whose song could easily be heard above the road from the north-facing slopes. I found 106 roosting at 490 m near the Nakaré River on 12/5/94. It was interesting that she travelled relatively quickly and frequently from region to region,

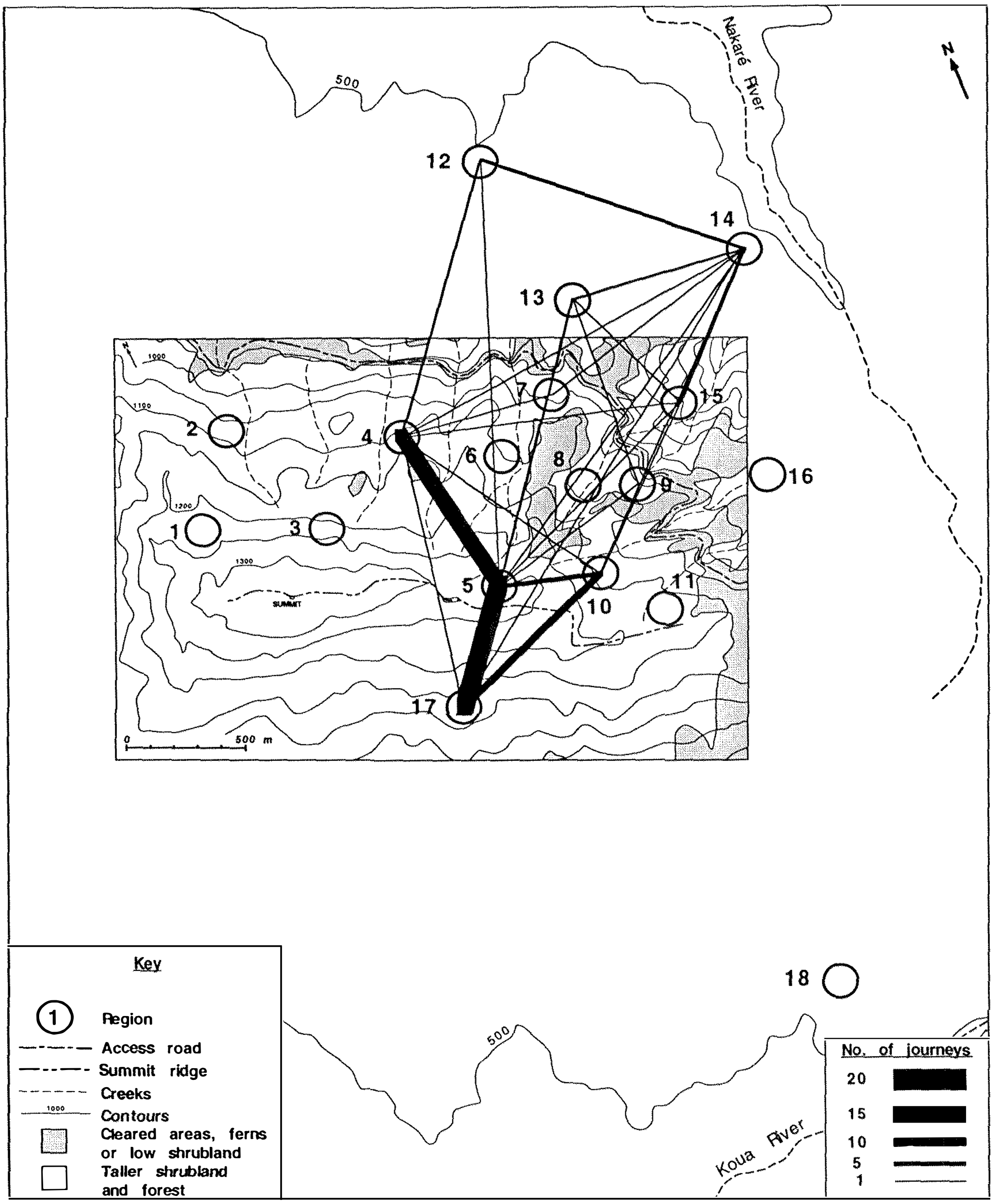
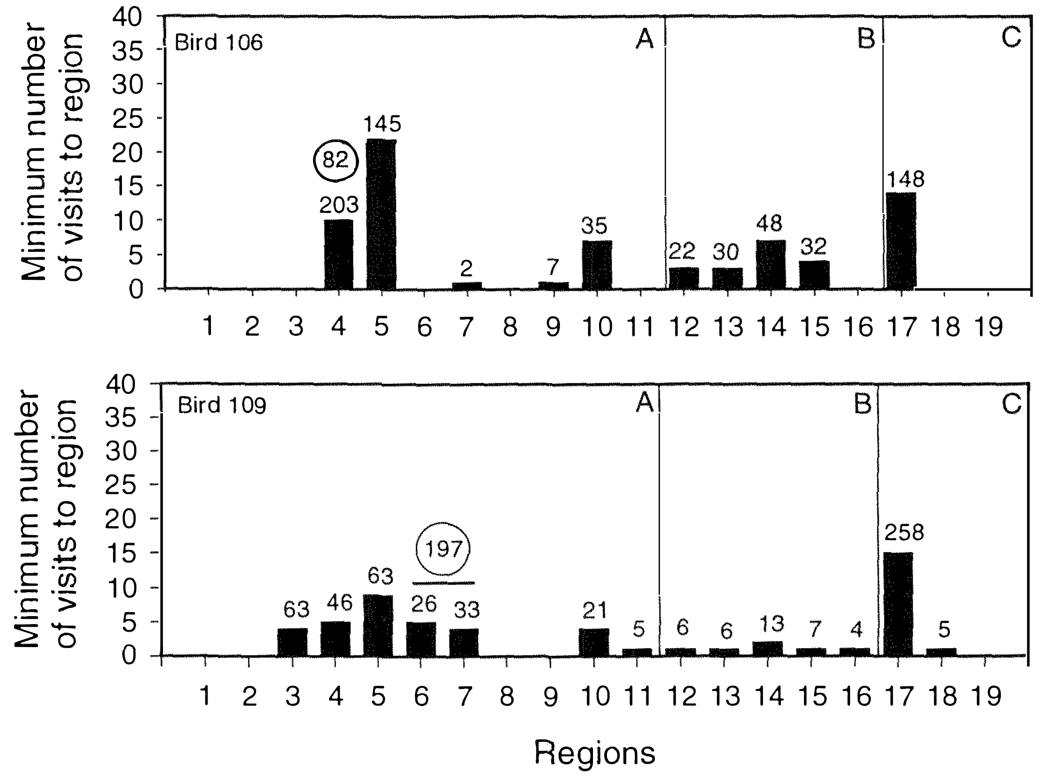


Figure 3-21. Graphic representation of the path diagram (in Appendix VIII) detailing the movements of female 106 at Pic Ningua after her partner 105 was killed. The thickness of a line running between two regions indicates the relative frequency that 106 moved back and forth between the two positions (see examples in inset). These movement data were collected from telemetry fixes only (methods in section 3.2.7) taken from roads around the peak, and are not intended to accurately indicate the home range used by 106. Also, the regions only indicated the general area that I estimated she was in (e.g., region 17 covered all the higher altitude forest on the south-facing slopes). Roost positions for 106 and an indication of her actual home range are in Figure 3-14.

Figure 3-22. Graphs summarizing the path diagrams (Appendix VIII) describing the movements of kagus 106, 109, 111, 119, 120 and 125 at Pic Ningua from the time they were first captured. Details of how the data were collected are in the legend to Appendix VIII. For birds 119, 120 and 125, each graph gives the observed frequency (bars) of visits to regions (region positions in Fig. 3-1). For females 106, 109 and 111, the observed frequency (bars) of visits to regions is from the time they lost their partners (estimated at 26/4/93 for female 111), and the number of days they spent with their partners is within the circles above the regions covering their combined home ranges (region 4 for bird 106, regions 6 and 7 for bird 109, and region 8 for bird 111). Numbers above bars not circled are estimates of the length of time (days) that birds (only after loss of partners for 106, 109 and 111; see above) spent in each region. The number of visits to regions, and the number of regions visited, are probably only minimum estimates because I did not locate a bird's position each day and birds could move considerable distances even in one day. For the same reason, the numbers of days spent in each region is only an average estimate. The vertical lines separate the regions into 3 blocks: 'A' = the north-facing slopes above the access road; 'B' = the north-facing slopes below the road; and 'C' = the south-facing slopes.



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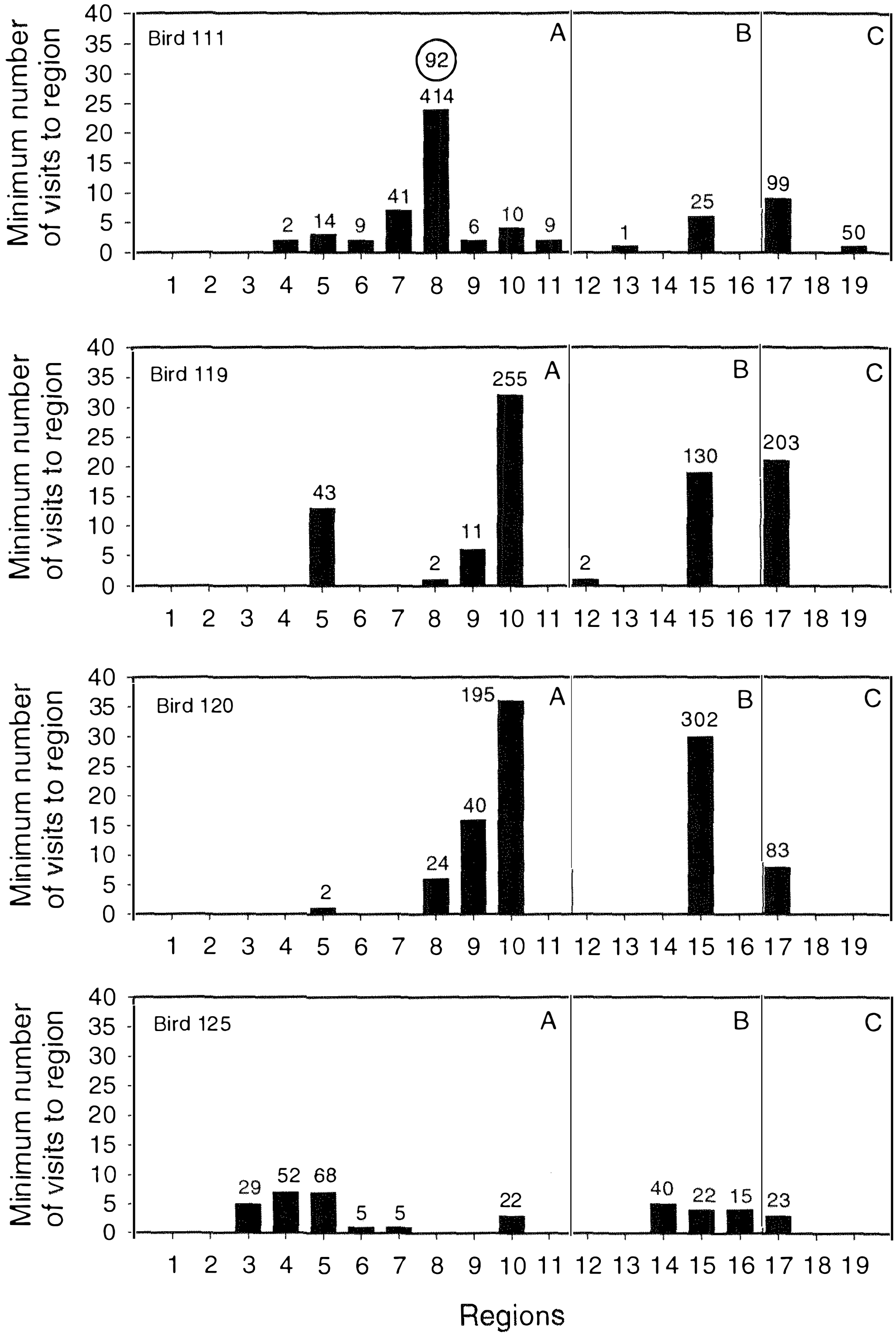

and often over long distances. For example, in October 1994 she completed a trip from near the summit ridge to region 14 and back again in at most nine days, a total map distance of about 7.0 km with a descent and ascent of around 750 m in altitude. Although she spent several weeks or more at a time in some regions, she was more or less constantly moving around the peak from the time she first left her home range. This was in dramatic contrast to her relatively confined movements within her home range the three months she was there with her partner 105. She also spent most of the 3.5 months after 105's death there, but during this period I located four of her roosts just outside her old home range (3 on 105's home range and 1 in a new area).

I recorded only one interaction between female 106 and another kagu, when I found her perching with bird 125 on her old home range on 12/4/94. Both birds stayed in region 4 for several days after 12/4/94, but female 106 moved to region 12 on about 17/4/94, while bird 125 stayed in region 4 for another two weeks. I found 106 roosting near the road in region 15 on four occasions but had no indication that she interacted with male 120 whose home range covered that area.

Bird 109

Female 109 was wounded by dogs in early August 1993. I took her to Nouméa for treatment and released her in region 7 on 7/8/93. I applied antibiotic cream to her back wounds several times after her release and she quickly recovered. Female 109 was less attached to her old home range (Fig. 3-13e) than female 106 as she only visited the area (regions 6, 7 and the eastern part of region 4) once after 13/12/93 (Appendix VIII). Like 106 she also travelled widely and more or less continually on the peak after the loss of her partner 110 (Figs. 3-22 and 3-23), and descended to both the Koua (once in February 1994) and the Nakaré Rivers (3 times from August 1994). Also like 106, she spent much time in region 5 and on the south-facing slopes, and exhibited considerable walking skills, for example she moved from region 18 at around 500 m to region 5 in at most five days, a map distance of over 4.5 km and an ascent of 750 m in altitude.

I recorded no interactions between female 109 and other kagus after she was wounded.

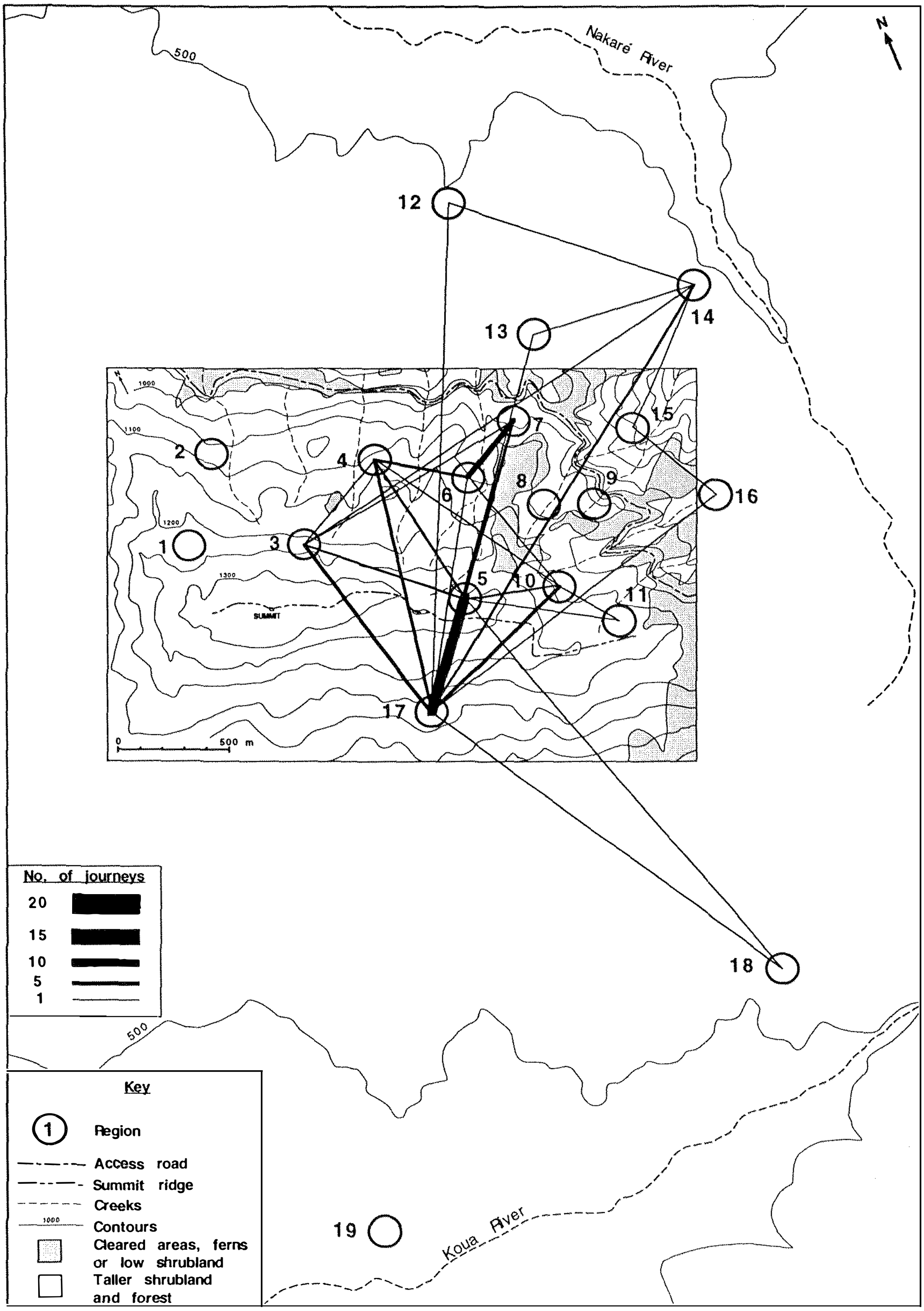

Figure 3-23. Graphic representation of the path diagram (in Appendix VIII) detailing the movements of female 109 at Pic Ningua after her partner 110 was killed. Roost positions for 109 and an indication of her actual home range are in Figure 3-15. The other details in the legend to Figure 3-21 also apply to the movements here for bird 109.

Bird 111

I first observed female 111 outside her old home range (region 8) on 2/8/93 three months after I recorded the first kagus attacked on 26/4/93 (Appendix VIII). Unlike females 106 and 109, she stayed relatively faithful to her old home range (Figs. 3-22 and 3-24), returning regularly up until 24/1/95 when she remained on the south-facing slopes. I found her there at 330 m a.s.l. (region 19, 6.5 km from, and 770 m in altitude below, region 8) on 9/4/95 perching with unknown bird 137. She had stayed near the Koua River since mid February 1995, to my knowledge her first descent to low altitude and to an area I had not heard kagus sing in. This was probably the third bird that she interacted with since late April 1993. The first was with male 124 (see above). She moved to region 15 on two more occasions (mid April and early August 1994) for brief visits after I lost 124's radio signal. The latter visit may have been related to male 120, and likely the second bird she interacted with (see *Bird 119 and 120* below).

Some of female 111's movements, as well as those of other birds, may have been reactions to my disturbing her at her roost (e.g., catching and weighing) as she sometimes moved large distances after these times. For example, I weighed her on 16/3/94 (region 8) and detected her in region 17 on the south-facing slopes for the first time four days later. On two subsequent occasions she moved to region 17 the same day that I captured her on the north-facing slopes, on 6/10/94 (in region 10, see *Birds 119 and 120)* and 30/12/94 (in region 4).

Birds 119 and 120

From the time I captured female 119 with male 120 in region 15 on 14/6/93, she travelled outside that region (Appendix VIII), and returned with decreasing frequency up until June 1994. After that time she passed through region 15 briefly on only three occasions. While outside region 15 she spent most time in regions 10 and 17. I first recorded her in the latter region in October 1993, then with increasing frequency until she nested there with male 120 in early December 1994 (Figs. 3-22 and 3-25). During the period that I followed her, she moved in a large but quite well defined area between regions 15, 10 and 17, except for a brief visit to region 12 in September 1994. She crossed the road a total of 20 times between regions 15 and 9, probably always directly between the two regions. Pair 119 and 120 often roosted near the road

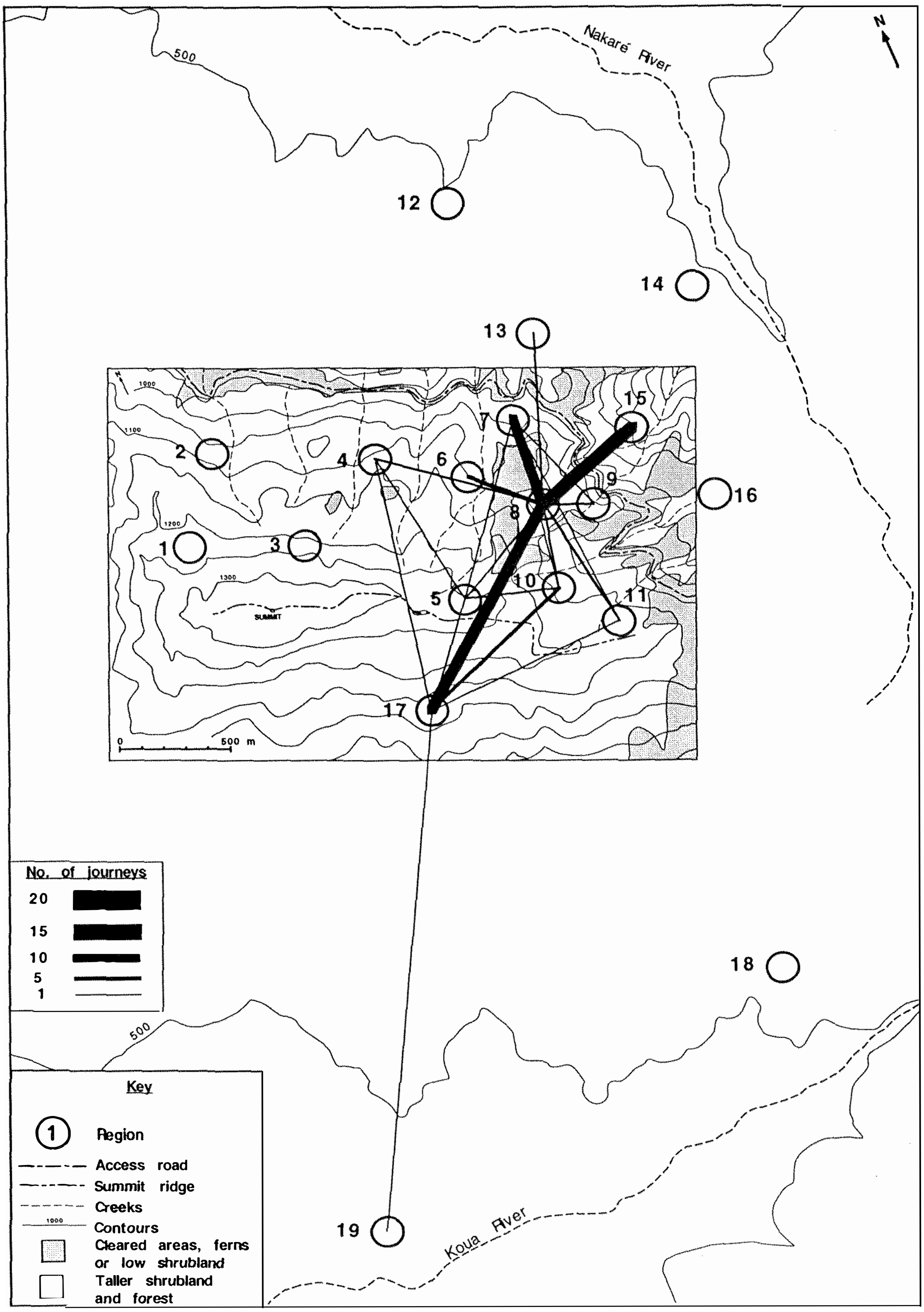

Figure 3-24. Graphic representation of the path diagram (in Appendix VIII) detailing the movements of female 111 at Pic Ningua after her partner was killed. Roost positions for 111 and an indication of her actual home range are in Figure 3-16. The other details in the legend to Figure 3-21 also apply to the movements here for female 111.

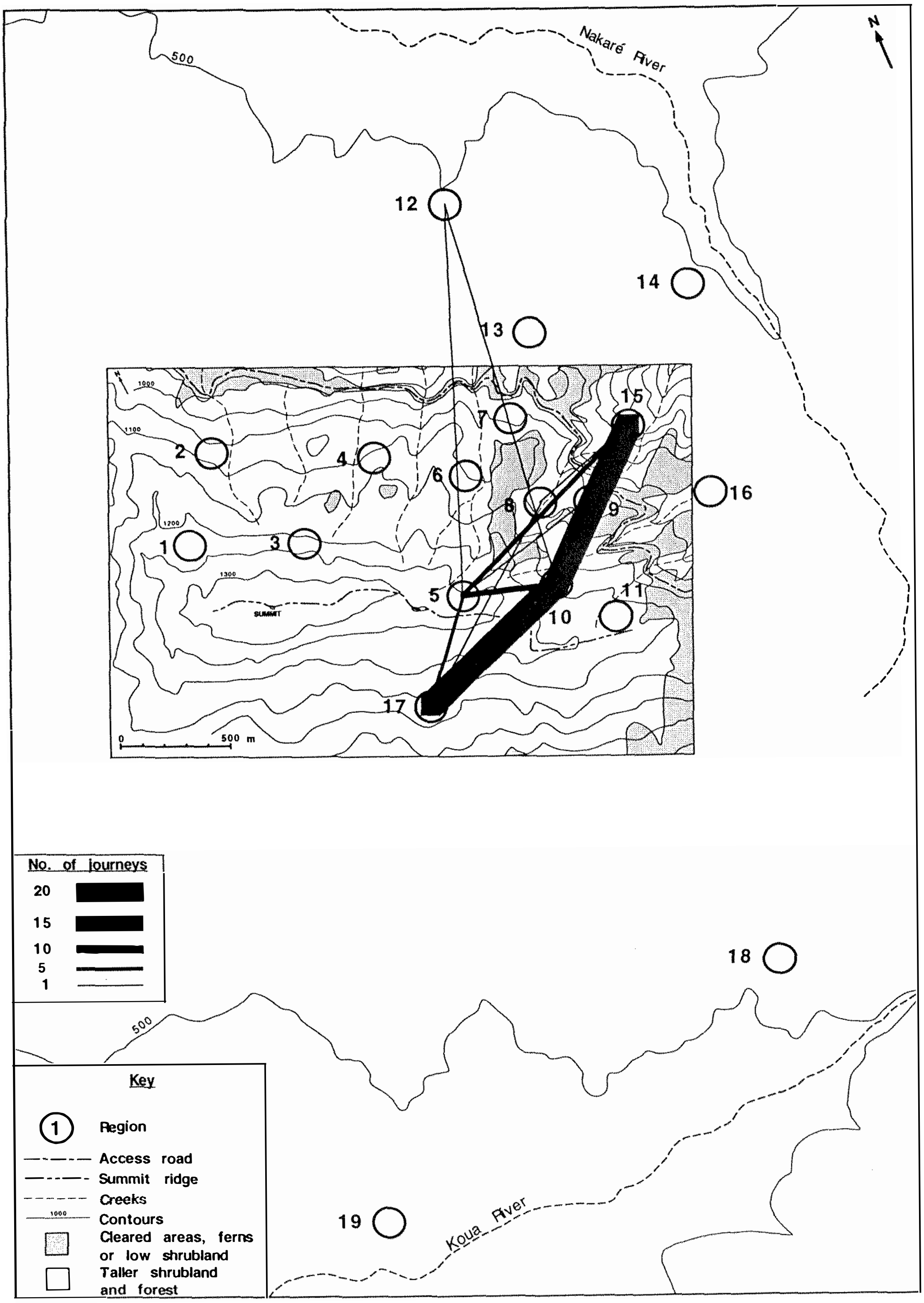

Figure 3-25. Graphic representation of the path diagram (in Appendix VIII) detailing the movements of female 119 at Pic Ningua. The line shown between regions 10 and 15 hides the lines connecting region 9 with regions 15 and 10. Roost positions for 119 are in Figure 3-19. The other details in the legend to Figure 5-21 also apply to the movements here for female 119.

in region 9 and crossed to region 15 in the early morning. From their movements, they also crossed at times in full daylight. During much of the time female 119 was outside region 15 she was not in contact with partner 120, for example this was the case for around three weeks in September/October 1994.

Male 120 moved in regions 9 and 15 for approximately four months after I captured him with partner 119 on 14/6/93 (Appendix VIII). His apparent reluctance to enter region 10 as bird 119 did suggested that his home range did not usually extend outside region 15. Also, pair 113 and 114, and possible pair 117 and 118, occupied region 10 sequentially up until early August 1993 (Figs. 3-13g and 3-18b). From the time I first recorded 120 in region 10 (on 31/10/93) he regularly travelled between there and region 15 until late September 1994 (Figs. 3-22 and 3-26), crossing the road 30 times.

Male 120's behaviour was interesting with respect to partner 119 and female 111. It seemed unusual that 119 spent so much time away from 120, even though partners at Parc Rivière Bleue tended to forage apart outside the main breeding season there (July-August) (Létocart 1991). It was possible that 119's behaviour was related to my disturbing her. Although they did not breed in 1993, pair 119 and 120 moved between regions 15 and 10 more or less at the same time between December and March 1994 indicating that they were probably often in close contact. During the brief period of milder weather in August 1994, 119 and 120 were also in close contact for about one week. Afterwards, 119 continued foraging mostly away from 120 until late October when 120 unexpectedly moved into region 17 with 119. The pair then stayed together in regions 10 and 17 until they nested in region 17 in early December 1994. Just before 120 moved to region 17 with 119, he may have been in close contact with female 111. He moved between regions 8, 9 and 10 for most of October and used two of 111's roosts, on 10/10/94 and 24/10/94 (Fig. 3-19). Female 111 was also present in regions 8 and 10 from 1-6 October when 120 was there, but my weighing her at that time may have prevented any possible longer term association. I weighed 111 on 6/10/94 and she left that morning for region 17, not returning until 19/10/94. I found her roost on 20/10/94, but did not approach closely and waited nearby until she left at first light. This had apparently disturbed her because at daylight she immediately returned to region 17. On 27/10/94, male 120 left region 8 and was with partner 119 in region 17 on 31/10/94. Also, in early

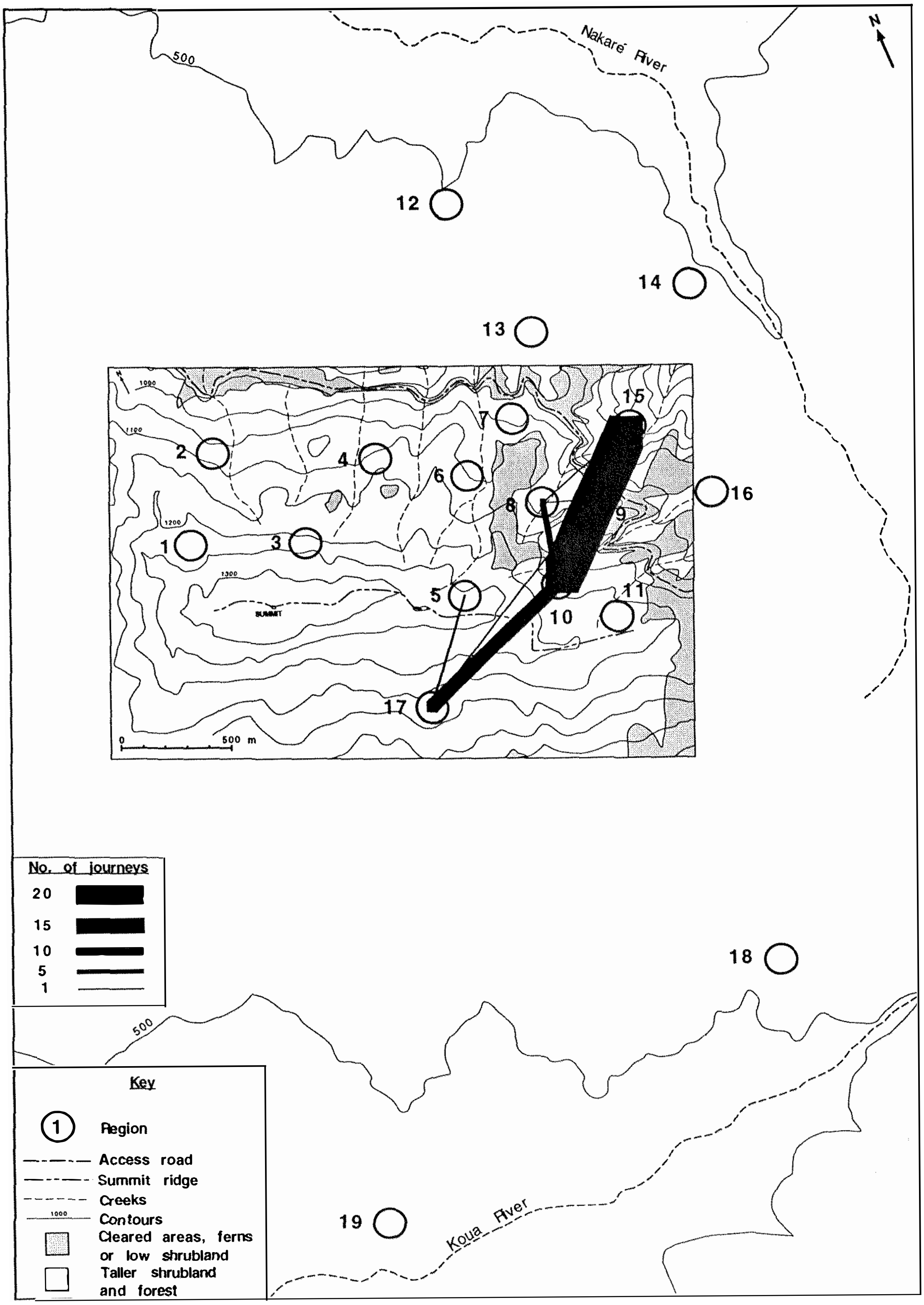

Figure 3-26. Graphic representation of the path diagram (in Appendix VIII) detailing the movements of male 120 at Pic Ningua. The line shown between regions 10 and 15 hides the lines connecting region 9 with regions 15 and 10. Roost positions for 120 are in Figure 3-19. The other details in the legend to Figure 5-21 also apply to the movements here for male 120.

November 1993 male 120 most probably interacted with female 111 as he also spent several days in region 8 and roosted about 12 m from 111 in region 9 on 9/11/93. This was the first time I had recorded female 111 in region 9.

Bird 125

I did not know if bird 125 was a new immigrant to the peak area. After I captured it on 14/4/94 perching with female 106 (Fig. 3-11), it descended below the road to the Nakaré River on seven occasions (Appendix VIII). It spent the longest period there (at least 20 days) from December 1994 to January 1995. Like females 106 and 109, 125 travelled more or less continuously on and around the peak, spending some time in region 3 which was rarely visited by the other birds (Figs. 3-22 and 3-27).

I only recorded one interaction between 125 and another bird, when I captured it perching with 106. I never heard 125 sing in spite being nearby on many mornings when it left its roost. I also attempted unsuccessfully to initiate its singing by playing duet song near its roost one morning.

3.3.10 Kagu movements, home ranges and interactions at Mt Cindoa

Birds 201, 202 and 206

Birds 201 and 202 shared a home range for just over four months from the time they were fitted with transmitters until 8/2/94 (Fig. 3-28). They defended it against the model kagu (Appendix IV), and duetted and roosted together, behaviour that suggested they were a pair and held a territory. On 22/2/94 I recorded 201 in region 2 (Appendix VIII, Fig. 3-2), and I only recorded it in region 1 again on two further occasions (22/3/94 and 26/7/94). It spent most time in region 2 but also visited region 3 twice. On the second occasion I recorded it there for three consecutive fortnightly telemetry fixes. Bird 202 stayed in region 1 throughout the study period. On 9/1/94 I found 202 roosting in a sheltered ground-roost with a new bird. The roost position (Fig. 3-28) was just to the southwest and outside of where I had recorded 202 up until then. I saw a new bird in region 1 on two further occasions (29/12/94 and 24/1/95) and it may have been the same bird 202 roosted with. I captured the bird I saw on 24/1/95 (bird 206) and it was a subadult or an adult. The size of the home range shared by 201 and 202 from October 1993 to 8/2/94 (before I first recorded 201 outside the area) was 9.6 ha.

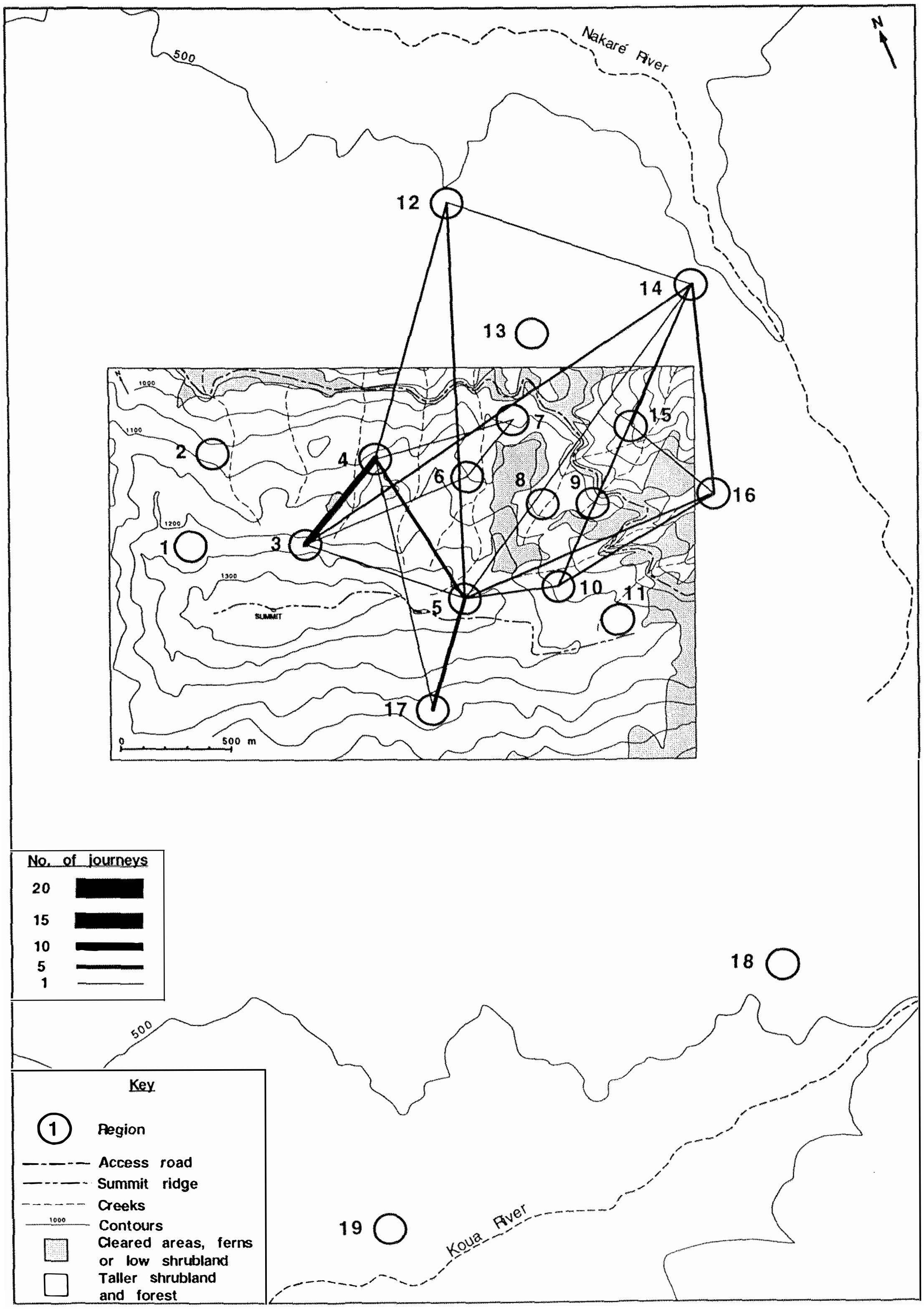

Figure 3-27. Graphic representation of the path diagram (in Appendix VIII) detailing the movements of bird 125 at Pic Ningua. Roost positions for 125 and an indication of its actual home range are in Figure 3-17. The other details in the legend to Figure 3-21 also apply to the movements here for bird 125.

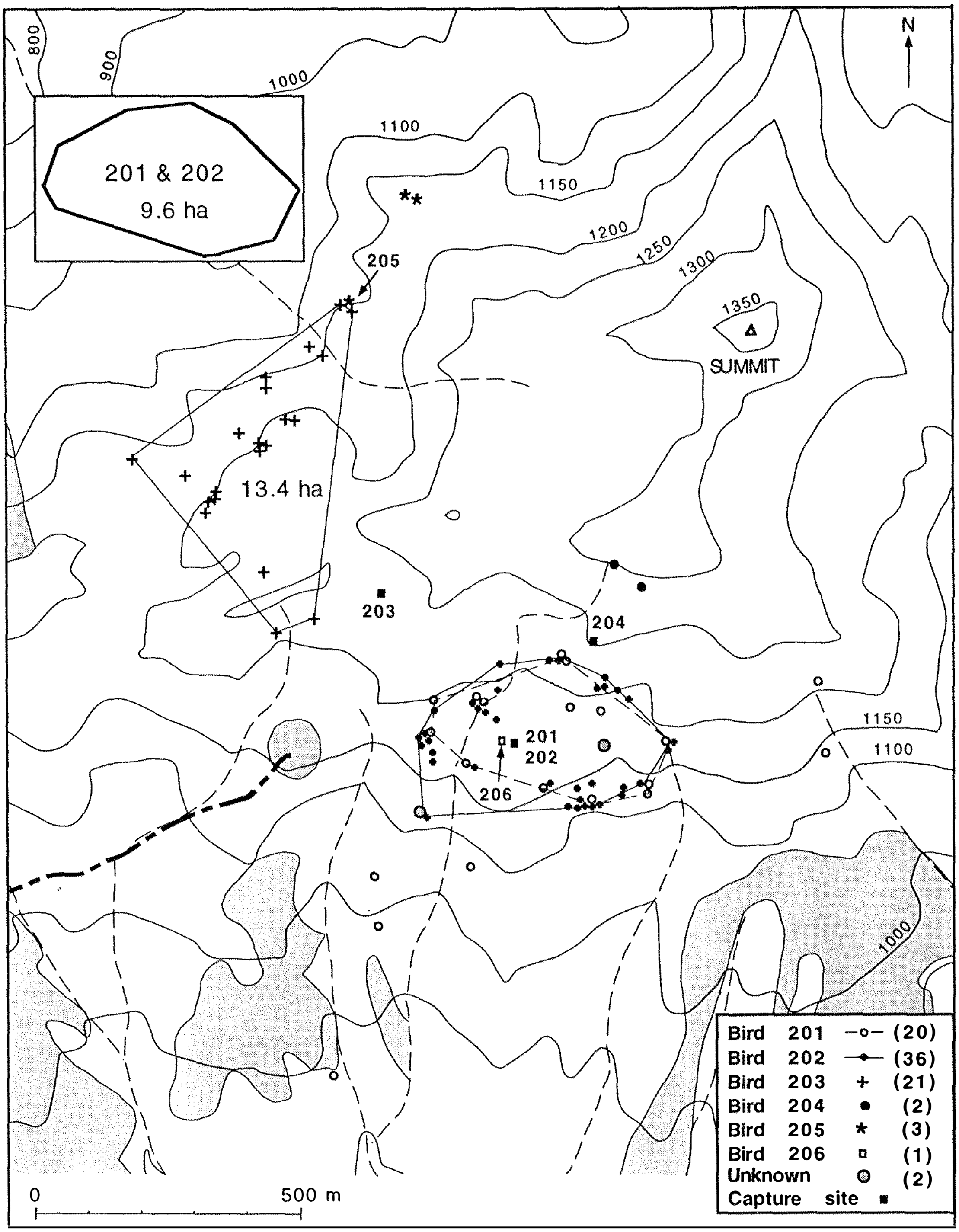

Figure 3-28. Roost and capture positions for kagus at Mt Cindoa from October 1993 to February 1995. Birds 201 and 202 were captured at the same position at the same time, and birds 205 and 206 were captured at their roosts (arrowed). I drew home range boundaries of individual birds (201, 202 and 203) by fitting minimum convex polygons around roost positions. The home range boundary for bird 201 is drawn around roosts it used in region 1 (Fig. 3-2) before it moved into regions 2 and 3 from February 1994 (see its movement records in Appendix VIII). The area (ha) of 203's home range is given within its boundaries, and the shape and area (ha) of 201 and 202's combined range before 201 left is in the inset in the upper left corner. No home ranges were drawn for birds 204, 205 and 206 because of lack of data. I only had one roost record for bird 206, but it may have been the unknown bird(s) I found roosting on two occasions in the same area at around the same time. Numbers of roosts for individual birds are in brackets in the Key.

Birds 203 and 205

I captured 203 on 6/10/94 outside the area I recorded it using during the study (Fig. 3-28). Its home range covered 13.4 ha. During the time I followed 203 I could not determine if it had a partner, although I heard birds duet on 203's home range. Bird 203 mainly roosted on the western and sunnier aspect of its home range where scrub vegetation was common, as were grasses in the undergrowth. On 12/7/94 I found 203 in a sheltered ground-roost with a new bird, 205 (Fig. 3-28), in the extreme north of 203's home range. I never recorded 205 within 203's home range, but located it roosting alone on two subsequent occasions further to the north of where I had captured it.

Bird 204

I captured 204 on 15/11/93 above the home range of 201 and 202 (Fig. 3-28), but removed its transmitter on 29/12/93 as I had sufficient birds to follow and it lived in an area more difficult to reach.

3.3.11 Variation in kagu bodyweights over time at Pic Ningua and Mt Cindoa

There was a definite seasonal trend in kagu bodyweights at Pic Ningua and Mt Cindoa (Fig. 3-29). Weights were highest at the end of the wet season around April and lowest around late October/early November in both 1993 and 1994 when conditions were driest. At Pic Ningua, this pattern was less distinct in 1994 when birds put on weight in August during a short period (interval 41) of milder wet weather (Figs. 3-3 and 3-8). Although sample sizes for individual birds were larger at the start of 1993 and I collected few weight data over the wet season then, birds almost certainly attained higher bodyweights in that period compared to the 1994 and (incomplete) 1995 wet seasons. Birds at Mt Cindoa (mean of the 8-weekly means = 850.93 g) were generally lighter than those at Pic Ningua (mean of the 8-weekly means = 920.05 g), and lost relatively more bodyweight by late October 1994 than did birds at Pic Ningua. This was in spite of two birds at Mt Cindoa (202 and 203) also increasing their bodyweights in August of that year (Fig. 3-30). Bird 205 at Mt Cindoa, who I weighed twice (12/7/94 and 29/11/94), was the lightest adult kagu (638 and 616 g, respectively). Although it appeared healthy, its breast and back bones were very prominent and it was obviously very thin.

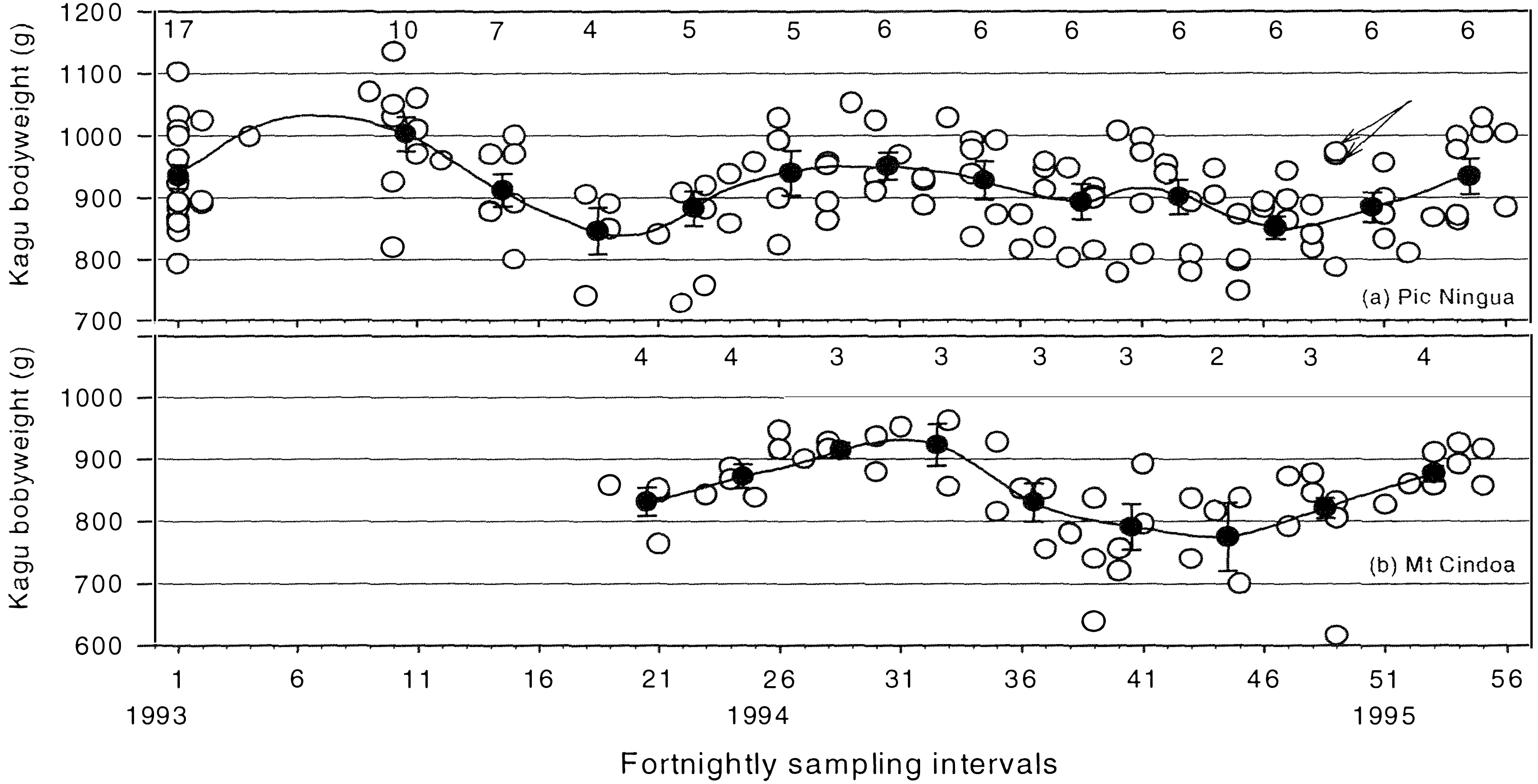

Figure 3-29. Kagu bodyweight data for Pic Ningua (a) and Mt Cindoa (b). I hand-drew the bodyweight curves through mostly 8-weekly means (method for drawing the curves is in section 3.2.9) (error bars ± 1 s.e.). Sample sizes (the number of individual birds) are along the top of each graph. I only used weight data for adult birds. The two weights for thin bird 205 (638 and 616 g) at Mt Cindoa were not used to calculate the means (section 3.2.9). Unfilled circles give all bodyweight records for individual birds (numbers of circles do not equal sample sizes). The arrows indicate the very similar weights (overlapping circles) of pair 119 and 120 just before they nested in early December 1994 (section 3.3.12).

Figure 3-30. Bodyweight records for individual kagus at Pic Ningua (birds 106, 109, 111, 119, 120 and 125) and Mt Cindoa (birds 201, 202 and 203). I excluded weight data for female 109 between intervals 16 and 21 because she was recovering from dog bite wounds then. Arrows on graphs for birds 119 and 120 indicate the weights of this pair just before they began incubating an egg in early December.

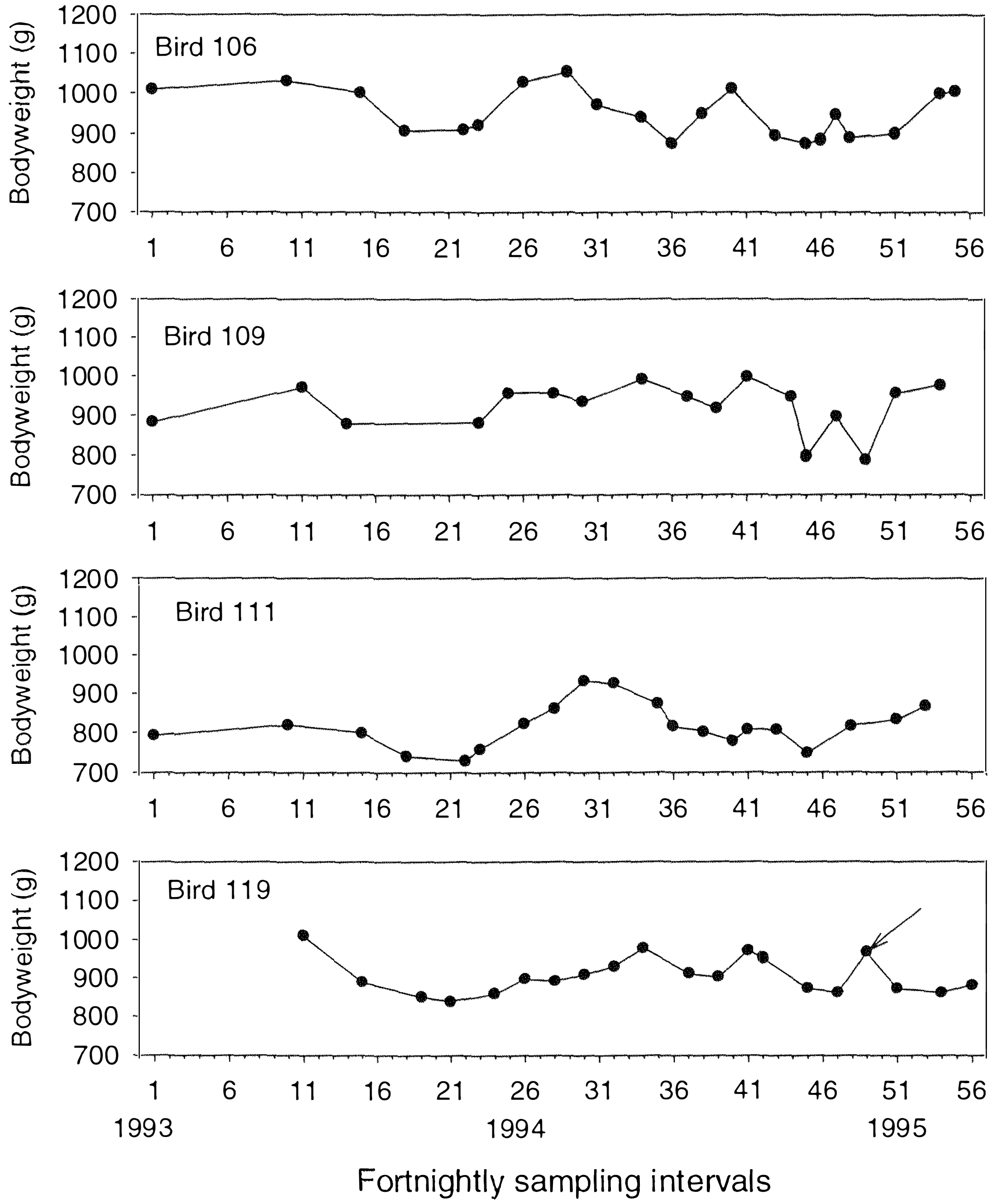

Figure 3-30 continued next page.

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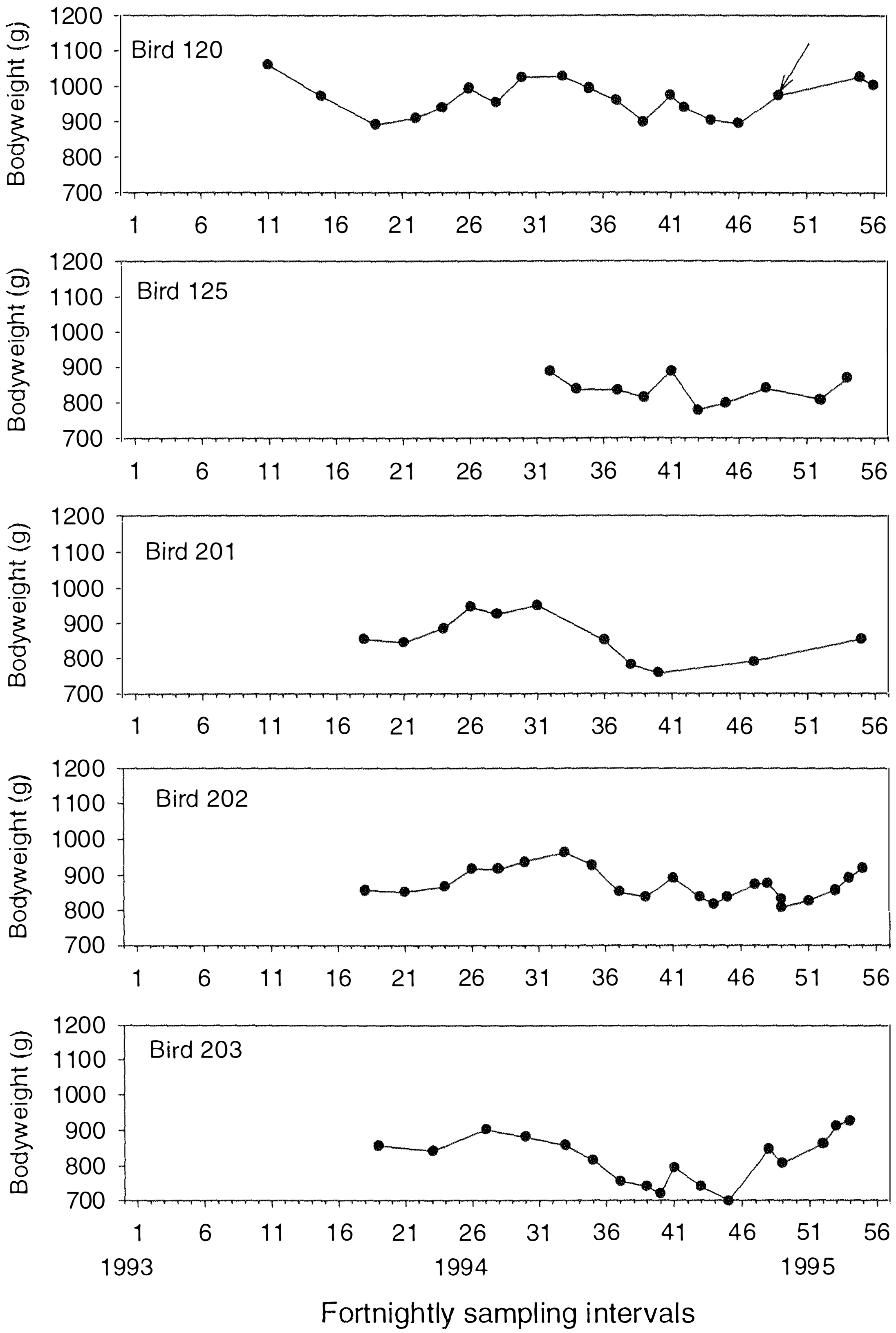


The seasonal trend for kagu bodyweights was less evident when I examined weight data for individual birds at Pic Ningua in 1994, but was clearly evident for individuals at Mt Cindoa in that year (Fig. 3-30). From late 1993, most birds at Pic Ningua had large home ranges and birds 106, 109 and 125 were more-or-less free ranging (section 3.3.9), and this may have led to greater bodyweight fluctuations for them. For example, the sharp declines in bodyweight for female 109 in intervals 45 and 49 were associated with her descents to the Nakaré River (Fig. 3-1). In repeated measures ANOVA analyses, 8-weekly means at Pic Ningua and Mt Cindoa were significantly different over time (Pic Ningua: Huynh-Feldt adjusted-$F_{[10, 30]} = 4.41$, $p < 0.001$, n = 5 individuals; Mt Cindoa: Huynh-Feldt adjusted-$F_{[7, 14]} = 5.36$, $p < 0.01$, n = 3 individuals). The 8-weekly means were not significantly different between Pic Ningua and Mt Cindoa over a similar time period (Repeated measures ANOVA: $F_{[1, 6]} = 3.39$, ns), nor was the pattern of variation in them over time between the two areas (Repeated measures ANOVA: 8-weekly means x Area interaction, Huynh-Feldt adjusted-$F_{[7, 42]} = 1.36$, ns).

3.3.12 Timing and frequency of kagu breeding attempts

I recorded the approximate egg-laying dates of two kagu pairs at Pic Ningua, but detected no breeding activity at Mt Cindoa. On 11/2/93 I found female 109 roosting on the ground with a young chick (bird 130). From its size and plumage, I estimated the chick's age to be four weeks. This would be consistent with my first record of it perching six weeks later on 25/3/93. Létocart (1991) stated that chicks first started perching on branches at 2-2.5 months of age. A chick four weeks old on 11/2/93 would have hatched on 14/1/93 from an egg laid approximately 34 days (Létocart 1991) earlier on 11/12/92. I knew of two other chicks (birds 122 and 123) on Pic Ningua raised in the 1992/93 breeding season, but as I first saw them in full juvenile plumage I was unable to estimate when they hatched. Juvenile plumage is complete at about four months of age (Létocart 1991), therefore bird 122 who I first captured on 7/4/93 hatched at least four months earlier in or before early December 1992.

The second egg-laying record was for pair 119 and 120. I saw the egg in the nest on 1/1/95 and the chick hatched on approximately 7/1/95, thus the egg was laid around 3/12/94. This was the first nest (Plate 3-4) described at high altitude, and was different from those found at Parc Rivière Bleue (Létocart 1991, section 1.4) because

Plate 3-4. Pair 119 and 120's nest on the south-facing slopes of Pic Ningua at approximately 1,125 m a.s.l. (see nest position on Fig. 3-19). Female 119 is incubating an egg. This is the first kagu nest described at high altitude and was completely protected from rainfall, unlike those described at Parc Rivière Bleue (Létocart 1991).

it was in a small natural shelter formed mostly by rocks and completely protected from the rain.

I also observed behaviour by three kagus in November 1992 at Pic Ningua which strongly suggested that there was a young chick or nest at the site. I came across the three birds by chance on the home range of pair 105 and 106 and close to the home range of pair 103 and 104. The birds never left the site for the over 60 minutes that I watched them from up in a tree. They gave frequent warning 'hisses' and reacted aggressively towards my day-pack which I had left on the ground.

Pair 119 and 120 both contributed to incubation, and care and defence of the chick, as has been described for captive (Brégulla 1987) and wild (Létocart 1991) birds. Létocart (1991) found that parents usually changed incubation shifts between 1000 and 1300 hrs. From monitoring the radio signals of 119 and 120, I recorded the times of two shift changes. On 3/1/95 female 119 took over incubation between 1100 and at 1200 hrs, and the next day (4/1/95) male 120 took over between 1130 and 1200 hrs. I observed each parent incubating the chick on the ground at night, and both parents used distraction displays to try and draw me away from it. I only observed the male feed the chick as he was less wary of my presence.

The chick remained motionless when I was present, but if I moved away it would sometimes run and hide nearby, for example under an exposed tree root. On one occasion the male fed it when I was only a few metres away, but only after making several close approaches to the chick beforehand. One morning at sunrise, the parents left the chick for approximately 20 minutes to sing some distance away (the singing was only just audible from where I was nearby the chick), and returned sometime after they ceased singing. Létocart (1991) reported that the incubating parent often left the nest (for up to 41 minutes) to sing with its partner.

3.3.13 Kagu roosting behaviour at Pic Ningua and Mt Cindoa

I drew home range boundaries of pairs and individuals (Figs. 3-12, 3-13 and 3-18) mainly using roost rather than daytime locations. Kagus tended to roost along and close to these boundaries rather than in the middle of their ranges, although this is probably in part an artefact of small sample sizes. An example of roosts confined to boundary areas was seen for pairs 115 and 116 (Fig. 3-13h) and 117 and 118 (Fig. 3-18b). Some birds also appeared to choose roosting areas because of their strategic positions, and this could be related to the acoustic attributes of an area for broadcasting song and listening to neighbouring kagus sing. For example, acoustic attributes were better where pair 101 and 102 roosted often at the top of a small 'hill' (bird 101 roosted 5 times on the same perch there) (Fig. 3-13a), and where female 111 generally roosted in the upper and lower areas of her home range (Figs. 3-13f and 3-16).

Kagus roosted in sheltered positions that ranged from those with little or no overhead cover other than the forest canopy to almost completely enclosed small natural caves. Unsheltered positions had little of no overhead cover other than the forest canopy (some were completely exposed to the sky in sites outside forest). I identified five types of sheltered and unsheltered positions (Table 3-5). Sheltered positions were (1) Dirt: against or in a cavity in a dirt bank [these were natural excavations (e.g., Plate 3-5) or those associated with sides of old roads]; (2) Leaf: on the ground under a palm leaf ; (3) Rock: up against large rocks or rock faces, or in natural enclosures or caves formed by rocks; (4) Root: under root structures formed by fallen trees, or under structures formed by living, exposed roots usually in association with sloping terrain; and (5) Tree trunk: up against or under a fallen tree trunk. Unsheltered positions were (1) perches on dead branches or tree trunks; (2) perches on living branches or trunks (e.g., Plate 3-6); (3) perches on raised roots; (4) perches on vine stems; and (5) roosts on the ground or rock in the open not up against any structure.

Live branches or tree trunks were used far more frequently than dead material for perches at Pic Ningua, but the situation was reversed at Mt Cindoa (Table 3-5). The use of dirt shelters was peculiar to Pic Ningua birds, but many of these sites were associated with old exploration roads in the forest or at the forest edge that were not present at Mt Cindoa. Roost positions on perches did not appear to be selected for any thermal benefits as they were usually in open locations over one metre above the ground with little vegetation (e.g., leafy branches) or other structures close to the roosting bird.

There were no significant differences in the diameter and height of perches used by kagus between Pic Ningua (mean diameter = 33.24 cm, s.d. = 18.26; mean height = 147.13 cm, s.d. = 57.44; n = 100) and Mt Cindoa (mean diameter = 30.35 cm, s.d.

= 11.07; mean height = 131.82 cm, s.d. = 33.82; n = 17) (only data from perches on branches or trunks were used to calculate the means).

Table 3-5. Numbers and percentages of roost types for sheltered and unsheltered roost positions used by kagus at Pic Ningua and Mt Cindoa. I only used one roost record per individual in an interval (sample sizes in Fig. 3-31), and excluded data when parents incubated chicks on the ground. Percentages may not add up to 100 because of rounding.

Study site	Roost position	Roost type	N	%Roost type	%Total roosts
Pic Ningua					
	Unsheltered	Dead branch/trunk	41	24.12	12.20
		Live branch/trunk	109	64.12	32.44
		Raised root	2	1.18	0.60
		Vine	2	1.18	0.60
		On ground/rock	16	9.41	4.76
			170	100.00	50.60
	Sheltered	Dirt	9	5.42	2.68
		Palm leaf	1	0.60	0.30
		Rock	121	72.89	36.01
		Root	33	19.88	9.82
		Tree trunk	2	1.20	0.60
			166	100.00	49.41
			336		100.00
Mt Cindoa					
	Unsheltered	Dead branch/trunk	20	66.67	25.32
		Live branch/trunk	9	30.00	11.39
		On ground/rock	1	3.33	1.27
			30	100.00	37.98
	Sheltered	Rock	45	91.84	56.96
		Root	3	6.12	3.80
		Tree trunk	1	2.04	1.27
			49	100.00	62.03
			79		100.00

Kagus at Pic Ningua and Mt Cindoa used sheltered roosts at considerably higher frequencies in the dry season than the wet season (Fig. 3-31a,b). At Pic Ningua, I recorded almost equal numbers of sheltered and unsheltered roost positions by kagus

Plate 3-5. Female 119 roosting in a 'dirt' shelter on the side of a creek bank at 810 m a.s.l. on 11/10/94. The shelter is below the access road on the north-facing slopes of Pic Ningua (roughly mid-way down the valley at centre-left in Plate 3-1). The thin, black radio-transmitter aerial extends outwards from 119's upper back region.

Plate 3-6. Bird 101 perching in an unsheltered position at approximately 1,170 m a.s.l. on the north-facing slopes of Pic Ningua on 19/4/93.

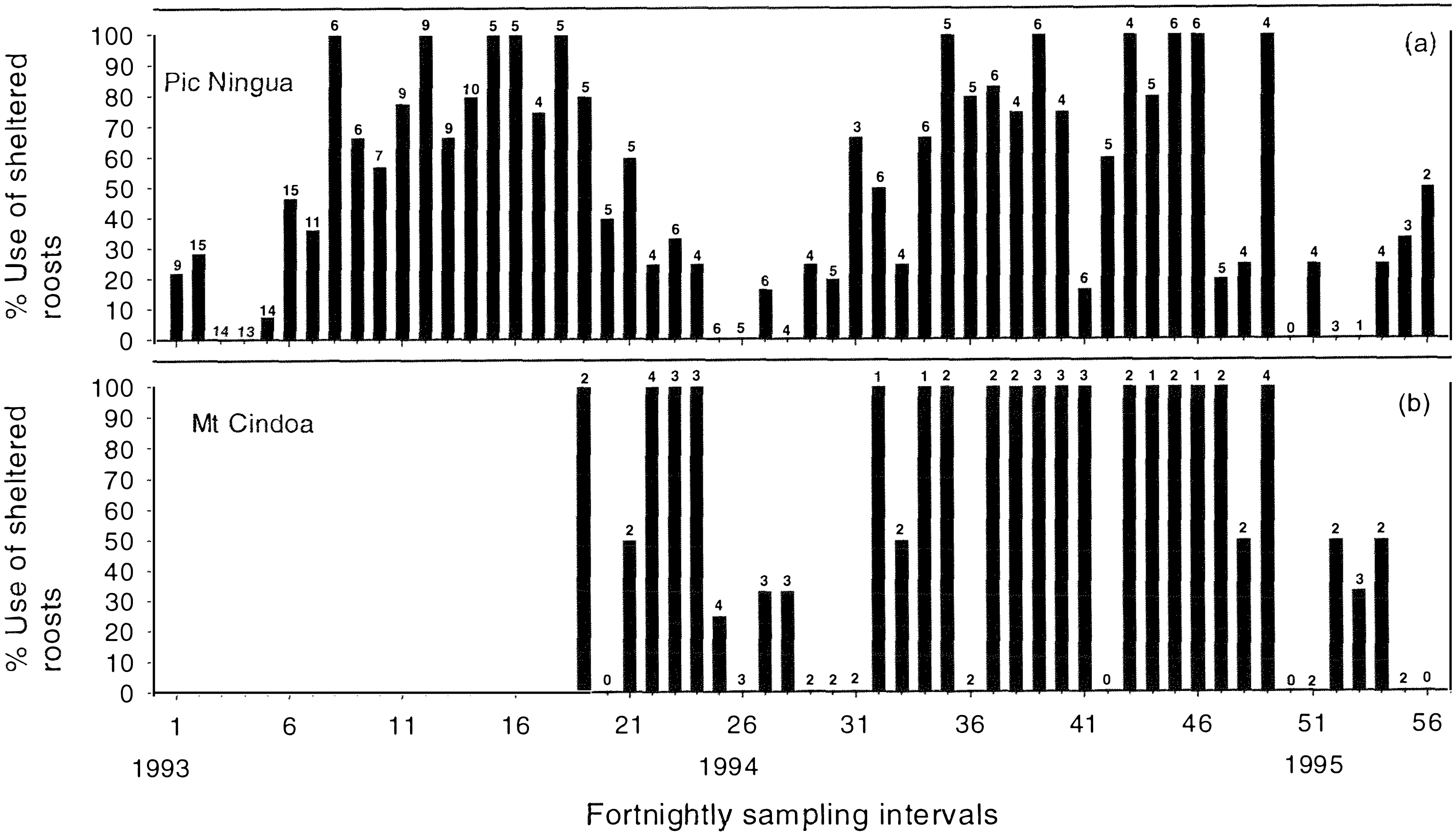


Figure 3-31. Percent use of sheltered roost sites by kagus at Pic Ningua (a) and Mt Cindoa (b). I collected data at Mt Cindoa only from interval 19. Sample sizes for the total number of roosts in intervals (one per individual kagu) are above bars (total numbers of roosts in each area are in Table 3-5). When n = 0 for sample sizes, I did not collect roost data in these intervals.

over the study period, but more sheltered roosts at Mt Cindoa (Table 3-5). When I compared the cumulative percentage-use of roost positions between years at Pic Ningua (year one = intervals 1-23 and 25-26: year two = intervals 27-49 and 51-52), kagus used sheltered roosts 55.15% of the time and unsheltered roost use 44.85%. At Mt Cindoa I recorded considerably more sheltered (n = 49) than unsheltered (n = 30) roosts over intervals 19-55 (Table 3-5). The cumulative percentage-use of the two types of roost position over one year (intervals 19-44, n = 24) was 66.32% for sheltered roosts and 33.68% for unsheltered ones. There was a significant difference between Pic Ningua and Mt Cindoa in the cumulative percentage-use of sheltered (49.31% and 66.32%, respectively) and unsheltered (50.69% and 33.68%, respectively) roost positions over the same time period (intervals 19-44, n = 24 as there were no data for two intervals at Mt Cindoa) (2 x 2 contingency table, $G = 5.96$, d.f. = 1, $p < 0.05$; NB: sample sizes for calculating the percentages were much smaller than desired, see p. 765 in Sokal and Rohlf 1981).

Variation in the mean altitude of roost sites at Pic Ningua for intervals 1-14 was low when sample sizes (numbers of birds) were relatively high and kagus only moved in small, fixed home ranges (Fig. 3-32). Variation increased considerably after interval 14 when sample sizes decreased and most of the birds I followed travelled widely on the peak.

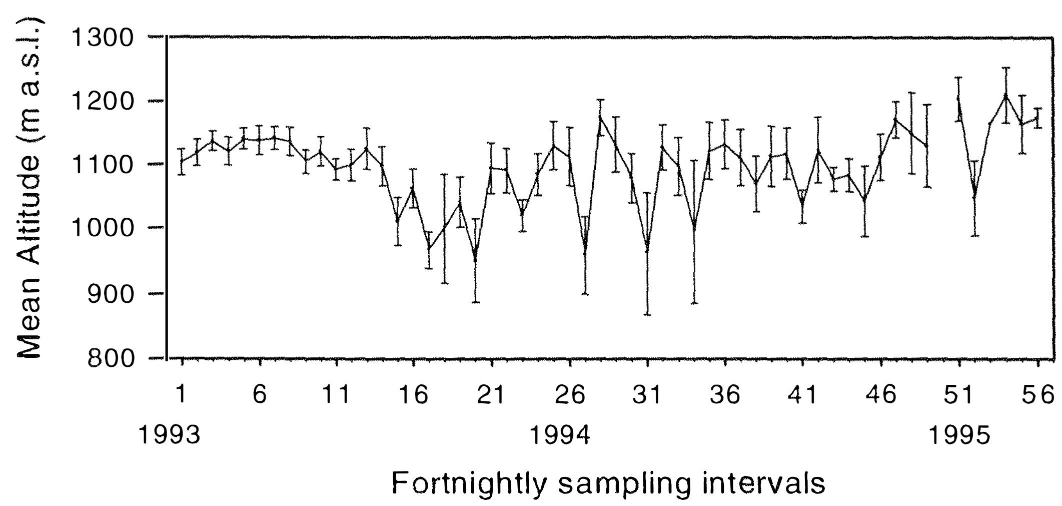


Figure 3-32. Mean altitude of kagu roost sites at Pic Ningua. Sample sizes for means are in Figure 3-31a (error bars = ± 1 s.e.). There were no data for interval 50, and no error bar for interval 53 as n = 1.

When I inspected all roost records (which sometimes included more than one record per individual in an interval) at Pic Ningua, seven individuals (birds 103, 104, 106, 109, 110, 111, and 129) roosted 11 times (sometimes only a few metres from family members) outside forest in relatively open areas. Two of the 11 roosts were in sheltered positions (e.g., Plate 3-7) and nine in unsheltered ones (e.g., Plate 3-8). I found the roosts between August and March in 1993 and 1994, and they were on the ground ($n = 7$) or on rocks ($n = 4$). Ten of the roosts were in shrubland and one in a cleared area amongst bracken-type ferns. Ten of 11 roosts were just outside forest (within < 50 m), and one on a rock under a shrub (for female 106 between the access road and region 12) well over 100 m from forest.

Re-use of a sheltered roost position was generally easier to detect than for an unsheltered one for two reasons: (1) substrate at the former was often protected from rain and free from leaf litter, and excrement had often accumulated on the ground. The build up and condition of excrement at some sheltered roosts indicated their use over many years; (2) I noticed that the consistency of kagu faeces was often associated with changing weather patterns: more liquid during periods of wet and warm weather when food supplies were high (possibly related to increased activity of internal parasites; Beugnet *et al.* 1995) but more like droppings at other times, particularly in very dry conditions. As kagus used sheltered roosts mostly in the dry season (Fig. 5-31), faeces deposited at these sites were more likely to be of the latter type. The reverse situation tended to apply for faeces deposited underneath perches. Therefore, the number of roost re-use records is only a minimum estimate, especially for unsheltered positions.

Birds at both study areas often selected roosts that had been used previously (Table 3-6), during or before my study began. Kagu re-use of sheltered and unsheltered roosts did not differ from expected values at both Pic Ningua ($\chi^2 = 0.02$, d.f. = 1, $n = 163$, ns) and Mt Cindoa ($\chi^2 = 1.27$, d.f. = 1, $n = 52$, ns), but overall re-use was greater at the latter (65.82%) compared to the former area (48.51%) (2 x 2 contingency table, $G = 8.92$, d.f. = 1, $p < 0.05$). The lower value at Pic Ningua was probably strongly influenced by the departure of females 106, 109 and 111 from their original home ranges after they lost their partners. To check this, I compared the frequency of the re-use of sheltered roosts for females 106, 109 and 111 inside and outside the home ranges they used before they lost their partners. Because I was more

Plate 3-7. A sheltered roost position used by female 109 in maquis less than 50 m from forest. The roost site is at centre-bottom of the photograph, in the open dirt-formed recess at the side of a small creek.

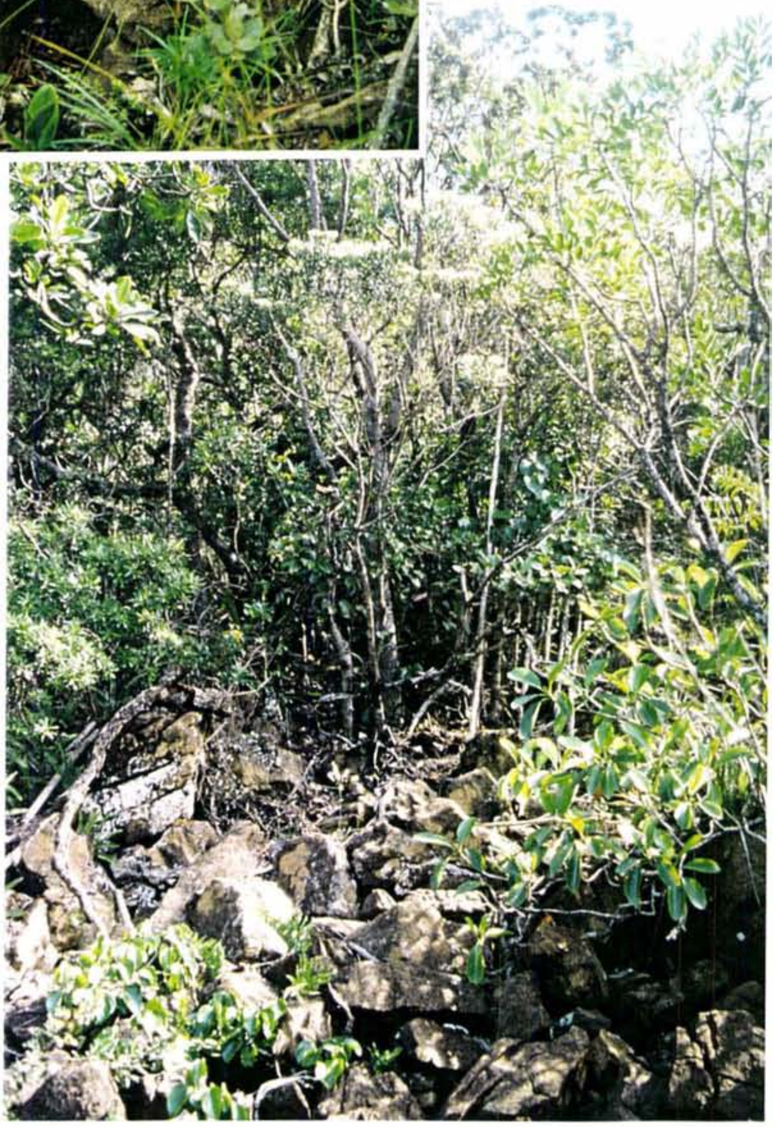


Plate 3-8. An unsheltered roosting position on rocks at 980 m a.s.l. used by kagu pair 103 and 104 with bird 129 on 12/2/93. The site was at the forest edge and had little canopy cover.

likely to detect re-use of sheltered roosts, I did not compare the re-use of unsheltered roosts. The three females (data were combined) roosted at sheltered positions used previously significantly less when they were outside the home ranges they had before they became widowed (Table 3-7) (2 x 2 contingency table, $G = 13.87$, d.f. = 1, n = 94, $p < 0.001$).

Table 3-6. Comparison of the re-use of sheltered and unsheltered roost positions by kagus at Pic Ningua and Mt Cindoa from 23/1/93 to 9/4/95. I only used one roost record per individual bird in an interval, and excluded data when adults incubated chicks on the ground.

Study area	**Roost type**	**Total roosts**	**Total roosts re-used**	
			No.	**%**
Pic Ningua				
	Sheltered	166	80	49.08
	Unsheltered	170	83	50.92
		336	163	100.00
Mt Cindoa				
	Sheltered	49	36	69.23
	Unsheltered	30	16	30.77
		79	52	100.00

Table 3-7. Comparison of re-use of sheltered roosts by females 106, 109 and 111 inside and outside the home ranges they used before they lost their partners (on 26/4/93 for female 111). Sample sizes for individual birds are in brackets.

Sheltered ground-roosts	**N**	**%**
Inside old home range		
Used previously (106=8, 109=7,111=17)	32	58.18
No evidence of previous use (106=5,109=8,111=10)	23	41.82
	55	100.00
Outside old home range		
Used previously (106=5,109=1,111=2)	8	20.51
No evidence of previous use (106=18,109=6,111=7)	31	79.49
	39	100.00

At Pic Ningua, I recorded 41 cases of an adult bird re-using a roost that I had recorded previously. Thirty-four of these were by the original user (3 with partners) and seven by different birds (3 were partners, and 4, as far as I knew, were non-family members). The 41 cases included 27 different roosts: 18 were re-used once, 5 twice, 3 three times and 1 four times. I also recorded 12 occasions when two adult kagus roosted together: one on the ground on an unsheltered rocky slope, one on the ground in a root shelter and 10 on perches. At Mt Cindoa, I recorded five (2 by the original user, and 3 by partners) cases of a bird re-using a roost that I had recorded previously. All the five roosts were different. I recorded two cases of two adult birds roosting together at Mt Cindoa (both times on the ground in rock shelters).

I only collected sufficient roost records (when all roost records were included) to allow a more detailed breakdown of roosting behaviour within a long-term home range for two birds (female 111: the area in Fig. 3-13f; and male 120: below the road in region 15) (Table 3-8). Even though female 111 travelled outside her old home range she returned to it regularly (Fig. 3-24). I recorded 66 of her roosts within her old home range from 2/2/93 to 31/1/95, and many of these were located in the early part of 1993 when I was trying to find her probable mate. Six of the seven first-recorded roosts that she subsequently re-used had been used previously, the exception was subsequently used eight times and was the highest re-use of a roost that I recorded. As this was a perch (a tree fern trunk) its first record may have also been a re-use but I did not detect it. Female 111's position on this perch was one of the highest above the ground (over 3 m) that I recorded. She could walk up the growing fern trunk from ground level. Other roosts female 111 re-used more than once during the study were mostly sheltered ones (a maximum of 5 re-uses). Although I had fewer roost records (n = 32) for male 120, he also tended to re-use sheltered roosts more than unsheltered ones.

I collected ten records of birds using the same sheltered (n = 8; 3 birds and 8 roosts) or unsheltered roost (n = 2; 1 bird and 2 perches) on a seasonal basis at Pic Ningua. At Mt Cindoa, I recorded two cases of inter-seasonal re-use of the same roost (n = 1 for both a sheltered and an unsheltered site, by different birds). Lack of mated pairs probably reduced records of the seasonal use of the two types of roost positions.

Table 3-8. Analysis of roost re-use at sheltered and unsheltered positions for female 111 (from 2/2/93 to 31/1/95 on the home range used up to 25/4/93) and male 120 (from 17/6/93 to 21/3/95 below the access road in region 15). The data for birds 111 (n = 66) and 120 (n = 32) included all their roost re-use records located in the above areas, therefore on occasions there may have been more than one record per bird in an interval. Data for male 120 are in brackets.

No. of times roost used after first found	**Sheltered roost**		**Unsheltered roost**	
	first record a re-use?			
	Yes	**No**	**Yes**	**No**
0	8 (6)	13 (5)	1 (4)	7 (7)
1	2 (2)	- (-)	1 (1)	- (-)
2	1 (-)	- (-)	- (-)	- (-)
3	1 (1)	- (-)	1 (-)	- (-)
4	1 (-)	- (-)	- (-)	- (-)
5	1 (-)	- (-)	- (-)	- (-)
8	- (-)	- (-)	- (-)	1 (-)
No. of roost records	30 (14)	13 (5)	7 (6)	16 (7)
No. of different roosts for each roost position	27 (19)		11 (13)	

3.4 Discussion

3.4.1 Meteorological conditions

Although large scale weather changes in the Pacific have considerable influence on weather patterns in New Caledonia, the strong seasonality in rainfall and air temperature that I recorded at my study areas probably occurred year-to-year and was highly predictable.

3.4.2 Social organisation

At Parc Rivière Bleue, Létocart (1991) found that pairs formed long-term relationships on relatively fixed territories, birds lived in families, and older offspring helped in territorial or chick defence. This type of social organisation might also suggest a monogamous mating system. Although my data were limited because of the loss of birds from dog attacks, they indicated that kagu social organisation at Pic Ningua might be the same as that at Parc Rivière Bleue.

For the first three months of my study, seven kagu pairs and bird 111 lived in mostly separate and closely 'packed' areas on the north-facing slopes of Pic Ningua. This was strong circumstantial evidence that the pairs held relatively fixed territories. Only pair 109 and 110 had dependent offspring therefore it was unlikely that the other pairs and female 111 lived apart because of breeding activity. Two other reasons suggested that pairs held territories. First, I caught at least one partner of most pairs when they reacted defensively to playbacks of duet song and the kagu model. Second, kagus tended to change roosts often and roost more around the boundaries of their ranges, possibly at 'strategic' sites. This was evidenced by the importance of roost rather that daytime positions in determining boundaries, however the latter positions almost certainly underestimated the foraging range of birds because they were conservative estimates of actual ones and sample sizes were very small. Predation avoidance has been suggested as one reason for frequent changes in roost use by birds (Chandler *et al.* 1995), but this would not appear to explain the more frequent roosting around home range boundaries.

I also collected evidence suggesting that at something like natural densities, pairs held relatively fixed territories year round. First, pair 109 and 110 lived together in the same area for over six months before 110 was killed. Second, although female 111 travelled from it, she returned regularly to her old home range in region 8 for nearly two years up until she may have re-paired in early 1995. Her high frequency of roost re-use also indicated that she had a good knowledge of region 8 and had lived there for some time. Third, male 120 also returned regularly to his old home range in region 15 below the access road until he nested with partner 119 on the south-facing slopes. Fourth, birds 202 and 203 at Mt Cindoa, as far as I knew, lived in their relatively well defined areas throughout the 74 weeks of my study there. Fifth, widowed birds (106, 109, 111) changed from living on small combined home ranges with their partners when kagu densities were high to using large, probably non-defended ones after they lost their partners and kagu densities were low. Also, pair 119 and 120 had an extensive and loosely defined combined home range that would have been too large to defend, and this may have been a consequence of the removal of neighbouring pairs. This suggested that a consequence of high bird densities was that kagu pairs spaced themselves on relatively fixed territories, and that as long as numbers remained high this type of social organisation prevailed. Sixth, I captured kagus using playbacks and the model not only during the first months (January-March) of my study, but in June, October and November. This indicated that birds defended territories (by song and physical confrontation) against intruding kagus throughout the year. Létocart (1991) noted that the reaction of birds to playback of kagu song (of an individual male) was mostly non-existent or weak outside the breeding season, however, birds still duetted at the Parc throughout the year (Létocart 1989). Also, my methods differed from Létocart's in two ways: I always played back duet song and I used a model kagu, and this may have increased the level of reaction of birds outside the breeding season. If pairs defended a resource(s) other than their mates then a lone male might be less of a threat to a pair's territory than another pair. Last, that kagus duetted at Pic Ningua was support for long-term pairbonds and year-round territoriality because these are common features of social organisations of duetting species (Farabaugh 1982).

The average size of a pair's home range at Pic Ningua (11.2 ha) was considerably smaller than that for four pairs at Parc Rivière Bleue (*c.* 20 ha, Létocart 1991). Although my sample sizes to establish home range boundaries were very small and my data were collected over only a short period of the year, home ranges close to the road were quite closely 'packed' and therefore Figure 3-12 may accurately indicate their actual sizes.

At least some of the pairs at Pic Ningua may have lived with independent offspring from the 1992 (e.g., juveniles 122 and 123) and earlier breeding seasons (e.g., birds 129 and 136). My observations of more than two adult/subadult birds roosting together and involved in territory defence at the same time were consistent with Létocart's findings that birds lived in families. That kagus lived in families at Parc Rivière Bleue implied that the parental investment that partners contributed for breeding activity extended well after offspring became independent. Increased frequency of extended parental care in tropical bird species might be due to the need to raise offspring that can better compete for resources that are more limited compared to those in more temperate climates (Emlen 1978). This does not seem a good explanation for extended parental care by kagus because, for example, they do not appear to compete intensively for space or mates, but rather establish territories in vacant areas. Also, extended parental care might be a consequence of other factors like slow development and the need for juveniles to acquire necessary skills for successful independent breeding (Lack 1968). Where all potential habitat is likely to be nearly always occupied, parents' fitness might be increased by allowing independent offspring to use the natal area as a base from which to look for and find a territory or partner, and not force them to disperse when they became independent. Any benefit (e.g., help in territorial defence) that these offspring may bring though, might be a consequence of parental tolerance and not the reason for it (Jamieson 1989). The kagu's social system may have evolved partly in response to saturation of habitat given their relatively predator-free status prior to human arrival.

Létocart (1991) described a case of pair dissolution at Parc Rivière Bleue that had similarities to the situation surrounding birds 201 and 202 at Mt Cindoa. A male (M1) at the Parc began to make excursions from his territory at about the time a new male (M2) was seen there with M1's partner (F1). When M1 returned, M2 retreated to the edge of M1 and F1's home range. M1 stayed away and nested with a new bird (F2). During F2's shift at incubation, M1 visited his old home range where F1 still resided. M2 left F1's home range permanently before M1 returned there with F2 (after their chick disappeared). This resulted in F1 also leaving permanently. The situation with birds 201 and 202 at Mt Cindoa remained obscure. It appeared from 201's movements from February 1994 that its partnership with 202 had ended, although it did roost on its old home range again. The appearance of a new bird (sex unknown) with 202 increased doubt as to whether it was still paired with 201.

Although little is known about pair dissolution in the kagu, it appears to occur in a way far less subtle than that based on direct confrontation where a new bird physically displaces a resident bird of the same sex. The latter occurs in species like the sedentary and territorial blue duck *Hymenolaimus malacorhynchos* (Williams 1991). Williams reported that unpaired birds were excluded from the territories of paired birds and defence against an intruder was only undertaken by the resident of the same sex as the intruder. Residents were regularly challenged resulting in changes to pair composition being common. Thus it appeared that blue ducks defended their territory and paired status against intruders of the same sex for the chance to reproduce as ejected birds often disappeared from the population (Williams 1991). It is unknown if sex-specific defence occurs in the kagu in response to a single intruder, but both partners, singly and together, defended their territory against an 'intruding' (playback of duet song) pair. This was consistent with a strong pairbond between partners and that birds showed little sexual dimorphism. Also, partners often foraged far apart which indicated that intruding males, for example, might not be a threat to unguarded females, at least outside the breeding season. This was also consistent with data from Parc Rivière Bleue which showed that unpaired juveniles travelled widely, crossing territories of other pairs (Létocart 1991). North Island brown kiwis *Apteryx australis mantelli* formed long-term pairs and exhibited similar behaviour to that of kagus (McLennan *et al.* 1987, Taborsky and Taborsky 1992). Unpaired brown kiwis also ranged widely including onto the territories of mated pairs, and confrontations between neighbours and pair dissolution were rare.

The fact that kagu partners shared territorial defence does not rule out mate guarding as a possible strategy influencing individual partners' behaviour. An indication that mate guarding might be involved comes from a pairs' duetting song. Duetting has long been thought to maintain pairbonds and/or act as joint territory defence (Levin 1996a,b), and it seemed likely that it functioned in the latter way at least in the kagu. More recently, it has been proposed that duetting might also function as acoustic mate guarding; the partner which initiates the song sings more for territorial defence but the response partner does so more to guard its mate (Levin 1996a,b). As male kagus generally initiate duets, females would be the sex who sing to mate guard. In this scenario, duets can still function as joint territorial defence behaviour.

The process of pair formation by kagus is more apparent. Widowed birds at Pic Ningua interacted with and appeared to search for other kagus. That three of these widowed birds (106, 109 and 111) roosted with new birds on or near their home ranges suggested that if new partners were available birds re-pair quite quickly and keep their territories. Birds 106 and 109 failed to re-pair, even though they travelled widely and visited areas near the Nakaré River where other kagus lived. Female 111 though, may have eventually paired with 137 on the other side of the peak. Birds 124 and 125 did not establish long-term relationships with the widowed birds they interacted with. The fate of bird 124 was unknown, but he may have been reluctant to cross the access road into female 111's old home range. That bird 125 (whose sex I did not know) did not pair with any of the widowed females also seemed strange, unless it was a female. It seemed possible that male 120 was also searching for a mate (while partner 119 was absent for several weeks) when he visited female 111's territory in October 1994 and used two of her roosts. This also suggested that 119's absence from 120 was unusual, and may have been caused by my disturbance. My results indicated that both female and male birds could move outside their territories in search of new partners. Female 115 and bird 202 may have also re-paired during my study, and I found them both roosting with new birds just outside their known home ranges.

Létocart (1991) suggested that home range boundaries of kagu pairs were formed by either: (1) forest limits; (2) the presence of neighbouring pairs; and (3) sufficient space to live and breed in the absence of (1) and (2). The first two factors appeared to be in operation at Pic Ningua as well. I had no evidence that birds regularly foraged in low shrubland (although they negotiated through and roosted in these areas) and the positions of home range boundaries suggested some may have been shaped by the access road. That boundaries were formed because of neighbouring pairs was strongly implied by pairs home ranges in Figure 3-12. Finally, I had not heard birds sing west of the home ranges held by 101 and 102, and 103 and 104, but suitable forest appeared to exist there. I knew little about kagu presence along the summit ridge south of the home ranges of pairs (101 and 102, 107 and 108, 115 and 116, and 113 and 114) which lived near there. These home ranges were not large suggesting they met the requirements of these pairs or that other pairs lived on their southern boundaries. Birds 126 and 127, for example, may have held territories south of pairs 115 and 116, and 113 and 114, respectively, as I only knew them in this area, although only for a short period in early 1993 (about 6 weeks).

A bird species' social organisation reflects the influence of ecological conditions on social competition, and within species variation in social structure in response to different conditions can occur (Davies and Hartley 1996). Features of kagu social organisation at something like natural densities were similar at Parc Rivière Bleue and Pic Ningua. These were (1) strong pairbonds between partners who held relatively fixed territories year round; (2) social competition which seemed to be based more around defence of a resource other than mates (e.g., space, food supply), for example male and female partners alone and together defended against playback of duet song outside the breeding season; and (3) apparently few aggressive disputes. Therefore these aspects of kagu social structure remained robust to different environmental conditions (e.g., air temperatures) between the two areas. This suggests that factors like for example the spatial and temporal nature of food supplies (*Chapter 5*) likely to influence social organisation were not different enough to bring about a detectable change in it between the two areas.

In a high density situation, the kagu's social organisation would seem advantageous if food was not generally abundant because birds foraged for most daylight hours when not involved in breeding activity. Long-term residency might also increase the food value of a territory if it results in more efficient foraging through better knowledge of resources (Partridge 1978). Reasons for holding a territory though may be complicated, and factors other than food and mate guarding like spacing behaviour to reduce infectious microparasites and predation risk might be involved (Stamps 1994).

3.4.3 Breeding

I was unable to determine the timing of the main breeding period at my study areas because of too few data from Pic Ningua and no data from Mt Cindoa. The two egg-laying records at Pic Ningua in early December might suggest pairs nested later in the year compared to those at Parc Rivière Bleue. Pair 119 and 120 made their first breeding attempt of the season in December, but pair 109 and 110's chick may have been the result of a re-nesting attempt. Pair 109 and 110 were the last pair I knew of to breed in 1992 so the others (e.g., parents of birds 122 and 123) that probably bred at Pic Ningua nested before December that year.

A later breeding date at high compared to low altitude appeared plausible in light of the environmental conditions there (discussed in section 7.2), but it does not explain why pairs 119 and 120, and 201 and 202 did not breed in 1993. One reason may have been the colder and drier conditions in November and the first half of December in 1993. Mean minimum air temperatures in forest did not climb above 12°C in 1993 until late December, whereas they reached that level in late November 1994, just before pair 119 and 120 nested in early December. Female 119 was also around 100 g lighter in early December 1993 compared to the same period in 1994, although she may have increased her foraging rate in preparation for incubation (section 3.4.5). Rainfall at Pic Ningua in November/December 1993 (intervals 21-24 = 59.5 mm) was considerably less than that in the same months in 1994 (intervals 47-50 = 174.5 mm). The lower bodyweights of birds at Mt Cindoa may have been associated with the lack of breeding activity I observed there.

Male 120 appeared to have had little influence in the choice of general area to nest in (nest position in Fig. 3-19) given that I had not observed him on the south-facing slopes until just before he nested there with female 119. Thus he probably followed 119 there after making contact with her again in late October 1994.

3.4.4 Sexual size dimorphism

Brégulla (1987) observed little difference in the usual body measurements (he did not carry out statistical analysis) between the male and female captive kagus, except that males tended to be larger. I found no significant size dimorphism between the sexes when I carried out analyses on my data, but this was based on only a small sub-set of the birds I captured. Further analysis on a larger data set may be possible if the feathers I collected from birds can be used to sex them. Also, different body measurements (e.g., combined head and bill length) than the ones I used may better indicate size differences, if they exist, between the sexes.

3.4.5 Variation in kagu bodyweights

Seasonal variation of mean kagu bodyweight at Pic Ningua and Mt Cindoa was clearly cyclical and at least 100 g in magnitude so it was most likely due to variation in the weight of body components like lipids rather than gut contents. I weighed most birds in the early morning after they had deposited a faecal sample (section 3.2.7) (frozen wet weights of faeces deposited in the early morning before sunrise can be over 30 g; section 5.2.3). Also, because the dog attacks caused the deaths of many kagus at Pic Ningua, I collected data on mostly non-breeding birds there at low densities. Thus effects of reproductive activity and intra-specific competition at least on bodyweight variation should have been minimal. I had little idea of bird densities at Mt Cindoa, but birds I followed there were also non-breeding.

Mean kagu bodyweight at Pic Ningua was highest at the beginning of my research when bird density on the peak was much greater than that for the remainder of the study. This was important because it implies that factors other than intra-specific competition were limiting bodyweights. In fact, changes in environmental conditions seemed to be closely associated with variation in mean kagu bodyweight. Highest mean bodyweight was recorded just after six weeks of more-or-less warm, wet cyclone-associated weather in intervals 3-5 (weight data were incomplete for several intervals over this period). This was the only long period of such conditions during the study, and may have allowed birds to obtain relatively high bodyweights. The rainfall data in Figure 3-3 appear to indicate why birds failed to achieve similarly high bodyweights in the 1994 wet season. There was a six week period (interval 26-28) between the passage of cyclones when most kagus lost bodyweight. Birds' bodyweights increased in the brief period of milder weather in August 1994, but their weights fell again when cold conditions followed. Bodyweights in the 1995 wet season remained lower than those in the 1993 wet season (my study finished before the end of that season). Rainfall data again indicate why this might have occurred; there was no cyclone and associated hot wet weather until very late in the season in mid March. Mean kagu bodyweight was lowest at the end of the driest period of the dry season in 1993 and 1994 (intervals 20 and 46), and started increasing in association with the substantial rainfall in intervals 21 and 47. This again suggested a close link between variation in kagu bodyweights and seasonal weather patterns. Bodyweight variation at Mt Cindoa had a similar pattern to that at Pic Ningua, and bird densities at the former area were probably relatively stable over the period of my study there. Thus kagu bodyweights had a positive relationship with weather-related factors (e.g., rainfall and temperature) and did not exhibit 'dry season fattening' to cope with periods of probable food scarcity. This suggested that food was at least predictable, even if scarce, in the dry season.

It was interesting that just before they nested in early December 1994, pair 119 and 120 increased their bodyweights relatively more than other kagus on the peak (Fig. 3-29). The pair may have increased fat deposition relatively more than that the of non-breeding kagus to prepare for the relatively long period of incubation ahead (section 3.1). If so, then the bodyweights of non-breeding kagus might have been below the level birds were able to reach given the food supplies available at that time. Meijer *et al.* (1994) found no difference in the annual bodyweight variation of non-breeding and breeding starlings in Holland.

There were no data to give an indication of how kagu bodyweights varied temporally at Parc Rivière Bleue, but they were likely to be low in association with hot and dry conditions (October/November) before the wet season (Y. Létocart pers. comm.). In a more temperate climate, bodyweights of breeding brown kiwis (McLennan 1988) and wekas *Gallirallus* spp. (Coleman *et al.* 1983, Beauchamp 1987) peaked in late winter just before they nested, and were lowest around December/January. This might have reflected a close relationship with their food supplies (section 5.4.2), but confounding effects were breeding activity and possible winter fattening. In *Chapter 5* I investigate how kagu food supplies varied throughout the year.

3.4.6 Primary moult

At Pic Ningua and Mt Cindoa, kagus undertook primary moult probably once a year (as in most birds, King 1974), usually starting in close association with the summer rainy season. In 1993, most birds at Pic Ningua began moult in late January/early February or later. Weather conditions then were hot and dry, and humidity was high (Fig. 5-3) before cyclone Polly brought the first heavy rainfall of the wet season in late February. In 1994, most birds began moult in the late December/early January period, coinciding with the arrival of hot, wet weather associated with cyclone Sarah in early January. Moult timing was also similar for birds at Mt Cindoa in 1994. My estimate for the average duration of primary moult in 1994 was approximately four months, and it took at least that long for birds 120 and 203, but was much shorter (roughly 2 months) for bird 201. If variation in length of moult is related to food supplies and changing bodyweight (as Emslie *et al.* 1990 suggested might be the case in cassin's auklet *Ptychoramphus aleuticus*), then moult could have been extended in 1994 because of the drier period in January/February between cyclones when the bodyweight of some birds decreased (Fig. 3-30). Birds at Parc Rivière Bleue appeared to undergo moult over the same period as birds did at my study areas (Létocart in litt., section 1.4). That birds obtain most of the nutrients for moult from their food (Blem 1990) and kagus at my study areas moulted when their bodyweights were around their highs, indicated that food supplies were abundant over the wet season.

Pair 119 and 120, with a young chick, had not began primary moult at 21/3/95, but the other four birds I knew at Pic Ningua had started at least before mid February. The pair had begun moult at around the same time as 106, 109 and 111 the previous year. Bird 110 who had a chick in early 1993 had also not begun moult at 18/3/93 when many other birds (some who could have raised offspring that breeding season 1992) had started moult around late January/early February. Moult in kagus does not appear to overlap with incubation. Chick rearing and moult did overlap at Parc Rivière Bleue, but only when chicks were raised from second or replacement eggs laid late in the year (section 1.4). Chick rearing may also be less energetically demanding than incubation; birds can lose considerable bodyweight during incubation (Létocart 1991, section 1.5). The average duration of primary moult in kagus at my study areas in 1994 was relatively short (*c*. 4 months) compared to some bird species in tropical climates (section 3.1). Bird 201 apparently took at most approximately ten weeks to moult in 1994, an extremely fast rate. It might have been possible though, that 201's moult was incomplete but that all 20 primaries (new and old) were fully grown.

3.4.7 Roosting behaviour

As kagus do at Parc Rivière Bleue (Létocart 1991), established pairs at Pic Ningua and Mt Cindoa used many different roosts around their home ranges and re-used certain of them. The re-use of roosts by kagus also supports the idea presented here that birds roosted in areas non-randomly, especially using sites around the boundaries of their home ranges. The amount of roost re-use must increase with the length of time a bird is resident in an area. Thus the higher use of previously unused roost sites by 106, 109 and 111 when they left the territories they had shared with their partners suggested they were not familiar with the areas they visited and that they had previously lived on their territories for some time.

One important difference between kagu behaviour at my study areas and Parc Rivière Bleue was the selection of roosting position. Kagus at my study areas used sheltered ground-roosts with high frequency in the dry season, in contrast to birds at the Parc who rarely roosted on the ground (Létocart 1991). No obvious environmental factor(s) appeared to constrain birds in their choice of either a sheltered or an unsheltered roost position at my study areas because the combination of mountainous terrain, often exposed rock, and primary rainforest meant there was no shortage of available shelters and perches. Sheltered positions might have been less available where Létocart studied kagus because the terrain was less rocky (pers. obs.). Kagus at Pic Ningua and Mt Cindoa were not attempting to avoid lethal overnight temperatures that force some small tropical birds such as green woodhoopoes (Ligon *et al.* 1988) to seek shelter. The fact that some kagus perched in unsheltered positions in intervals when most birds used sheltered positions indicated this. Cold temperatures are less of a problem for larger birds because they loose less heat per unit area than small birds (Calder and King 1974), however birds larger than kagus like vultures may seek more favourable microclimates in north temperate winters (section 3.1).

Wind chill and low humidity are likely more important than radiation loss in causing weight decline in roosting birds (Elkins 1983, Walsberg 1986, Webb and Rogers 1988). At 0°C, weight loss for blackbirds was reported to be four times as great in windy conditions as in calm weather (Elkins 1983). Walsberg (1986) found reduced wind chill provided five times the thermal benefit for phainopepla (small passerines of *c.* 25 g) than did protection from radiation loss. I did not measure the thermal attributes of sheltered and unsheltered roost positions. However, wind chill at many sheltered positions would have been considerably less than that for birds roosting on unsheltered perches because of shelter and that wind speed is generally least near the ground (Moore 1945). The combined effects of wind, cold and dry conditions and low humidity would have almost certainly increased overnight weight loss for a perching bird compared to that for one using a sheltered roost (Walsberg 1986). Kagus also appeared to roost in sheltered positions more when their bodyweights were declining, and at times when humidity and rainfall tended to be low.

My results suggest that kagus at Pic Ningua and Mt Cindoa sought shelter mainly from wind chill in colder weather. First, the lack of overhead cover (other than forest vegetation) at many sheltered roosts suggested that birds were mostly seeking to reduce wind chill rather than radiation loss. Second, until human arrival in New Caledonia there appeared to be few, if any, resident predators which could prey on adult birds (*Chapter 4*), so it is less likely that predation has been an important factor influencing roosting behaviour. Also, there is probably a positive association between altitude, kagu numbers and use of sheltered roosts on the island, which indicates that present-day predation risks and roosting behaviour at high altitude are not closely associated. Third, birds were solitary roosters therefore roost site selection is little influenced by social factors like dominance hierarchies in communal roosts. Fourth, at Pic Ningua and Mt Cindoa I observed a close negative association between use of sheltered roosts and minimum temperature. Last, the use of sheltered ground-roosts was uncommon at the lower altitude Parc Rivière Bleue (Létocart 1991) where minimum air temperatures are generally several degrees higher that those at Pic Ningua and Mt Cindoa (*Chapter 5*). Wind speeds are higher at altitude and at a maximum during the night (Proctor *et al.* 1988, Thomas and Proctor 1997), therefore also probably exacerbating colder conditions for kagus at high altitude compared to those for birds at the Parc.

Acclimation to ambient temperatures might also explain some of the variation in use of sheltered roosts like the increased use of perches during the milder weather in August 1994 when minimum temperatures were still quite cold. Although birds did put on bodyweight at that time and humidity increased (see Fig. 5-3), if kagus make relatively rapid physiological adjustments (e.g., possibly increased insulation of superficial tissues; Calder and King 1974) for cold resistance, then a sudden temperature rise in cold months might seem like warm conditions even if the increased temperatures were still low.

3.4.8 Kagu movements and interactions

Some kagus, particularly unpaired birds before they established territories, travelled many kilometres to new areas at Parc Rivière Bleue (Létocart 1991, Y. Létocart pers. comm.). However, there were no data to predict that widowed birds at Pic Ningua would leave their territories and travel so extensively and frequently after they lost their partners. Females 106 and 109 showed little attachment to the home ranges they held with their partners after starting to travel widely on the peak, in contrast to female 111 who returned regularly. Female 119 also travelled far from region 15 where I captured her with partner 120, but less extensively than the other three widowed females. Male 120 exhibited the most sedentary behaviour after the dog attacks, remaining mostly in regions 10 and 15.

Létocart (1991) observed that female kagus were more likely to leave their territories than males because of human disturbance (e.g., being captured). Female 111 probably left her territory on several occasions because I captured or disturbed her at her roost (section 3.3.9), but I was unsure if this was the reason females 106, 109 and 119 travelled widely on the peak. Birds 106 and 109 travelled on a relatively continual basis, even to low altitudes. It is difficult to imagine that my catching them could have been largely responsible for this behaviour because they also travelled in-between the times I captured or disturbed them at their roosts. I also captured or disturbed birds 202 and 203 at their roosts at Mt Cindoa most fortnights (e.g., I weighed bird 202 22 times over an 18 month period; Appendix IV), but they apparently did not leave their small home ranges. There was little evidence that the events related to dog predation caused females 106 and 111 to initially leave their territories as they remained on them for over three months after their partners died or disappeared. Female 109 should have had most reason to leave as she was wounded by dogs on her old home range. Birds may have been more likely to leave their territories because of disturbance once they lost their partners and/or kagus were reduced to low densities.

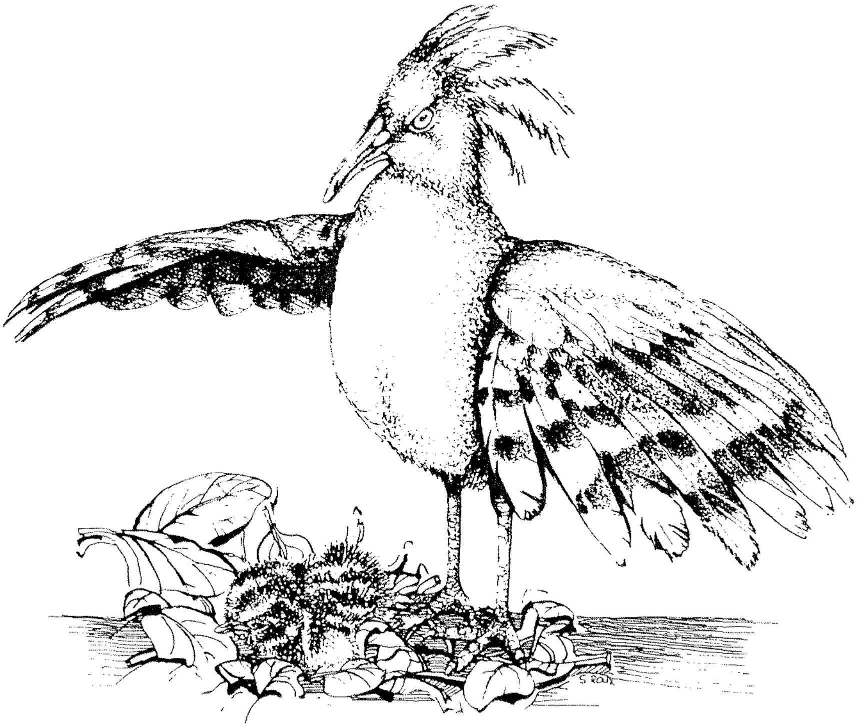
A search for other kagus appeared to be an important factor causing widowed birds to leave their territories and travel widely at Pic Ningua. Females 106 and 109 both spent time below the road and near the Nakaré River where others kagus lived. I found female 115 and bird 202 outside the areas they had moved in previously when I found them roosting with unknown birds. The most dramatic example was female 111 who I found roosting with a new bird at 330 m and 6.5 km from her old territory. Another example appeared to be male 120 who visited female 111's territory when his partner 119 was absent. Additional support for this 'search' hypothesis was that both 106 and 109 lost considerable bodyweight on some occasions when they descended into the Nakaré River valley, so travelling to this region appeared to incur a cost. In spite of this, they made six and three visits, respectively, down into the valley.

Although pair 119 and 120 's movements may have also been influenced by my disturbing them, by 1995 they had moved their combined home range away from region 15 where I first captured them to one that included region 10. The situation in region 10 was interesting as it appeared to be the home range of three pairs (113 and 114, 117 and 118, and 119 and 120) in succession. Territorial brown kiwis also extended their home ranges when their neighbours were preyed upon (Taborsky and Taborsky 1992). Thus although kagu pairs may have fixed territories when their densities are high, they might move to more preferred areas when these become vacant, or new pairs might quickly establish there.

Kagu movements at Pic Ningua also showed that birds would and could readily migrate between patches many kilometres apart. Although birds moved through shrub vegetation to reach forest, they probably mostly used forested corridors.

4

Kagu deaths caused by dog attacks at Pic Ningua and the question of whether dog predation played an important role in kagu decline



4.1 Introduction

One of the first steps in arresting or reversing a threatened species' decline is to determine the causal factor(s) involved (Caughley 1994). For some species the factor(s) is clearly evident (see Atkinson 1989 for examples related to introduced animals on islands). However, for many threatened species it may be extremely difficult to identify the main causal factor(s) (Caughley 1994). One reason being that remaining animals are often in the safer areas of the species' potential range where factor(s) causing the disappearance or decrease in other areas are reduced or absent. For example, this was the case for Lord Howe Island Woodhen *Tricholimnas sylvestris* (Miller and Mullette 1985) and probably New Zealand's Takahe *Porphyrio mantelli* (Bunin and Jamieson 1995). The kagu also appears to be an example of this. In *Chapter 2* I provided strong circumstantial evidence that kagus were mostly in safer areas because of the positive association between their numbers and the distance from human settlements. Thus the habitat used by an endangered species may not be its ideal habitat, but instead the last refuges for it (Olson 1989).

The kagu evolved in the absence of mammalian predators, but potentially had avian and reptilian predators (section 4.4.2) before human arrival in New Caledonia. Defence behaviour by kagus may have evolved to minimise the risk of predation from these types of predators. For example, when threatened or to protect chicks, birds open their wings and show the black and white banded primary feathers (Plate 4-1). When captured and unable to stand, birds also show the banded primaries by the unusual behaviour of fanning both wings forward in a shield that generally covers their heads (Pouget 1875, pers. obs.). Captive birds have been described to crouch and exhibit this behaviour when frightened but not actually held (Bennett 1863, Sarasin 1913). Also, in nest or chick defence adults may flap their wings on the ground in a typical distraction display, feigning injury (Hunt 1996b). Birds have been described attacking dogs as they captured other kagus (Pouget 1875). These defence behaviours though, are ineffective against predation by dogs *Canis familiaris* who can easily capture the birds (e.g., Sarasin 1913).

With humans came an array of associated factors detrimental to kagus that probably started the species' decline. Reasons cited other than the obvious loss of habitat included capture and predation by humans and introduced predators (e.g., Pouget 1875, Sarasin 1913, Warner 1948, Jeggo 1978). Dog predation had long been cited as important in causing kagu decline (Pouget 1875, Sarasin 1913, Jeggo 1978, Brégulla 1987, Seitre and Seitre 1990), but little quantitative evidence was available. Most evidence was anecdotal or circumstantial, or of single kills by stray (e.g., Létocart 1992) or hunting (e.g., M. Bull pers. comm.) dogs. Field research at Parc Rivière Bleue from 1980 by Létocart (1991 1992) provided valuable information about the effect of introduced predators on wild kagus there, and circumstantial evidence to suggest that hunting activities by people (e.g., for feral pigs *Sus scrofa* and rusa deer *Cervus timorensis*) in kagu habitat were extremely detrimental to birds. However, the data were insufficient to allow the main causes of kagu decline to be identified with any degree of confidence. In 1993, a serious predation event at my study area on Pic Ningua provided hard evidence to support the idea that dogs had played an important role in kagu decline.

In this chapter I describe in more detail the dog predation event that occurred at Pic Ningua in 1993 (Hunt *et al.* 1996c, reprint in Appendix IX). This was the first documented case of multiple kagu deaths caused by dogs. In light of this new evidence, I then use the discussion to address the question of whether dog predation has played an important role in kagu decline in the hope that this might help to make clear what management actions are needed to ensure kagu persistence in the wild. I do this by first trying to establish what kagu distribution had been in the past, then use information about their recent distribution (Hunt 1996a, *Chapter 2*), about their spatial and social organisation (Létocart 1991, *Chapter 3*), and about factors that could or did affect kagus to see if a case for an important role of dog predation in kagu decline exists. Here, I am not concerned with the obvious effect of habitat loss on kagu numbers, but rather the reason for the contraction of birds within their potential range.

4.2 Methods

The methods I used for following kagus at Pic Ningua (e.g., radio-tracking), and details about individuals that were known there are in *Chapter 3.* Although an in-use road ran close to the forest on Pic Ningua, I classed access to the peak as moderate (Appendix [illegible]) in the generalised linear modelling analyses in *Chapter 2* because it was a private road and its use was restricted. In the text, individual kagus are identified by their ID Nos., and additional information on birds (e.g., sex, age) is in Appendix IV.

4.3 Results

4.3.1 Description of the attacks on kagus

In 1993, 20 kagus were found dead (n = 15) or wounded (n = 5) at Pic Ningua in four distinct attack episodes: three episodes between late April and late May, and one in early August (Table 4-1). Four of the wounded birds subsequently died, and the fifth one (bird 109) completely recovered after treatment with antibiotics. The remains of two other birds (132 and 134) were found sometime after they had died. Eighteen of the 22 birds wore radio-transmitters, and the four non-radio-tracked birds (131, 132, 133 and 134) were found by chance. The remains of the birds found dead (n = 17) consisted of feathers only (n = 5), feathers and one or more separate body parts (n = 6), partly eaten carcasses (n = 4; birds 107, 117, 123 and 131) (Plate 4-2), and dead but uneaten carcasses (n = 2). Two of the partly eaten birds could have been scavenged by rats *Rattus* spp. as only a small area of the breast of each bird was eaten and no bones were damaged. The sex of a bird did not appear to affect the risk of it being attacked as both males and females were killed.

The dead or wounded birds were found over a large area (Fig. 4-1), including one (female 123) on the south-facing side of the peak, although she may have been wounded on the north-facing side where I first captured her (Fig. 3-11). I found seven radio-tracked individuals who had partners (101, 102, 107, 109, 113, 114, and 116) outside the home ranges they used before they or their partners were attacked (Figs. 4-1 and 3-12).

All transmitters on attacked birds were undamaged and working, but some of the attachment cords were bitten through on eaten carcasses. Several leg bands on eaten carcasses contained single tooth marks presumably from feral pig or dog bites.

After the August attack episode, I knew of only five birds (four females and one male, all fitted with transmitters) at the study area. At 31 March 1995, I had only found two new birds (124 and 125) there, who I captured on 27 November 1993 and 12 April 1994, respectively, and also fitted with radio-transmitters. As I only recorded bird 124 below the road on the north-facing slopes, and 125 spent time there

Table 4-1. Details of the 22 dead (n = 17) or wounded (n = 5) birds found at Pic Ningua in 1993. Column 1: kagu identification number. Column 4 briefly describes the state kagus were found in. Column 5: 'T/B' = fitted with a transmitter and leg bands; 'B?' = may have been banded; '----' = not fitted with a transmitter or banded. Birds 104 and 123 may have been wounded before the date I last thought them unharmed. The condition of the remains of birds 132 and 134 indicated that they had died several weeks or months before they were found.

Bird	**Date last thought unharmed**	**Date found attacked**	**Brief description of attacked birds when found**	**Transmitter / Bands**
First attack episode				
103	12/4	26/4	Dead (feathers, head, foot, digestive tract)	T/B
105	14/4	27/4	Dead (feathers, one wing)	T/B
107	20/4	27/4	Dead (wings, head, and legs on carcass)	T/B
101	19/4	27/4	Dead (feathers, section of leg)	T/B
108	20/4	28/4	Wounded, later died	T/B
102	19/4	28/4	Dead (feathers)	T/B
104	29/4	2/5	Wounded, later died	T/B
Second attack episode				
113	5/5	9/5	Dead (feathers)	T/B
131	?	9/5	Dead (wings, 1 leg, and head on carcass)	----
114	5/5	9/5	Dead (feathers)	T/B
122	5/5	9/5	Dead (feathers, digestive tract)	T/B
Third attack episode				
116	20/5	21/5	Dead (intact)	T/B
133	?	23/5	Dead (intact)	----
Fourth attack episode				
110	1/8	5/8	Dead (feathers, head, one foot)	T/B
109	1/8	5/8	Wounded, later recovered	T/B
121	29/7	5/8	Wounded, later died	T/B
115	29/7	5/8	Wounded, later died	T/B
117	4/8	8/8	Dead (virtually intact)	T/B
118	4/8	8/8	Dead (feathers)	T/B
123	8/8	10/8	Dead (virtually intact)	T/B
Approximate date of death unknown				
132	?	21/5	Dead (feathers)	B?
134	?	12/10	Dead (head, feathers)	B?

Plate 4-1. Bird 101 using its wings in a defence display after being disturbed at night on its perch. Note bird 101's extended banded primaries and its crest feathers displayed roman-casque-like rather than fanned as in Plate 3-2.

Plate 4-2. Male 107 shortly after he had been killed by dogs on the north-facing slopes of Pic Ningua (107's position is marked on Fig. 4-1.). This was unlikely to be a pig-scavenged carcass as pigs probably left little else other than feathers.

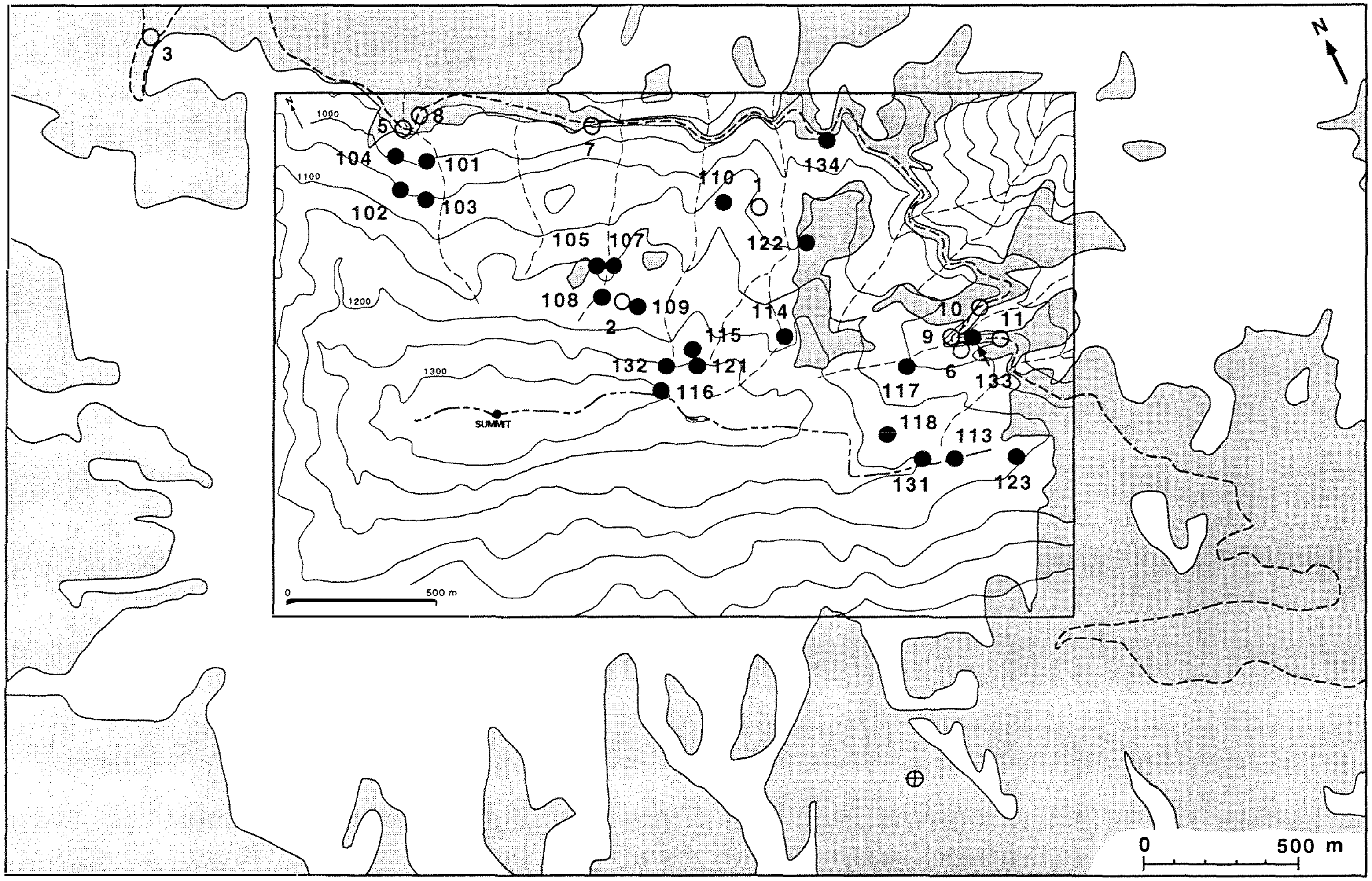


Figure 4-1. Pic Ningua summit area showing positions where wounded and dead kagus were found (black dots), and where dogs were heard or seen (unfilled circles). Numbers beside circles correspond to the respective bird ID Nos. and dog observation records in Tables 4-1 and 4-2 (dog observation No. 4 is outside the map area). The tribal village from where dogs B-E strayed is located approximately 4 km southwest of the summit. '⊕' = listening site used for the survey on the south-facing side of the peak. Key to map details is in Figure 3-1.

soon after I fitted it with a radio-transmitter, both birds could have migrated to the study area from lower down in the Nakaré River valley (Fig. 3-1).

4.3.2 Evidence for dog predation

Eleven observations of dogs (barking or visual sightings) were recorded at the study area between late January 1993 and 31 March 1995 (Table 4-2, Fig. 4-1). I was present at the study area over this period for, on average, four days each week. I found dog scats in only two locations at Pic Ningua during the time I spent there: several recent scats on open ground near dog observation No. 8 and the road (Fig. 4-1) during the period of the attacks, and one fresh scat on 3 October 1993 on an old mining track near the other scats and just outside the forest. Kagu remains (feather shafts) were in all the scats. I identified five different dogs at the study area: a lost hunting dog (white coloration, dog A in Table 4-2) that mine staff identified and observed descend from Pic Ningua the day before (25/4/93) I found the first attacked birds, and four dogs (B, C, D, and E in Table 4-2) that belonged to a hunter from the tribal village in the valley on the southern side of the peak (see Fig. 4-1 legend). Descriptions by mine staff of dogs (B, C and D) they observed at the study area just before the second attack episode matched my own observations of the same dogs two weeks later at the time of the third attack episode.

Wounds on kagus were consistent with dogs bites because circular puncture marks were in the skin on and around the back region of all wounded and (intact) dead birds. I noticed no injuries around the head regions of attacked birds. The feather remains of bird 132 appeared less than a few months old and its death may also have been caused by dogs. A dog-related death for bird 134 seems likely as only the head was present.

A dog or dogs clearly caused the death of bird 133 who I found on 23 May in vegetation a few metres from the road. Obvious signs of a chase and capture by a dog(s) were indicated by dog and kagu footprints and kagu feathers on the road next to where I located the bird. I had seen three dogs at the same location the previous evening (Table 4-2, Fig. 4-1). Dog footprints (identified by Michael Bull) were only observed near one other dead kagu, the feather remains of bird 113 found approximately 350 m from the road. The footprints were on a muddy track where they were easy to detect.

Table 4-2. Dog observation records (barking or visual sightings) at the study area on Pic Ningua between January 1993 and March 1995. Observations 3-6 were made by mine staff.

Observation number	Type of observation	Date	Number of dogs	Dog identity code
1	barking	12/3/93	1	?
2	barking	20/4/93	1	?
3	sighting	25/4/93	1	A
4	sighting	27/4/93	1	A
5	sighting	4/5/93	3	B, C, D
6	sighting	7/5/93	1	B
7	sighting	20/5/93	1	C
8	sighting	20/5/93	2	D, E (killed)
9	sighting	22/5/93	3	B, C, D
10	sighting	22/5/93	2	B, C
11	sighting	24/5/93	1	B (killed)

I killed two dogs on the road at the study area, on 20 and 24 May 1993 (Table 4-2, Fig. 4-1). Kagu remains were in the (full) stomach of one dog, but as maggots were also present it may have just eaten a kagu carcass rather than a newly killed bird.

It seems improbable that pigs, who move relatively noisily through forest, could capture healthy adult kagus. However, they did feed on kagu carcasses as I found pig scats containing kagu remains (feather shafts and bone) at the study area after late April 1993. No fresh pig scats I inspected after early May 1993 contained kagu remains.

Feral cats *Felis catus* hunted in forest at the study area, but the wounds on kagus were not characteristic of cat attacks. For example, I did not observe head and neck injuries on birds, but such injuries were found on a newly released captive-bred juvenile killed by a feral cat at Parc Rivière Bleue (Y. Létocart pers. comm.). Also, I did not find kagu remains in cat scats I inspected at the study area.

4.3.3 Survey of kagus on the south-facing slopes of Pic Ningua

In 1992, local hunters told me that they had heard many kagus sing in forest on the south-facing slopes of Pic Ningua. To check if my presence or activities at the study area had led to the dog attacks, I surveyed part of the south-facing slopes for kagus after August 1993. The forest there was closer to the tribal village from where dogs

B-E had strayed. The presence of many surviving kagus on the south-facing slopes would strongly suggest my research activities on the north-facing slopes had increased the risk of birds there being attacked.

I listened for early morning kagu song from the area where hunters had heard kagus sing (Fig. 4-1). On 21 mornings between 17 October 1993 and 1 February 1994, I only heard one kagu pair sing (on 30 December). This pair was unknown to me as none of my radio-tracked birds were near the location the pair sang from. At Mt Cindoa, birds had sung on each morning (n = 12) I spent there over the same period.

I heard no non-radio-tracked birds sing again at higher altitudes on Pic Ningua after 30 December despite many mornings spent there during the period when kagus sing. Thus I only knew of the unknown pair who sang and the seven radio-tracked kagus at higher altitudes on Pic Ningua after the dog attacks, whereas at least 35 birds had been there before late April 1993 (section 3.3.2). This suggested that dogs attacked kagus on both sides of Pic Ningua and not just on the north-facing slopes.

4.4 Discussion

4.4.1 Dog attacks at Pic Ningua

There seemed little doubt that dogs caused the deaths of at least 19 of the 21 kagus known to have died at Pic Ningua. The numbers killed were almost certainly higher as kagus without transmitters had also been on the peak. That four dead birds not fitted with transmitters were found by chance suggested this was the case.

Lost hunting dog A seen at the end of April could have been responsible for the first attack episode. The four dogs from the tribal village certainly appeared responsible for the second and third attack episodes as they were seen at the study area around those times. I did not see or hear dogs at the study area around the time of the August attack episode, therefore the dog(s) possibly reached the north-facing slopes without using the access road and may have also come from the tribal village.

It was a disturbing coincidence that dogs attacked kagus on the north-facing slopes soon (three months) after I started intensive research work there. Kagus on the slopes were numerous before the attacks (*Chapter 3*), indicating that there had been no large scale predation of birds in that area for many years given the kagu's low annual fecundity. Kagus fitted with transmitters and leg bands did not seem more at risk from dog predation because birds without them were also attacked. The lack of kagus on the south-facing slopes suggested that dogs had attacked birds there as well, therefore my research activities were unlikely to have attracted dogs to the peak. Dogs may have started attacking kagus on the south-facing slopes then moved to the north-facing slopes in search of more prey. I had no evidence that my marked walking tracks in the forest were used by dogs.

I found seven attacked birds outside their previously known home ranges, suggesting that this phenomenon was predation-related. Dogs may have chased and/or carried the birds to the locations where I found them, or the birds moved there themselves after being wounded. The remains of bird 107 included the head, indicating that it was chased and/or carried to the site by a dog(s) as pig scavenged carcasses probably consisted of little else other than feathers. Although adult kagus are easy prey for dogs, the circumstances surrounding the death of bird 133 suggested that some birds defended themselves by running to try and escape these predators.

The hunting behaviour of the dogs at Pic Ningua indicated that dogs are a serious threat to kagus. In two of the four attack episodes wounded birds were left alive to die later, and this may have also happened to many of the birds found dead. Thus the dogs appeared to have attacked more birds than was necessary for their immediate food needs, assuming that birds with bite marks were or could have been captured. I had no evidence that dogs buried kagu remains or whole carcasses, as a stray dog did with New Zealand brown kiwis *Apteryx australis mantelli* (a similar-sized flightless forest bird) that it killed (Taborsky 1988).

Two behavioural aspects of the stray dogs from the tribal village were important: they probably hunted in a pack which should have facilitated the finding and capture of birds, and they made repeat visits to forest at a much higher altitude than where they originated. Although the map distance from the village to the study area was not large (4 km), the dogs ascended from 200 m to probably around 1,300 m (bird 116 was found dead at 1,280 m). They climbed over 1,000 m in altitude demonstrating that kagus at higher altitudes (where many unprotected birds now remain, *Chapter 2*) are also at risk from predation by stray dogs originating at lower altitudes. The lost hunting dog may have killed birds, but it left the peak and apparently did not return. In contrast, the stray dogs made repeat visits to the peak to hunt, evidenced by sightings of the same individuals at the second and third attack episodes but not in-between these times. The dogs probably returned to the peak because of successful hunting on previous visits, which would be consistent with other studies showing increased search times by predators in an area after encountering prey there (Stephens and Krebs 1986). Thus several dogs almost exterminated kagus from the mountain top forest on Pic Ningua.

The dog attacks at Pic Ningua may not be an isolated event. Dog-related deaths of non-radio-tracked kagus would be difficult to detect because they would occur in forest where any remains would be quickly removed by pigs. The situation seen with brown kiwi may not be unlike that of the kagu. There has been growing evidence after the first reported brown kiwi deaths from dog predation (Taborsky 1988) that such incidents are a continuing problem and dog predation could be the main reason for that species' decline in certain areas (Miller and Pierce 1995).

I next review the history of kagu decline and try to identify the factor(s) that may have helped shape the current kagu distribution.

4.4.2 Past kagu distribution

The extent of kagu distribution on mainland New Caledonia when Melanesians arrived over 3,000 years ago (Guillaud and Sémah 1997) was unknown, but the island is generally assumed to have been almost completely forested then (Jaffré and Veillon 1994). Because kagus appeared to be generalists in the types of rainforest they inhabited (Jeggo 1978, Thiollay 1989) (birds have been known in recent times in coastal and inland forests and at most altitudes; Cherrier 1990, Hunt 1996a) and the soil and litter prey they ate (*Chapter 5*), their potential habitat covered much of Grande Terre at the time.

Potential predators of kagus were present before Melanesian arrival. For example, there were the extant New Caledonian crow *Corvus moneduloides* (a known pillager of other birds' nests; Délacour 1966, Létocart 1992) and the mainly forest-dwelling blue goshawk *Accipiter haplochrous* (Thiollay 1993) which hunts within rainforest (Létocart 1992), extinct reptiles (a terrestrial crocodile *Mekosuchus inexpectatus* and tortoise *Meiolania* sp.; Balouet and Alibert 1989) and birds (two *Accipiter* sp.; Balouet and Olson 1989), and the possibly extinct flightless New Caledonian rail *Tricholimnas lafresnayanus* (no confirmed sighting since 1890; Hannécart 1988).

There was no evidence that New Caledonian crows or blue goshawks preyed on kagus, and the extinct reptiles may not have been a significant threat in the mountainous terrain that made up much of the island. However, large lizards were also likely to have been present in New Caledonia in the past (a fossil was discovered in 1983 and legends about them are common in indigenous Kanak culture; Balouet and Alibert 1989). These animals might have also preyed on the eggs and chicks of kagus but little is known about their presence on Grande Terre.

Balouet and Olson (1989) suggested *R. orarius* was a lowland species and *R. jubatus* a highland one. If they were separate species (see section 1.4), the ability of *R. jubatus* to live in forest at all altitudes implies that if *R. orarius* also lived in forest it must have excluded *R. jubatus* from those areas. Nevertheless, *R. jubatus* may still have lived extensively in the island's forests since humans arrived given that *R. orarius* sub-fossils are not known later than around 2,000 BP.

A considerable amount of forest on Grande Terre had disappeared due to Melanesian fires by the time Europeans arrived (Morat *et al.* 1986, Mittermeier *et al.* 1996), and Kanak people snared and ate kagus (Bennett 1863). Although it was not taboo in Kanak culture to eat the birds, they played an important role in the traditions of certain tribes (Hunt 1996b). Dogs were not present until Captain Cook introduced them at Balade (north of Pouébo, Fig. 2-1) in 1774 (Pisier 1974, Gargominy *et al.* 1996). Two Tahitian dogs were given to the chief of the Balade tribe and are thought to have survived and reproduced successfully (Dousset-Leenhardt 1978). If this was so, Kanaks probably used them for hunting kagus soon after their introduction. If not, Kanaks were using dogs for this purpose after 1853 (Pouget 1875), indicating that snaring of birds was less efficient. The first Polynesian rats *Rattus exulans* were thought to have arrived with Melanesians around 3,000 B.P. (Atkinson 1985), but these rats may not necessarily have arrived on Pacific islands with the earliest known human invaders (Holdaway 1996). The ability of kagus to co-exist with the more dangerous ship rat *Rattus rattus* (see *Introduced mammalian predators* below) suggested any affect on kagu distribution by *R. exulans* was probably limited. Warner's (1948) opinion was that neither Melanesian hunting or the Polynesian rat had been a serious threat to kagus.

Kagus were probably still widespread in forest and in greater numbers in 1774 compared to today, especially as dogs were only introduced then. Cherrier (1990) though, suggested that European settlement may have resulted in increased kagu numbers as Kanaks turned to different, more easily obtained food sources. Kagu distribution and abundance was little known from the time of European settlement in 1853 until the survey in 1991 (Hunt 1996a, *Chapter 2*). Part of the difficulty in obtaining accurate demographic data on the kagu population has been the contraction of kagu distribution into more remote areas (Jeggo 1978) and the difficulty in detecting kagu presence unless birds sing (Cherrier 1990).

Given that a widespread kagu presence in rainforest was likely when Europeans arrived, a large decline in their population has occurred and now birds only live in a very small area of their potential range at anything like former densities. Europeans introduced potential predators and/or competitors (rats, cats, pigs, dogs and rusa deer) and an efficient means to capture kagus using dogs, created a market for the sale of live birds, and increased forest fragmentation by logging (Thiollay 1989), forest clearance, road building and the direct or indirect burning of large areas of vegetation in association with mining and logging operations (Sarasin 1913, Warner 1948). In the next section I discuss what effect these factors may have had on kagu decline.

4.4.3 Factors potentially shaping kagu distribution

Fragmentation of rainforest

Approximately 20% of mainland New Caledonia remains forested (section 1.3), and much of this is fragmented (excluding the effect of fragmentation by roads, which I discuss under *Degradation of habitat* below) (Jeggo 1978, pers. obs.), thus negative effects of patch size and isolation have probably affected at least some resident bird species (Henrik 1994). Fragmentation may result in declining bird numbers for various reasons such as increased predation (e.g., Yahner and Scott 1988) and/or greater vulnerability to localised extinction from stochastic events because of small isolated populations (Burkey 1995). Such processes would mean that remaining populations would be those in larger, more contiguous areas of habitat. However, this does not appear to be the case for kagu distribution. High numbers of kagus occurred in small (< 1,000 ha) areas of forest (e.g., Dent de St. Vincent. Mt Cindoa, Pic Ningua, Koum), and there were few kagus in some large tracts (e.g., Panié Massif, Col des Roussettes, Col d'Amieu, Mts Dzumac) (Hunt 1996a). Thus patch size and forest fragmentation do not appear to be good predictors of kagu numbers (also observed by Jeggo 1978), which supports the idea that the main reason kagus have persisted in their present areas was because they were in safer rather than larger tracts of forest (Jeggo 1978, Thiollay 1989, Hunt 1996a).

Degradation of kagu habitat

Here, I use the term degradation to include damage by introduced animals, selective logging and fragmentation by roads. The effect of mining operations (mainly for nickel) on forest in New Caledonia has mostly been its destruction by clearance or fire (section 4.4.2), along with habitat fragmentation by mining roads.

Densities of introduced mammals (rats, feral pigs and rusa deer) who potentially degrade kagu habitat are not known, but kagus live in forest where probably at least two of the above three taxa are permanent residents (pers. obs.). Therefore, rat, pig and deer damage (singly or combined) to the forest understorey does not make forest uninhabitable for kagus.

Selective logging has been the most common form of forestry practised in New Caledonia, where it is legally restricted to below 800 m and not permitted on steep slopes (M. Boulet pers. comm.). Much forest remained intact after a selective logging operation (Jeggo 1978), but logging roads and cleared areas also remain for many decades or longer (pers. obs.). I found few kagus in selectively logged forests on the 1991 survey (Hunt 1996a, *Chapter 2*), so factors associated with this type of disturbance make forest unsuitable to support birds at pre-logging levels in the long term. The situation at Parc Rivière Bleue offered a clue about what might be responsible for this. Logging was most recently carried out in the upper Rivière Bleue region, terminating in 1978. In 1980, when kagu protection measures were introduced at the Parc (see *Introduced mammalian predators* below), the positions of 42 birds were known there (Létocart 1992). Most pairs sang from older logged forest, especially in the Moi de Mai valley, and birds singing in the upper Rivière Bleue region were mostly lone males (female kagus appear more likely to leave their territories because of disturbance than males; section 1.4). By 1991, most birds singing in the upper Rivière Bleue region were duetting pairs (Létocart 1992). The management measures introduced for kagu conservation at the Parc had probably assisted the return to high kagu densities in logged areas there (Létocart 1992).

Fragmentation by roads and the associated influx of human activity (e.g., for hunting introduced mammals) and non-human predators (e.g., cats and dogs) may be one reason that kagus have disappeared or remained at low numbers in many areas (Thiollay 1989). Little is known about the effect of this type of fragmentation on resident native forest fauna, in New Caledonia or elsewhere (May and Norton 1996).

Human hunting and capture of kagus

Kagus were sought after for aviaries both locally (Brégulla 1987) and overseas (Pouget 1875, Sarasin 1913) from soon after European settlement in 1853. Numbers of kagus caught for this purpose must have been considerable because 94 different captive birds were recorded and banded on Grande Terre in a survey between 1977 and 1982 (Brégulla 1987). Capture of birds was reduced substantially after about 1977 when the existing strict kagu protection laws (section 1.2) were enforced. In 1991, I knew of at least one bird who had been captured and offered for sale (Hunt 1992), but I had no evidence of actual transactions or that birds were still being deliberately hunted for food. Some kagus accidentally killed by hunting dogs though probably had been eaten by hunters (Warner 1948, M. Pandolfi pers. comm.).

Kagus in more easily accessible locations such as coastal areas were captured first (Marié 1870, Pouget 1875). The combined impact of human hunting and capture of kagus on localised, less remote populations was probably substantial.

Introduced mammalian predators

Rats are probably widespread at all altitudes in New Caledonian forests, but their densities were unknown. They lived in the low altitude Parc Rivière Bleue (Létocart 1992), and I often noticed their caches of empty nut shells on the ground at Pic Ningua (above 950 m in altitude), but rarely saw them at night in forest there. The Polynesian rat has not been documented preying on kagu chicks or eggs, but it preyed on the eggs and chicks of ground-nesting seabirds (Wirtz 1972, Booth *et al.* 1996). Ship rats (a dangerous predator of birds nests and present in New Caledonia before 1912; Atkinson 1985) may exclude the smaller and weaker Polynesian rat from forest at Parc Rivière Bleue as the former were only caught in forest there (Létocart 1992). The Norway rat *R. norvegicus*, present on the island (Atkinson 1985), has not been seen in forest at the Parc (Létocart 1992), so the ship rat may be the main potential rat predator of kagus. Some evidence suggested that ship rats might be predators of kagu chicks rather than their eggs (Létocart 1992); eggs in 11 unprotected (no rat poison laid nearby) kagu nests at Parc Rivière Bleue were not attacked by rats, but chick survival rate increased when rat poison was laid around 13 kagu nests (within a 100 m radius of nests when incubation began and again one week before the chicks hatched). However, the large increase in kagu numbers in the Parc, mostly from nests not protected by rat poison, indicated that rat predation had not been an important factor causing kagu decline there. Rats may also compete with kagus for soil and litter prey like snails (Warner 1948).

Feral cat scats were widespread on tracks and roads over the island (Thiollay 1989, pers. obs.). I found scats on my walking tracks in the forest at Pic Ningua up to 1 km from the road, confirming Fitzgerald and Karl's (1986) finding that feral cats travel some distance into unbroken tracts of dense vegetation. There has been only one documented case of cat predation on a kagu (a one-year-old bird, section 4.3.2), and no records of them killing chicks or mature adults. Feral cat diets worldwide mostly consist of mammalian prey when these animals are present, and this is consistent with my inspection of cat scats at Pic Ningua which contained mostly rat or mouse *Mus musculus* fur. Australian feral cats took mammals up to 2 kg in bodyweight (Paltridge *et al.* 1997), therefore cats can potentially prey on adult kagus.

Feral pigs were widespread in the island's forests (Thiollay 1989, pers. obs.), and they caused considerable rooting damage to the forest floor in many areas (e.g., at Parc Rivière Bleue; Létocart 1992). Feral pig rooting causes extensive damage to rainforest vegetation in Australia and Hawaii, and pigs compete with native fauna like North American turkeys *Meleagris gallopavo* (reviewed in Pavlov *et al.* 1992). Miller and Mullette (1985) presented strong circumstantial evidence that pig predation was the major factor in the decline of the Lord Howe Island woodhen; the distributions of the two species did not overlap and remaining birds were in areas inaccessible to pigs. In New Caledonia though, kagus co-existed with pigs (e.g., at Parc Rivière Bleue and my high altitude study areas). However, eggs in two of the 26 kagu nests Létocart (1992) observed at Parc Rivière Bleue from 1986-1991 were assumed eaten by pigs based on evidence of nest damage. Along with rats, pigs may also compete with kagus by reducing their food supplies (Warner 1948, Hay 1986, Létocart 1992, *Chapter 5*).

Dogs were numerous throughout Grande Terre in association with human presence, and I often saw them walking unaccompanied along road margins, especially in the vicinity of human settlements. In tribal villages, dogs have become an integral part of tribal life since their introduction. Official control of stray dogs was minimal, even in the three towns (Nouméa, Poya, and Pouembout) where dog registration was a requirement. When pigs became feral, and rusa deer were introduced, the use of dogs for hunting in forest also increased. The dog-related deaths of many kagus at Pic Ningua were the first direct evidence that dogs were a serious threat to the birds. This supported past observations (section 4.1), and circumstantial evidence suggesting this from Parc Rivière Bleue. Management there by predator control, a halt to hunting game, and kagu introductions since 1980 had reversed kagu decline (section 1.2). Predator control included shooting and poisoning cats, pigs and dogs. It was difficult to pinpoint the main factor(s) responsible for the increased kagu numbers at the Parc because the management of humans, introduced predators and kagus had been carried out simultaneously. However, hunters and stray dogs had been eliminated from the Parc or were very rare there. The change in the numbers of cats and pigs there is unclear, but their presence in areas subject to poisoning and shooting (along and close to roads; Létocart 1992) has probably been reduced (Y. Létocart pers. comm.).

The lack of kagus in the northern regions of Grande Terre (Hunt 1996a), particularly on Panié Massif, may also be circumstantial support for dogs being important kagu predators. This was because the occurrence of dogs and/or hunters with dogs may have been much greater there than in the southern parts of Grande Terre (Seitre and Seitre 1990, pers. obs.). Local people commonly cited packs of stray and/or feral dogs as the reason for the disappearance of kagus from Panié Massif (Seitre and Seitre 1990, Hunt 1992). A considerable amount of other qualitative evidence also pointed to a greater dog problem in the north. I observed deer carcasses in the Tipindjé River south of Hienghène that locals said resulted from these animals trying to escape packs of dogs. Men from the tribal village of Haut Coulna (on the southwest side of Mt Panié) regularly shot stray dogs in forest around their village because they killed deer (G. Bouerou pers. comm.). Also, a higher density of tribal villages exists near forest towards the north of Grande Terre, where dogs were also first introduced (section 4.4.2).

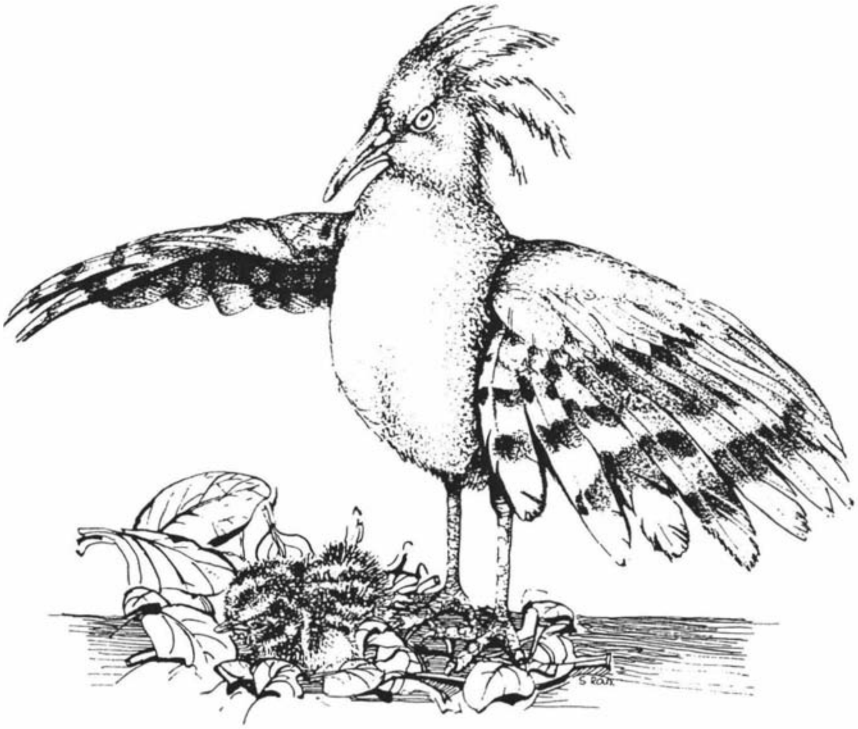
4.4.4 Conclusion

A substantial decline in kagu numbers within potential habitats has occurred since European settlement in New Caledonia, for example in selectively logged forests. The effect of Melanesian presence, other than habitat destruction, on the distribution of kagus before Europeans arrived is largely unknown. Although the data were few and mainly circumstantial and/or negative evidence, they suggested that kagu decline since 1853 was related to humans and/or dogs. First, the data failed to implicate mammalian predation or competition from animals other than humans and dogs, the effects of habitat fragmentation, or habitat specialisation by birds. Second, circumstantial support for dog predation (with or without humans) was the kagu distribution pattern in 1991; more birds in remoter areas. This pattern would be consistent with a widespread kagu distribution in forest before human arrival and subsequent greater predation on adults in areas closer to human activity. Fraser *et al.* (1995) demonstrated in stream fish that predation can cause such population fragmentation. This process would also explain the anomalous lack of kagus in the northern regions even in large and remote tracts of forest, in association with an increased frequency of dogs and/or hunters in those areas compared to forest elsewhere. Given these two points and that dogs are dangerous predators of kagus, predation by dogs (alone and with humans) appeared to be the parsimonious explanation for kagu decline. However, one should not draw conclusions about causal agents of decline from associations (Caughley 1994), and further research is needed to see whether rats, cats and pigs are serious resident predators of kagus.

The spacing behaviour of kagu pairs, which might reflect the nature of their food supplies (section 1.5) and be facilitated by the kagu's apparent ability to live for long periods without drinking water (Hunt 1996b), may have provided protection from rapid extinction (Jeggo 1978). Most rail species have broken distributions in close association with water (Taylor 1996), and this may have been the case for many of the flightless rail species that became extinct throughout the Pacific (Steadman 1989 1995), including in New Caledonia (*Porphyrio kukwiedei* Balouet and Olson 1989, and possibly *T. lafresnayanus*), after animal invasions. Clumped distributions near water may have made many rail species more vulnerable. A similar set of circumstances to those of the kagu may have enabled the brown kiwi to persist in a relatively widespread distribution in Northland, New Zealand. The recent arrival of ferrets *Mustela furo*, dangerous introduced predators of kiwis and resident in forest (McLennan *et al.* 1996), in southern Northland may have caused the apparently recent large reduction in brown kiwi numbers in that area (Miller and Pierce 1995).

5

Diet and feeding ecology of kagus, and the influence of pig foraging on birds' food supplies



5.1 Introduction

The foraging behaviour of an animal is an important factor influencing its reproductive success because it plays a large role in making available the energy resources required for reproduction. The link between foraging behaviour and an animal's fitness though has received little attention in birds (Frey-Roos *et al.* 1995), although it is known that birds' bodyweights, which reflect foraging success, affect their fitness (section 3.1). In this chapter I describe the relationship between kagus' diets and their food supplies over time at Pic Ningua and Mt Cindoa, along with associated variation in the reproductive activity (measured by egg numbers in faeces) of an important intestinal parasitic nematode *Cagourakis dorsalata* specific to kagus (Petter *et al.* 1988). I also look at the potential for competition between feral pigs *Sus scrofa* and kagus for food supplies at Pic Ningua and present pitfall trap and climate data from Parc Rivière Bleue.

Most studies investigating temporal variation of arthropod abundance in tropical rainforests have focused on insects and used above-ground collection methods such as light-traps or sweep nets (e.g., Wolda 1978a,b, Wolda and Fisk 1981, Frith and Frith 1985, Wolda 1987). Few have investigated temporal variation of soil and litter arthropod abundance in tropical rainforests at higher altitudes. Leakey and Proctor (1987) and Thomas and Proctor (1997) investigated the abundance and biomass of soil and litter taxa at a range of altitudes in sample plots on ultrabasic mountains in the tropics, but not temporal variation.

Wolda (1978a) found decreased year-to-year fluctuations in insect abundance with increased physical stability of the environment (e.g., humid forests), in both temperate and tropical regions. Seasonality in insect abundance though occurs in most, if not all, tropical rainforests and is suggested to be closely related to climatic conditions (Wolda 1978a, Wolda 1988). Rainfall is usually cited as the primary weather-related factor varying abundance (Wolda 1978a, Wolda 1988, Frith and Frith 1985, Braby 1995), especially where seasonal variation in temperature is minimal. Humidity and photoperiod are also thought to be important (Wolda 1988). Seasonal variation in abundance tends to be weaker with decreasing latitude, and within the tropics is weakest in relatively non-seasonal areas (Wolda 1988).

Studies in the tropics have shown or suggested that in areas with alternating dry and wet seasons food abundance for birds declines in the dry season, sometimes dramatically (section 3.1). This is consistent with patterns of insect abundance in tropical forests (see above). Because seasonal weather patterns (e.g., rainfall) in many tropical areas are very similar year-to-year, variation in food supplies for birds there might also be highly predictable (Fogden 1972). Food supplies for kagus might be predictably low each year in the driest months of September and October, and high in the wet season. This would be consistent with seasonal variation in kagu bodyweights at Pic Ningua and Mt Cindoa (section 3.3.11), and Yves and Henriette Létocart's observations (section 1.4) that kagus appeared to become satiated at times only in the wet season.

Apparently monogamous relationships like the kagu's are the commonest mating system in birds (Lack 1968). Emlen and Oring (1977) predicted that monogamous and evenly spaced breeding pairs should occur where resources are spatially uniform and sufficiently abundant in time, and where there is shared parental care. The spatial and temporal nature of kagu food resources was not well known, but from Emlen and Oring's theory I predicted they would be available year round and relatively evenly dispersed (section 1-6).

Avian diet studies often have two main aims: (1) to establish quantitatively what food an animal eats; and (2) to test some aspect of foraging theory to try and explain why an animal has a particular diet. Addressing the former presents logistical difficulties like the time involved, and biases towards 'hard-bodied' prey items in diets. This probably explains the lack of these types of studies in the literature (Rosenberg and Cooper 1990). One reason for addressing the second aim might be to see if an animal is attempting to efficiently exploit its food resources (Stephens and Krebs 1986). This could provide an insight into whether the animal's resources were scarce or abundant (Emlen 1966 1968, Klomp 1980). A factor which must be considered in 'optimality' studies is that a prey's abundance in the environment might not be closely correlated with its availability for its predator because of factors like habitat structure (e.g., background coloration; Kelly 1996) and prey defence techniques (e.g., cryptic and/or noxious prey; Shettleworth *et al.* 1993). A predator may also not use available prey in a random way because of differential preference for prey, which might be due to innate factors (Shettleworth *et al.* 1993), tradition (Galef and Allen 1995), frequency dependent preference for prey types (Krebs 1991), nutritional requirements (Pulliam 1975) or parasitism (Lozano 1991).

Environmentally-related (e.g., seasonal) variation in food abundance and type also must be considered when investigating diet selectivity (Emlen 1966).

Emlen (1966, 1968) predicted that an animal will move towards diet specialisation when food is abundant, and become less specialised when food is scarce. He suggested an animal may also specialise on a prey item because it is common even though it might be less profitable per item than other less abundant available items. Schoener (1971) predicted that increased energy needs (e.g., because of cold conditions) had the same effect on prey selectivity as variation in food abundance, so decreased selectivity could potentially occur with constant food supplies and increased energy needs (e.g., for moult). Reaction to increased energy needs and/or reduced food supplies could also be more efficient food assimilation and different foraging behaviour to increase the numbers of the same prey types caught (Schoener 1971), without potentially changing diet selectivity.

Although animals might not attempt to forage optimally (Krebs 1991), many studies suggest that they do (reviewed in Stephens and Krebs 1986), for example by taking larger, more profitable prey (e.g., Kelly 1996) and foraging in higher food density areas (Frey-Roos *et al.* 1995). Selection to forage efficiently might be strongest when food resources are scarce (Grant and Grant 1996, Rundle and Vamosi 1996), which for many tropical forest birds might be the driest periods of the dry season (see above). Therefore if kagus foraged according to theory (and taking into account their bodyweight variation; *Chapter 3*), they might be least selective in the driest months of September and October, and most selective in the wet season.

Diets of individuals could also be affected by trade-offs associated with factors like breeding activity (e.g., parents might feed larger prey to chicks), predation risk (e.g., Krebs 1980), competition (inter- and intraspecific) and specific nutritional requirements (Pulliam 1975). Most of my data came from non-breeding kagus, therefore any immediate demands from reproductive activity were minimal. It was possible that disturbance (my presence and the dog attacks) did influence diets of the birds who travelled widely on Pic Ningua compared to the diets they would have had if living on home ranges with partners. Predation risk was unlikely to have affected the choice of general foraging areas used by kagus when they lived on relatively small home ranges, as most of the kagus did at Mt Cindoa. Also, decisions about patch-use and the choice of prey should have been little affected by predation risk, or by intraspecific competition as kagus were generally solitary foragers. Potential interspecific competition from feral pigs and rats *Rattus* spp. (*Chapter 4*) may have affected kagu diets, but this would probably have affected most birds in an area similarly given the widespread presence of pig rooting. Nutritional requirements might result in partial preferences to give a balanced diet (Pulliam 1975), however there is some evidence that the amount of food or energy for birds' growth and self maintenance is of greater importance than specific nutrients (Brodmann and Bollmann 1997).

Parasitic nematodes cause mainly morbidity rather than direct mortality in red grouse *Lagopus lagopus scoticus* (Hudson *et al.* 1992, Dobson and Hudson 1994) and snowshoe hares *Lepus americanus* (Murray *et al.* 1997). Therefore important effects of high levels of infection might be reduced bodyweights, and changed foraging behaviour (Lozano 1991). The main parasite affecting kagus is the species-specific intestinal nematode *C. dorsalata* (Nematoda : Heterakidae) (Vassart 1988, Petter *et al.* 1988). Beugnet *et al.* (1995) reported large infestations of these parasites in three captive-bred juvenile kagus that died, but although wild birds can have large concentrations of *C. dorsalata* eggs in their faeces (*c.* 30,000 per g) no obvious adverse effects of the parasite on wild birds was known. Kagus also have a caecal-specific parasite *Brachylaima* sp., but it has been observed only infrequently in wild birds (Beugnet *et al.* 1995).

Feral pigs may potentially compete with kagus for food supplies, indirectly by rooting damage to the forest understorey and/or directly by eating the same prey (section 4.4.3). Therefore pigs might have an important effect on kagus especially when their food supplies are scarce. Hone (1988) found that the frequency of pig rooting was positively correlated with altitude, which may be related to the higher incidence of pig rooting in wetter areas (Hone 1995). Animals reported in stomach contents of feral pigs foraging in forest include Amphipoda, Blattidae, Chilopoda, Coleoptera, Diplopoda, Diptera larvae, Hemiptera, Lepidoptera, Orthoptera, Phasmatoidea, Reptilia (geckos), earthworms and snails (Thomson and Challies 1988, Pavlov *et al.* 1992), which are also taxa that kagus eat (section 1.4).

My specific aims were to (1) describe seasonal variation in kagu diet and *C. dorsalata* egg numbers at Pic Ningua and Mt Cindoa; (2) describe seasonal variation in kagu food supplies at Pic Ningua, Mt Cindoa and Parc Rivière Bleue; (3) identify periods of high and low food supplies; (4) try and establish if kagus foraged as theory predicted to efficiently exploit their food supplies in meeting their energy needs in response to changing environmental and physiological conditions; (5) investigate the potential for competition for food supplies between feral pigs and kagus; and (6) compare food supplies and kagu diet at Pic Ningua and Mt Cindoa with that at Parc Rivière Bleue.

Here, I use the definitions of prey abundance, availability and use of Johnson (1980), and summarized by Kelly (1996). Prey abundance is the number of prey in the environment. Prey availability is the portion of the abundance accessible to the predator. The portion of available prey eaten by the predator are the prey used.

5.2 Methods

5.2.1 Collecting kagu faecal samples at Pic Ningua and Mt Cindoa

Although kagus regurgitate pellets (Létocart 1989), mostly consisting of whole snail shells and hard body parts of large Carabidae (Y. Létocart pers. comm., pers. obs.), I rarely noticed them at roost sites, especially in the dry season. Therefore faecal analysis was required to investigate kagu diet as I did not plan to observe birds foraging. An advantage of this type of analysis was that relatively non-intrusive and repeated sampling from the same individuals could be carried out year-round (Rosenberg and Cooper 1990). Also, because I rarely disturbed birds during the day, my activities probably had only a minimal effect on birds' foraging behaviour.

When I located a kagu roost (section 3.2.8) I collected any fresh faecal material present, which was virtually always. As I generally found the roost of an individual bird every fortnight, I also collected a faecal sample (fresh faeces collected from one individual at one roost site) from it at similar frequencies. It was relatively straightforward to gather up a sample from the ground under a bird's perch or at its ground-roost site, and I often scraped faecal material from litter or substrate to obtain the maximum amount possible. Samples were often contaminated with the substrate (e.g., forest floor detritus) they were deposited on. At ground-roosts which had been used previously, I was careful to avoid contaminating the fresh sample with the remains of older deposits. I placed a faecal sample from an individual bird into a plastic 'zip-top' bag at the site, and froze it the same day. Before importing the faecal samples into New Zealand, I weighed (to 0.1 g on an electronic balance) the frozen samples then placed them into 95% alcohol in individual plastic containers. Samples were usually between 10 and 20 g in weight.

Before freezing a faecal sample on the day I collected it, I removed a small amount (1-2 g) for parasite analysis (section 5.2.2).

5.2.2 Analysis of parasites in faecal samples

Parasite analysis was carried out on faecal samples I collected at Pic Ningua and Mt Cindoa (section 5.2.1) by scientists at the Parasitology Laboratory of the Centre de Coopération International en Recherche pour le Développement (C.I.R.A.D.), New Caledonia (Beugnet *et al.* 1995, my and C.I.R.A.D.'s unpublished data). This work was instigated by Frédéric Beugnet, C.I.R.A.D.

Before freezing a fresh faecal sample, I removed 1-2 g and placed it in 100% formaldehyde. I gave samples to the C.I.R.A.D. laboratory weekly for analysis. The coproscopic methods used to quantify parasite egg numbers per gram were described in Beugnet *et al.* (1995), and accuracy was ± 50 eggs per gram. The eggs of several parasite species were recorded in the faecal samples (Beugnet *et al.* 1995), but I only present data here for *C. dorsalata*, whose eggs were by far the most common.

5.2.3 Sorting faecal samples and quantifying prey numbers

I analysed a subset of the faecal samples I collected at Pic Ningua by arbitrarily limiting the number of samples to be analysed from different birds in each interval to five, and from the same bird to one. This mostly only removed samples collected before the dog attacks began when the numbers of study birds I followed was over ten. The number of faecal samples I collected in each interval once the dog attacks began was usually five or fewer, but never less than two (no faecal samples were collected in interval 50 as I was absent from the field then). I analysed all samples I collected at Mt Cindoa because there were never more than four per interval.

I analysed each faecal sample separately because per-sample measures with their associated variances are recommended to describe a species' diet (Rosenberg and Cooper 1990). Before I sieved a faecal sample I carefully broke it up in alcohol by pressing it with the base of an approximately 3 cm diameter plastic container, after adding a small amount of dish washing detergent to help aid separation. Animals in samples were already well broken up so it was unlikely that I damaged animal parts by doing this, but rather separated them from the high percentage of soil in the sample. I then sieved the sample through four 70 mm diameter stacked sieves (mesh sizes from top to bottom were approximately 1.0, 0.5, 0.3 and 0.2 mm) with water. When the (frozen) weight of a faecal sample was over 20 g, I usually took an approximately 20 g subsample (I weighed subsamples to the nearest 0.01 g) to sieve and sort.

I sorted the contents of the 1.0 and 0.5 mm sieves separately in a petri dish with 8 mm parallel sorting lanes formed by thin strips of silica gel. I examined the material in batches when there was a large amount of it, sorting it under a 1.5 x 10 power binocular microscope lane by lane with the aid of tweezers. I separated out animal parts which I could later use to establish the presence and/or number of prey, and stored them separately in alcohol.

I did not sort through the contents of the 0.3 mm sieve as this material contained very few recognisable animal parts (I kept this material and returned it to the sample container with the 'discarded' sorted material for possible future use). For example, small parts like Isopoda, Diplopoda and Amphipoda mandibles were caught in the 0.5 mm sieve, and worm chaetae passed into the 0.2 mm sieve.

I took a subsample (*c.* 1.31 g) from the 0.2 mm sieve and counted worm chaetae in it. When the total weight of material in the sieve was less than 1.31 g, I recorded its weight and later calculated the relative number of chaetae present. I distributed the subsample as evenly as possible (in a small amount of alcohol) over a petri dish with 6.0 mm parallel lanes formed by thin strips of silica gel. I counted all earthworm chaetae I could see (without disturbing the contents after I began counting) under a 2.5 x 10 power binocular microscope. I found very few worm chaetae in the material I checked that passed through the 0.2 mm sieve.

I catalogued the animal parts I had sorted out from a faecal sample after I had sorted all samples. I formed a reference collection of different animal parts by taping them with clear tape onto white filing cards (Y. Létocart pers. comm.), and used this collection when identifying the prey the parts came from. I mostly used parts of animals from the pitfall trap reference collection (section 5.2.6) to establish which prey the parts on the faecal sample reference cards came from.

I quantified the minimum number of most of the prey in a faecal sample using a range of key body parts depending on the type of animal (Moreby 1987), as is usual practice in diet analysis of faecal samples from ground-feeding birds taking mostly invertebrate prey (e.g., Colbourne and Powlesland 1988, Itämies *et al.* 1996) (Table 5-1). I sometimes used a combination of body parts to determine the minimum number of prey eaten (Table 5-1) which resulted in non-integer values per sample (e.g., Amat 1986, Jenni *et al.* 1990). This method has been found to reduce bias compared to the use of integer values only and better estimates actual prey numbers (Jenni *et al.* 1990). With Blattidae, for example, if two mandibles (0.5 animals each) and seven tibia (0.17 animals each as all tibia were similar in shape) were counted in a sample, I recorded 1.17 prey. Front tibia for certain taxa (e.g., Carabidae, Scarabaeoidea) were readily distinguished from mid and hind tibia and counted as 0.5 animals when mandibles underestimated the numbers eaten. There needed to be in excess of two mid/hind tibia per one front tibia for the former to contribute (0.17 prey for each one) to prey numbers. For example, two front and five mid/hind tibia were also recorded as 1.17 prey. Because it was difficult or impossible, I did not quantify Arachnida other than Araneae, nor Diplopoda, Gastropoda (snails), Scincidae or Tipulidae pupae, but only recorded them as present or absent. Although I recorded Diplopoda mandibles, these were in a low percentage of samples compared to the presence of Diplopoda exoskeleton. Thus, as it was likely that I had failed to detect many of these difficult-to-see mandibles I did not quantify them. Amphipoda and Isopoda mandibles were similar in size to Diplopoda mandibles but easier to detect in samples, and the frequency of their other body parts suggested the mandibles were a reliable indication of actual numbers of these animals eaten.

To obtain a rough indication of the biomass of prey items in kagu diet, I used the average biomass for an individual (total biomass/total abundance) in taxa captured in the pitfall traps (see section 5.2.7). This underestimated the actual average biomass of individuals in at least some taxa in kagu diet (e.g., Curculionoidea, Hemiptera and larvae) because I knew by visually comparing sizes of body parts of these prey that kagus generally fed on larger animals than those that commonly fell into the traps. To present and analyse the diet data and make a comparison with the pitfall trap samples, I organised the data the same way as I did for the pitfall trap samples (sections 5.2.6 and 5.2.14). I needed three additional categories for diet data (unidentified adults and larvae, and Scarabaeoidea larvae) because I did not record them in the pitfall traps.

Table 5-1. Body parts used to quantify the main taxa in faecal samples (see text for more details on methods used to quantify prey).

Taxa	Body part(s) used to quantify prey
Amphipoda	mandible
Araneae	fang
Blattidae	mandible, tibia
Chilopoda	head/forcipules
Coleoptera	mandible/femur/tibia
Dermaptera	mandible, forceps
Diplopoda	mandible
Hemiptera	
Reduviidae	fore leg parts
Nymphs	head, eye, leg
Hymenoptera	
Formicidae	body section (head, thorax, abdomen)
Apoidea	tibia
Pompilidae	mandible
Isopoda	mandible
Larvae	mandible/head/complete larva/last segment
Neuroptera larvae	mandibula
Orthoptera	mandible
Phasmatoidea	mandible
Scincidae	vertebrae
Unidentified adult	mandible

5.2.4 Pitfall trapping for soil and litter fauna

Pic Ningua

I installed nine sets of pitfall traps at nine different sites in forest at Pic Ningua (Fig. 5-1). When choosing the sites on the north-facing slopes, I attempted to install each set of traps on the home range of a different kagu pair to see how food supplies varied spatially as well as temporally. As I did this at the beginning of my study, I selected sites based on only a limited knowledge of kagu home ranges.

At each pitfall trap site I installed ten traps in rows of 3-4-3 within a 10 m grid (Moeed and Meads 1985). Each row was approximately 3 m apart, as were traps within rows. For each individual trap, I dug in a 250 mm long x 100 mm diameter

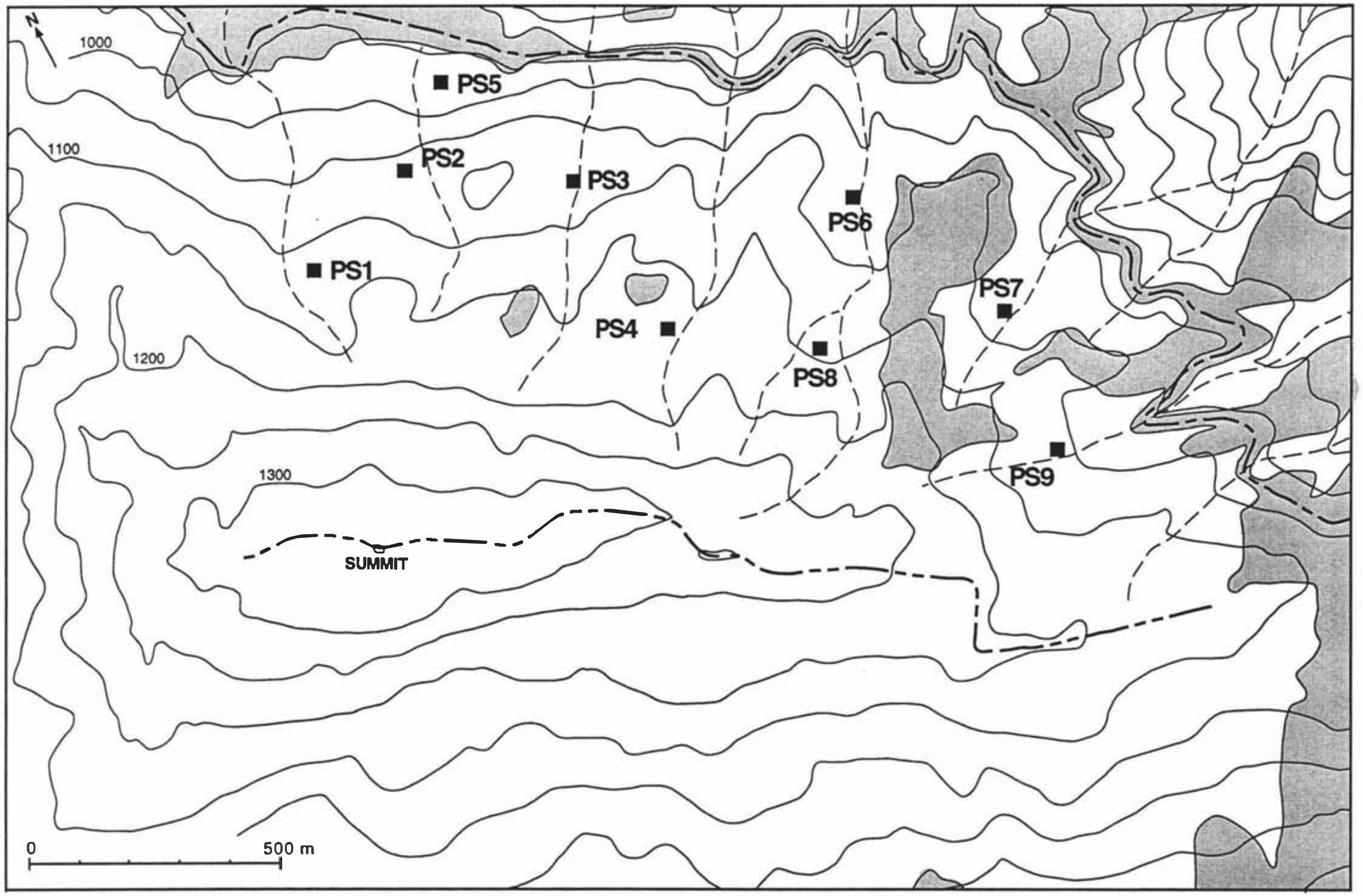


Figure 5-1. Positions (black squares) of nine pitfall trap sites (PS1 to PS9) at Pic Ningua. Key to map details is in Figure 3-1.

within rows. For each individual trap, I dug in a 250 mm long x 100 mm diameter PVC liner, the top of which was level with the ground. I did this at least ten days before installing the collecting containers (500 g white plastic yoghurt pots) to minimise possible 'digging-in' disturbance effects (Digweed *et al.* 1995). However, there was little visual evidence of disturbance to the ground after I installed a trap as I had placed soil on a plastic sheet and discarded any excess material outside the 10 m grid. The rim of the yoghurt container rested neatly on the exposed rim of the PVC liner. The inside diameter of the container was 94 mm, giving a total trap area for the ten traps at each site of 694 cm^2. I also drilled a group of nine 2 mm drain holes into the upper area of each container. I pegged a 150 x 150 mm plywood cover approximately 50 mm above each trap to keep rainfall and leaves out. The trap liquid (a mixture of ethylene glycol and 5% formaldehyde, J. Chazeau pers. comm.) was 15-20 mm deep.

I set the traps permanently from 25/1/93 (beginning of interval 1) to 19/3/95 (end of interval 56). I emptied the trap contents every fortnight almost always on the last day (Sunday) of each interval. On the few occasions that I could not empty the traps on this day I did so within a few days before or afterwards. When emptying a trap, I retained the material caught in a 1 mm sieve and put it immediately into 95% alcohol. I returned the drained liquid to the trap or replaced it if it had been diluted by rainwater or had deteriorated. Afterwards on the same day, I drained off the liquid in the samples and replaced it with fresh 95% alcohol before storing the samples. I combined all material caught at each site in each fortnight (a sample). I removed Scincidae from trap material and individually labelled them before storing them in 100% formaldehyde prior to their identification by Brian Gill (Auckland Institute and Museum).

Mt Cindoa

I permanently installed two sets of pitfall traps at Mt Cindoa (Fig. 3-2) (as per the methods above except that I set the traps on the day I installed them) during intervals 19-55. I emptied the traps once a fortnight. For logistical reasons, I usually emptied traps on the first day (Monday) of an interval, and the samples were recorded as being collected in the previous interval.

Parc Rivière Bleue

I permanently installed two sets of pitfall traps at Parc Rivière Bleue (Fig. 5-2) (as per the methods for Mt Cindoa) during intervals 26-56. I chose locations high enough to avoid the annual flooding that occurs along the creeks in the area after heavy rainfall (Y. Létocart pers. comm.). I emptied the traps once a fortnight, usually on the second-to-last day (Saturday) of an interval, and the samples were recorded as being collected in the same interval.

5.2.5 Description of pitfall trap sites

I described each pitfall trap site at the three study areas in four ways by (1) recording its altitude; (2) measuring the downhill slope; (3) measuring the basal area of trees (> 4 cm dbh) in a 10 m grid over the site; and (4) obtaining soil analysis on three 10 cm diameter x 10 cm deep soil samples taken across the centre of each site. I removed any surface litter before taking a soil sample. Soil analyses were carried out by the Territorial Soil Analysis Laboratory, Bourail, New Caledonia.

5.2.6 Sorting pitfall trap samples and identifying animals

Before sorting a pitfall trap sample I washed it with water over a 2 mm sieve. I kept any material (suspended in water) that passed through the sieve in case it was required for later use, although the animals were too small for potential kagu prey and amounted to only a fraction of the total animal biomass in the sample. I sorted the material caught in the sieve by eye on a clear plastic tray placed over a laminated sheet of 1 mm grid paper and counted each animal. I built up a reference collection of morphologically similar 'species' and used this to catalogue the animals in the samples.

Many of the animals in the reference collection were only identified in broad taxonomic categories, one exception being Coleoptera which were often identified to superfamily or family. I created three data sets for the presentation and analyses of the data at Pic Ningua. The first one contained as many taxonomic categories as possible to show the range of animals captured in pitfall traps and recorded in kagu faeces, but still only identified down to a minimum of family level. Then I collapsed these categories to 28 for presentation of each category in the text as a separate graph. All correlations between the numbers and dryweight biomass of animals at Pic

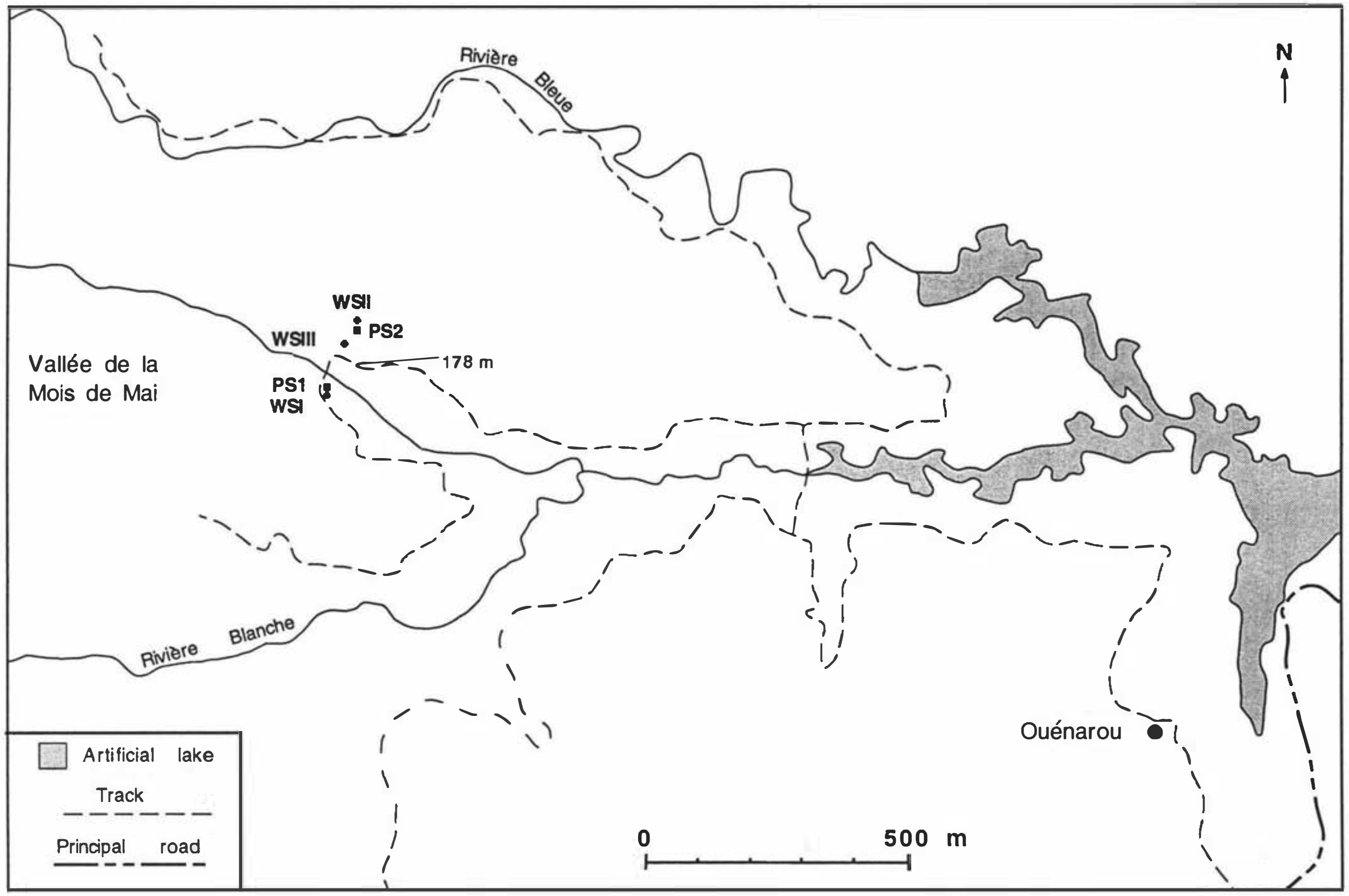


Figure 5-2. Positions of the two pitfall trap sites (PS1 and PS2, black squares) and three weather stations (WSI, WSII and WSIII, black crosses) at Parc Rivière Bleue. The park headquarters are situated at Ouénarou. To indicate the height (a.s.l.) of the pitfall trap sites, a 178 m reference point is arrowed.

Ningua for each of the 28 taxa in pitfall traps were significant (partly due to my methods for calculating biomass, section 5.2.7), therefore I only graphed data for animal numbers as faecal data were also presented this way (section 5.2.3). Finally, I collapsed the 28 categories into 15 for data analysis and to enable a comparison with diet data (method of selection of the 15 categories is in section 5.2.14). I presented the Mt Cindoa and Parc Rivière Bleue data in only one of these three data sets, graphs of the 28 categories.

5.2.7 Estimating animal dryweight biomass

I chose methods to estimate the total dryweight biomass of animals in pitfall traps which only involved the destruction of a very limited number of animals to conserve the valuable collection. The methods I used were (1) calculation of the average dryweight (mg) biomass of an individual in a morphological species after drying (at 60°C for 48 hrs to constant weights) and weighing (on electronic scales to the nearest 0.0001 g) a known number of animals. I only used this method for Amphipoda, common Gryllidae and 'dung beetles' (Scarabaeoidea: Hybosoridae and Scarabaeinae) because they occurred in relatively large numbers. I estimated the average dryweight of an individual of each of these three categories for each pitfall trap site. I did this by drying all the respective animals collected in the same four intervals (9, 25, 41 and 56). These four intervals covered a range of seasonal weather conditions; (2) I measured the body length (excluding appendages such as legs or antennae) of each individual of a morphological species and calculated its dryweight biomass using known weight-length relationships (Rogers *et al.* 1977, Gowing and Recher 1984) or those I calculated myself after drying and weighing a small number (sample sizes varied depending on the rarity of animals but were at least n = 5 individuals) of different sized animals. I calculated power, exponential and linear functions for each regression equation and chose the one that best fitted the data, which was almost always a power function; and (3) for certain morphological species which varied little in size I estimated the average dryweight biomass for individuals by measuring a subset (sample sizes varied) of them, then calculated dryweight biomass from known length-weight relationships or those I calculated myself (see above).

I used length-weight relationships for all invertebrates except snails (I recorded the greatest diameter of their shells) when calculating my own regression equations, and measured all animals by eye on the 1 mm grid sheet to the nearest millimetre. I used widest head width for estimating Scincidae dryweight biomass. I measured head width under a microscope fitted with a micrometer or obtained the measurements of those Scincidae I had deposited at the Auckland Institute and Museum from Brian Gill (measured with vernier callipers, B. Gill in litt.). I only had smaller Scincidae specimens from which to obtain dryweights and preferred not to use regression equations to estimate the biomass of larger animals deposited at the museum. I used 350 mg for the average dryweight of all individual Scincidae, which underestimated the actual average.

5.2.8 Effects of feral pig foraging on kagu food supplies at Pic Ningua

I used two methods to investigate the possibility that feral pigs in forest at Pic Ningua might be competing with kagus for prey. First, I compared the abundance and biomass captured in pitfall traps between sites little or not and highly disturbed by pig rooting. In the first year of emptying pitfall traps at Pic Ningua I noticed that sites were differentially disturbed by pig rooting, and that fewer animals tended to be captured at disturbed sites. To obtain a quantitative idea of the level of pig disturbance at pitfall trap sites, in intervals 29-56 I recorded fresh pig rooting within 1 m radius of individual pitfall traps when I emptied them each fortnight. During this period, I had placed pig exclosures (for an experiment not presented in this thesis) around five individual traps at four of the more disturbed sites (PS1, PS3, PS5 and PS6), therefore I only recorded pig rooting at the five traps outside the exclosures at these sites. Based on the record of pig disturbance in year two and my observations at sites in year one, I classified each pitfall trap site as highly, moderately or little or not disturbed by pig rooting.

Second, I carried out a qualitative analysis of the animals eaten by feral pigs at Pic Ningua. I collected pig faecal samples regularly in forest on the peak from 29/8/94 to 5/3/95. I did this as I walked through the forest in the course of my kagu research, and found most faecal samples on well used pig tracks. I only collected what looked like reasonably fresh faeces, although some samples may have been several weeks old.

I sieved samples individually and collected the contents caught between a 2.5 and a 1.5 mm sieve. I then separated out the hard animal parts that could be used to identify taxa and stored them in 95% alcohol in individually marked containers. I used my reference collection of animals captured in pitfall traps at Pic Ningua (section 5.2.6) to identify which taxa the separated-out parts came from. I also quantified where possible (methods as for kagu faecal samples, section 5.2.3) the total number of animals of each taxa in each sample.

5.2.9 Hand searching litter around pitfall trap sites

Pitfall trapping may not give an accurate indication of community composition for a number of reasons like biases in animals captured arising from differences between sexes, in activity patterns and in trap avoidance (Topping and Sunderland 1992). Therefore, I carried out hand searches of forest litter over one year to check if the pitfall trap samples represented the types of daytime animals present and to obtain an indication of what prey kagus might encounter in the litter. In intervals 1-26, I searched the litter for 30 minutes in an approximately 50 m radius around up to eight different pitfall trap sites [PS1 and PS3-9, sample sizes were $n = 8$ except in intervals 6, 9 and 25 ($n = 7$), and 1 and 20 ($n = 4$)]. I did not search within about 10 m of an individual pitfall trap. I pulled away a small area (*c.* 0.3 m^2) of litter without disturbing the soil underneath and caught by hand any arthropod except the numerous Amphipoda and Orthoptera. I did not turn over heavy objects such as rocks or dead wood to find animals as kagus were not known to do this. I also did not glean prey from substrates (e.g., tree trunks) above the forest floor which kagus were known to do (Létocart 1989). I immediately placed the captured animals in 95% alcohol, and then replaced the litter I pulled away. I also noted the numbers of Scincidae I saw under litter, but did not attempt to capture them. I counted, identified and categorised (using the pitfall trap reference collection) all captured animals.

5.2.10 Estimating worm activity

Earthworms were thought to be an important part of kagu diet at Parc Rivière Bleue (Létocart 1989). Pitfall traps were unlikely to give an accurate indication of worm activity in the top soil layer and thus the potential availability of these animals for kagus. To obtain more information, I estimated the level of activity of casting worms by counting their casts (this method did not detect activity of non-casting earthworms). I counted casts in three 700 mm diameter (1.16 m^2) circles around each of eight pitfall trap sites (PS1 and PS3-9) in forest (each circle was up to about 5 m from the nearest trap and outside the 10 m trap site grid). I determined the circumference of each circle within which I counted casts by using a 350 mm length of string placed around a permanent wooden reference peg which I had placed in the centre of the circle. I counted casts in intervals 27-56 at the eight trap sites on the day that I emptied the traps. I did not count small casts (< about 15 mm in diameter) as they were often difficult to distinguish from surrounding soil. After counting casts I smoothed over the soil within the circle. In conditions of moderate to heavy rain casts were generally destroyed, thus if rain fell the day before I counted them it probably lowered the relative number of casts recorded compared to records from intervals when no rain fell just before I counted casts. The effect of rain in this way was more likely over the wet season.

5.2.11 Soil moisture

I determined soil moisture at pitfall trap sites at Pic Ningua, Mt Cindoa and Parc Rivière Bleue by calculating percent H_2O saturation of soil I collected. At Pic Ningua in intervals 1-27, I collected soil fortnightly at most of the eight pitfall trap sites where I carried out litter searches [sample sizes were eight except in intervals 1 and 22 (n = 4), 27 (n = 5), 16 (n = 6) and 6, 19-20 and 25 (n = 7)] (section 5.2.9). Thus I collected soil throughout an interval. In intervals 28-56, I only collected soil at four pitfall trap sites (PS1, PS5 and PS8-9), and did this only on the day I emptied the traps (section 5.2.4). At Mt Cindoa and Parc Rivière Bleue, I collected soil at both of the pitfall trap sites at each area every fortnight, also when I emptied the traps.

A soil sample from each pitfall trap site consisted of two duplicate subsamples each made up of three 5 x 2.5 cm soil plugs. I placed each subsample in a zip-top plastic bag (collected subsamples averaged about 50 g). I weighed the subsamples on an electric balance to the nearest 0.1 g, up to five days later.

I calculated percent saturation in subsamples by first air-drying them indoors in their open plastic bags at Pic Ningua after recording their collected weights, then re-weighed them. I used this method because I did not have access to a drying oven, and although it would have resulted in some variation in dry weights in association with changes in weather it probably gave a reasonable indication of soil weights in very dry conditions. I then soaked the air-dried subsamples in water overnight, filtered off the excess water (by hanging the bags upside down and draining water off through a tissue paper wick) and recorded their saturated weights. I calculated percent saturation of each subsample [(collected weight - dry weight) x 100 / saturated weight - dry weight] then averaged the two figures to obtain percent saturation for a soil sample. My estimates of percent saturation for a soil sample probably underestimated that in natural conditions at Mt Cindoa (soil was less well established at the collection sites there and samples contained much organic matter) as some figures were more than 100%. When this occurred I adjusted percent saturation figures to equal 100%.

5.2.12 Meteorological data at Parc Rivière Bleue

I measured rainfall and temperature fortnightly (when I emptied pitfall traps) at Parc Rivière Bleue from the time I installed pitfall traps there (section 5.2.4) (Fig. 5-2). The temperature gauge (at PS1) was installed as per those at the other two study areas (3.2.3). PS1 had a sunny aspect and temperatures there would probably have been higher on average than those at PS2. I installed a raingauge (a 5-litre plastic container with a 92 mm collection funnel) to a free-standing stake at each trap site from interval 26 to 56, and one nearby on the ground outside the forest from interval 31 to 56.

5.2.13 Humidity at Pic Ningua

I measured average daily humidity in forest once a week on a hand-spun hygrometer at two sites (near PS5 and PS9, Fig. 5-1). I calculated average humidity for the day at each site from two readings (one in the early morning usually before 0800 hrs and one in the early afternoon usually between 1300-1400 hrs). I multiplied the two readings by constants (maximum x 0.63 and minimum x 0.37, supplied by the Nouméa Meteorological Service), then added them together to obtain the daily average humidity. I calculated the weekly percent humidity by averaging the readings from the two sites, then the mean percent humidity for each interval from the weekly averages. I estimated one mean weekly percent value in each of three intervals (3, 16, 22 and 27) because of rain or a broken hygrometer, and only recorded one mean weekly percent value in interval (50).

5.2.14 Analyses

I calculated mean *C. dorsalata* egg numbers in each interval for adult kagus using only one record per individual bird. When there was more than one record per individual in an interval, I averaged the values for individuals before calculating the mean for all birds in that interval.

The ('wet') weights of frozen faecal samples ranged from around 2 g to over 30 g, but were generally well above 10 g (Pic Ningua: mean weight = 15.43 g, s.e. = 0.389, n = 249; Mt Cindoa: mean weight = 16.73 g, s.e. = 0.661, n = 80). I standardized the data to account for this variation by adjusting the number of animals quantified in each faecal sample to values per 10 g. I did not simply use a 10 g subsample because it might have resulted in the loss of certain data, for example rare prey in faeces. All the faecal data presented here were based on the adjusted values, which underestimated the actual total numbers of animals I recorded as I mostly adjusted values downwards. I also standardized numbers of worm chaetae in samples to values per 1 g.

I organised pitfall trap and faecal data at Pic Ningua into the same 15 categories so a meaningful comparison between both data sets could be made (section 5.2.6). I only chose taxa for which individuals could be quantified in faecal samples (I excluded unidentified adults), but also tried to form the minimum number of categories which could adequately describe the data while still retaining the variation in the data. In preliminary analyses, homogeneity values across intervals (see below) were very similar between the same data set separated into 15 and 25 categories, therefore I used 15 categories. I chose the 15 categories mostly because they were numerically the main groups which kagu used. The 'Other adult' category consisted of Neuroptera (very rare in samples), and Isopoda and Hymenoptera adults which had similar distributions. Orthoptera species were mostly Gryllidae with small numbers of Tetrigoidea and Stenopelmatidae. I kept separate those Coleoptera families which were relatively common in kagu diet and/or pitfall trap samples (Carabidae, Curculionoidea, Melolonthinae and Hybosoridae/Scarabaeinae), and combined the rest in Other Coleoptera. I combined all larvae into one category. Kagus ate high percentages of litter and/or soil dwelling larvae at certain times of the year, but these animals were few in pitfall traps. Therefore I also examined diet data without larvae, adjusting percent occurrence calculations for the lower number of total animals present where necessary. I only separated the Pic Ningua pitfall trap (n = 9 sites) and faecal (n = or > 2) data into the 15 categories for statistical analyses because only sample sizes for these data were adequate within intervals.

To compare seasonal variation in animal numbers and dryweight biomass between study areas, I calculated the wet-season-peak/dry-season-low ratios (Bell 1985) for these two variables at each area. I used only the maximum and minimum values in intervals 27-55, but did not use interval 26 (although I collected data at the three areas in this interval) because this was the first data collection period at Parc Rivière Bleue and I always captured proportionally more Scincidae in traps when I first set them. To get an indication of how species diversity changed over time at Pic Ningua in the pitfall traps, I calculated the total numbers of morphological 'species' in intervals in all traps (n = 90) in most of the 28 categories (section 5.2.6) (I only counted one life stage for a taxa and chose the one that kagus used most, for example I used Diptera larvae but not Diptera adults, and I excluded Acari). Numbers of morphological species would have considerably underestimated the actual numbers of species present in the samples. For example, I counted all animals in both Blattidae and Araneae as only one 'species'.

Because samples sizes for the number of pig faecal samples and the numbers of animals quantified per sample were small, I only present the taxa I identified as percent occurrence data in samples and give the total numbers of animals quantified in each taxa.

I used two main analyses on faecal and pitfall trap data in intervals using the 15 categories (or 14 for diet data without larvae). First, I looked at the homogeneity of diet and pitfall trap data across the 15 categories in intervals. To measure this I chose the Shannon-Wiener diversity index (Magurran 1988)

$$H' = -\sum p_i \ln p_i$$

(where p_i is the proportion of the i^{th} taxa category). Although H' has received criticism as a species diversity index, it has the advantages of taking into account both richness and evenness and, because *H'* values for a number of samples are normally distributed, parametric tests can be used for significance testing (Magurran 1988, Luo *et al.* 1994). Here, I used *H'* as a measure of homogeneity across percent-occurrence categories (recently used this way by Luo *et al.* 1994). Because I used the same categories for both pitfall trap and diet data, I also made a qualitative comparison of *H'* values in intervals between the two data sets by graphing them together. I calculated *H'* for individual trap sites and faecal samples then calculated the mean and standard error for each interval for both data sets. I also calculated a multivariate coefficient of variation (*CVp*) (Van Valen 1978)

$$CVp = \sqrt{}(\Sigma s_j^2 \,/\, \Sigma x_j^2)$$

(where s_j^2 and x_j^2 were the variance and mean for the j^{th} category within each interval) for both data sets for each interval. For *CVp,* I first calculated the mean and standard deviation for individual taxa (using percent occurrence data) for both the pitfall trap and faecal data in each interval. I then calculated the *CVp* value for each interval for both data sets. I used the *CVp* values to see how variation in homogeneity arose. For example, did high diet homogeneity result from all kagus using a wide range of categories or by different individuals using different sets of categories (Kincaid and Cameron 1982)?

Second, as the diet and pitfall data were in two-way contingency table format (intervals x categories), I used correspondence analyses (SAS CORRESP procedure) as an exploratory tool (Greenacre 1981) to look for patterns in these data. I carried out two analyses on the frequency of animals in the 15 categories (columns) in each interval (rows): one analysis for faecal samples and one for pitfall trap data. I produced two plots for each analysis to avoid overlapping data points: one positioned the intervals, and one positioned the 15 categories.

I used repeated measures ANOVA (SAS GLM procedure) (additional details in section 3.2.9) to test for between- and within-subject effects and interactions between these two types of effects for abundance, biomass and homogeneity in pitfall trap samples. I first tested to see if these data were approximately normally distributed using SAS UNIVARIATE procedure, and log-transformed data where necessary to achieve approximate normality. I could not use repeated measures ANOVA on diet data in intervals as the same individual kagus were not sampled in each interval, although the data were still time series.

5.3 Results

5.3.1 Environmental conditions

Humidity in forest at Pic Ningua was usually above 80%, dropping below this level in the drier months of the dry season (Fig. 5-3) in each year, and in the wet season in 1994 when conditions became dry between the passage of two cyclones (Fig. 5-3).

Soil moisture at Pic Ningua (Fig. 5-3), Mt Cindoa (Fig. 5-4) and Parc Rivière Bleue (Fig. 5-5) showed a general positive association with rainfall. Soils at all sites were very dry by the end (late October) of the extended dry period in 1994, dropping to below 20% before rain fell in early November (interval 47). I observed fronds on ferns and leaves on juvenile trees wilting in late October 1994, a phenomenon which has been reported before in a tropical forest (Longman and Jeník 1987).

Fortnightly maximum air temperatures in forest at Parc Rivière Bleue were almost always several degrees or more above those at Pic Ningua (Fig. 5-6), and approached 32°C in 1994. Minimum air temperatures in forest at the Parc were usually about 2°C or more above those at Pic Ningua, but fell to similar levels of around 4°C in late July/early August 1994. Winter minimums at the Parc in August 1994 were some of the lowest recorded there, for example the lowest mean monthly minimum temperature recorded in forest in the upper Rivière Bleue valley (160 m a.s.l., Fig. 5-2) from November 1986 to September 1987 was 11.7°C in September (Bonnet de Larbogne *et al.* 1991). Bonnet de Larbogne *et al's.* site though, was in a well forested area along the river whereas my site was in a sunny aspect surrounded by open shrubland.

Rainfall at Parc Rivière Bleue (Fig. 5-5) had a similar seasonal distribution to that at Pic Ningua and Mt Cindoa (Figs. 3-3 and 3-4). In intervals 31-55 (a 50 week period), I recorded 1,568 mm of rainfall outside forest (WSIII) at the Parc, which was intermediate between that recorded over the same period at Pic Ningua (917 mm) and Mt Cindoa (2,181 mm). The annual average rainfall at the Parc in the upper Rivière Bleue valley (see above) for the period 1975-1987 was 3,181 mm (Bonnet de Larbogne *et al.* 1991). Rainfall in intervals 31-55 at the three study areas was highly

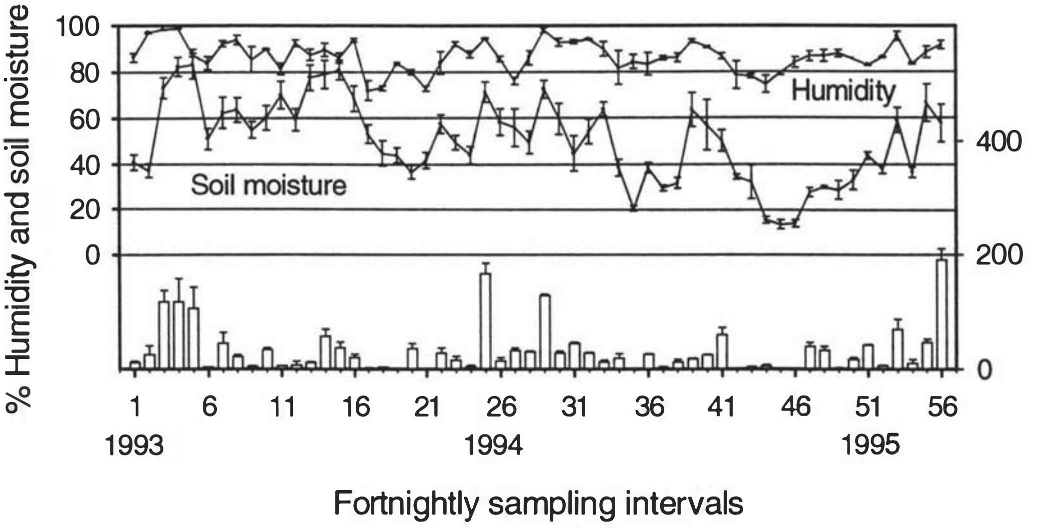


Figure 5-3. Humidity (top line), soil moisture (lower line) and rainfall in forest (unfilled bars) at Pic Ningua for intervals 1-56. N = 2 for all humidity means except in interval 50 when n = 1. Sample sizes for soil moisture are in section 5.2.11 (error bars on lines ± 1 s.e. and on bars = 1 s.e.). Rainfall data (see Fig. 3-3) are given here again for comparison with humidity and soil moisture.

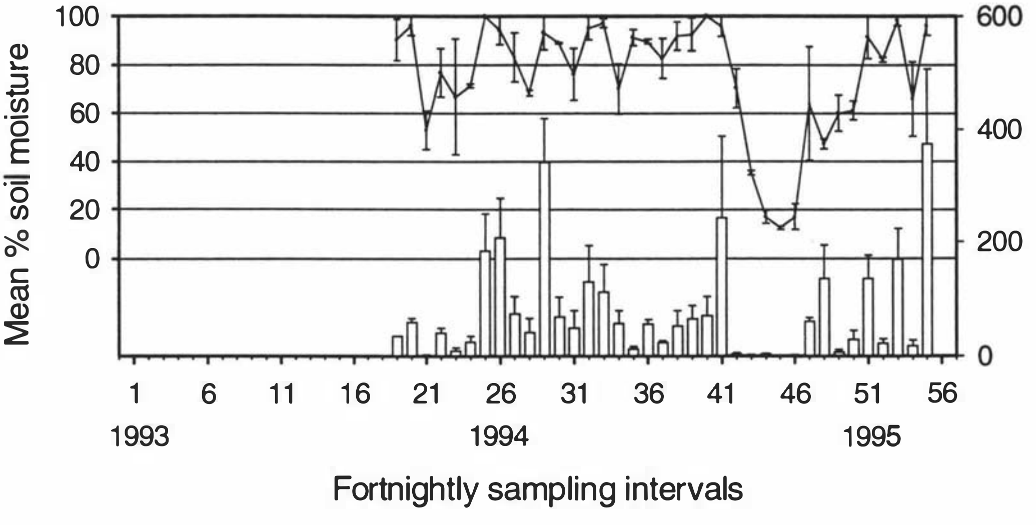


Figure 5-4. Soil moisture (line) and rainfall in forest (unfilled bars) at Mt Cindoa for intervals 19-55. Rainfall data (see *Chapter 3*) are given here again for comparison with soil moisture. N = 2 for soil moisture means; error bars on lines ± 1 s.e. and on bars = 1 s.e..

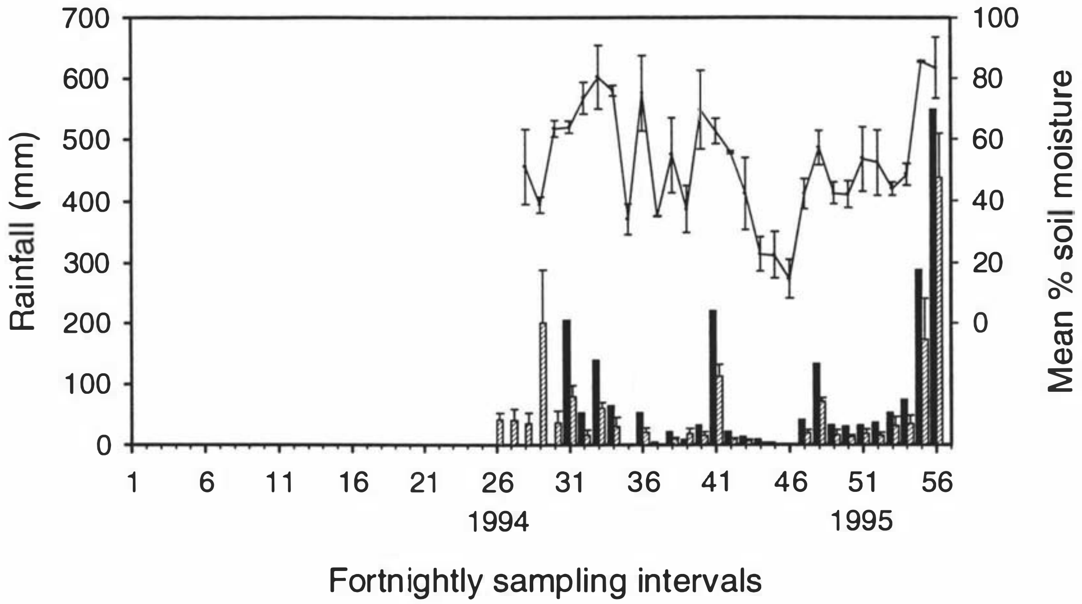


Figure 5-5. Soil moisture (line, intervals 28-56) and rainfall (bars) at Parc Rivière Bleue (n = 2 for all means; error bars on line ± 1 s.e. and on bars = 1 s.e.). Hatched bars (intervals 26-56) give mean rainfall at the two forest weather stations (WSI and WSII), and the black bars (intervals 31-56) the rainfall outside forest (WSIII).

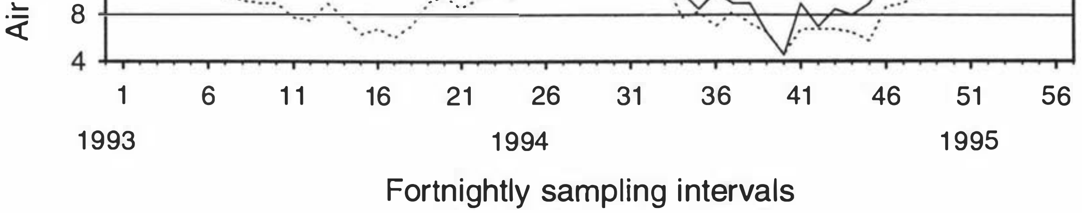


Figure 5-6. Absolute maximum and minimum air temperature (continuous lines) in forest at Parc Rivière Bleue (WSI) in intervals 26-56. Absolute maximum and minimum air temperature in forest at Pic Ningua (dashed lines) (see Fig. 3-7) are also graphed for comparison.

correlated (Spearman correlation coefficients: Pic Ningua and Mt Cindoa, $r = 0.89$; Pic Ningua and Parc Rivière Bleue, $r = 0.74$; Mt Cindoa and Parc Rivière Bleue, $r = 0.73$; $n = 25$, $p < 0.0001$).

5.3.2 *Cagourakis dorsalata* egg numbers in kagu faeces

Mean numbers of *C. dorsalata* eggs in kagu faeces were generally highest in warmer months of the year at Pic Ningua (Fig. 5-7), especially so in interval 35 (21,150 eggs per gram in late May 1994, $n = 2$). Although the sample size was low in interval 35, relatively high egg numbers were also recorded at Mt Cindoa at about the same time in interval 36 (20,750 eggs per gram, $n = 2$), where sample sizes of two were common. The seasonal pattern of variation in egg numbers at Mt Cindoa was mixed, and probably influenced by the very low sample sizes. However, *C. dorsalata* egg numbers in intervals there were generally much lower than recorded at Pic Ningua. Interestingly, *C. dorsalata* adults were relatively numerous in the faeces I collected from very thin bird 205 (section 3.3.11).

Avian nematodes like *C. dorsalata* often require one or more external hosts at some stage in their life cycles (Rausch 1983). At Pic Ningua, *C. dorsalata* egg numbers appeared to be more common in faeces in warm, wet conditions. To see what prey may be significantly associated with *C. dorsalata* egg numbers at Pic Ningua, I tested for correlations between *C. dorsalata* egg numbers and 25 taxa in kagu faeces at Pic Ningua (see Fig. 5-8) to see what taxa might be potential external hosts. There were two significant positive correlations (Spearman correlation coefficients, $p < 0.05$, $n = 48$, intervals with sample sizes < 3 excluded): with Carabidae ($r = 0.50$) and Oligochaeta (chaetae numbers, $r = 0.52$).

5.3.3 Characteristics of pitfall trap sites

Pitfall trap sites varied noticeably in certain of the measured characteristics (Table 5-2), for example in pH and % organic carbon values. These values were generally lower and higher, respectively, than those found on an ultrabasic mountain in Malaysia (Leakey and Proctor 1987). Sites in my study not noticeably disturbed by pig rooting generally had low pH values. Exceptions were PS2 and PS4 (Pic Ningua) and PS2 (Parc Rivière Bleue), which had either relatively steep slopes where litter tended to be shifted downhill leaving soil exposed or were on quite flat terrain where

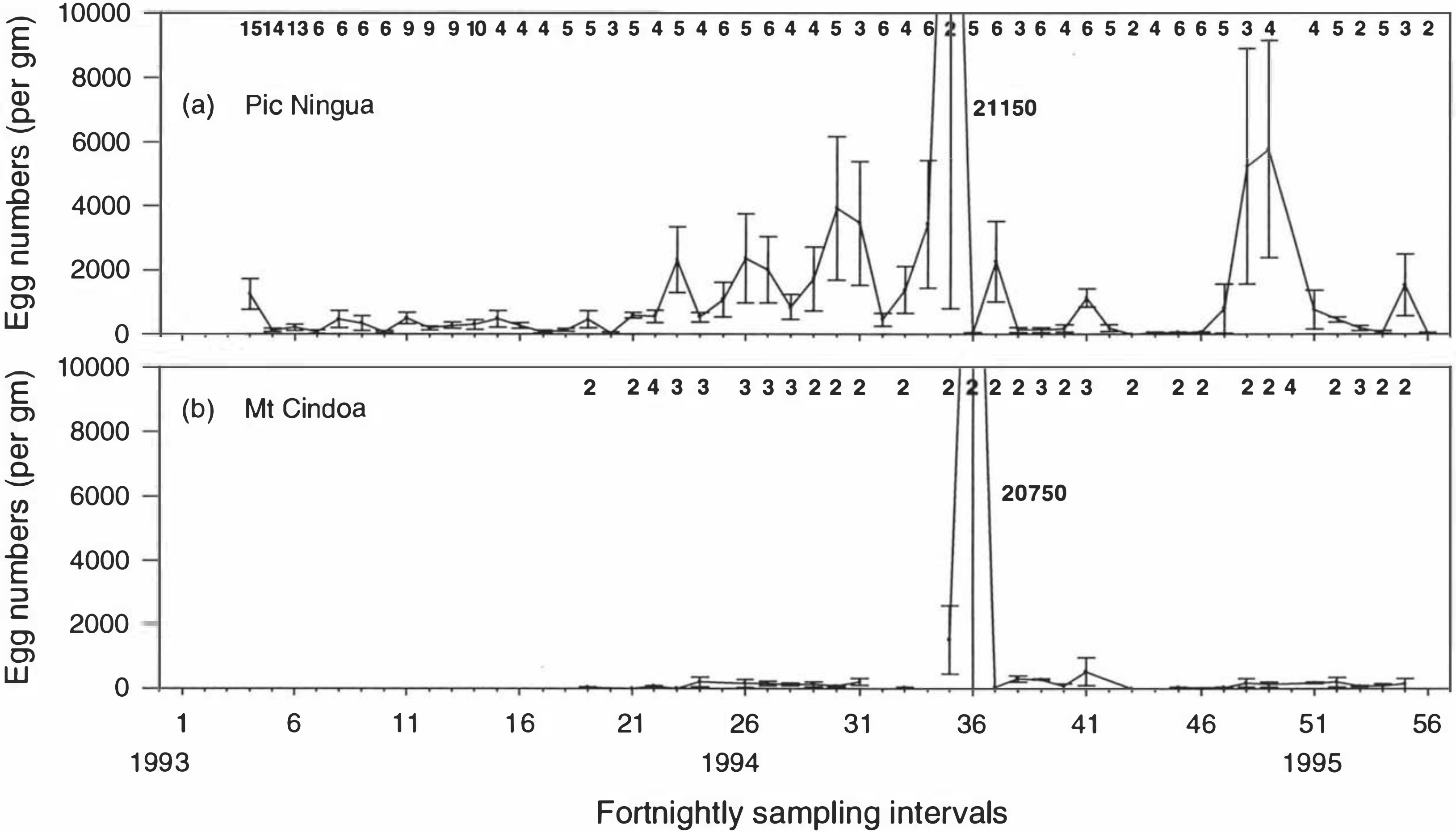


Figure 5-7. *Cagourakis dorsalata* egg numbers per gram (accuracy ± 50 eggs) in faecal samples collected from kagus at Pic Ningua (a) and Mt Cindoa (b). One data point on each graph is outside the range of the y-axis (their values are shown on the graphs). No data were collected at Pic Ningua in intervals 1-3 and 50, nor at Mt Cindoa in intervals 1-18, 32, 34, 44, 50 and 56. Sample sizes (numbers of faecal samples from different birds) are along the top of each graph. Error bars ± 1 s.e..

Table 5-2. Characteristics of the 13 pitfall trap sites at Pic Ningua (PS1-PS9), Mt. Cindoa (PS1-PS2), and Parc Rivière Bleue (PS1-PS2). Column 3 gives the down-hill slope over the 10 m² grid at each trap site. Column 4 gives the basal area of all trees > 4 cm dbh within the 10 m² grid centred over each trap site. The much higher basal area for PS2 at Mt Cindoa was due to three large trees within the grid. Columns 5-12 give results of the soil analyses for each site. A '**' in column 1 indicates sites that received high damage from pig rooting, '*'= moderate damage, and no asterisk = little or no damage.

Site No.	Altitude (m)	Slope	Basal area (cm²)	pH (H_2O)	Organic carbon (%)	Nickel (mg / 100g)	Exchangeable bases				Mg/Ca
							Ca	Mg	Na	K	
							(meq / 100 g)				
Pic Ningua											
**PS1	1120	16°	8889	4.2	89.31	10	3.02	5.06	0.20	0.06	1.68
PS2	1070	25°	5407	5.0	42.64	50	1.13	6.65	0.13	0.11	5.90
**PS3	1080	<5°	3996	5.3	70.18	60	6.24	12.59	0.27	0.16	2.02
*PS4	1170	6°	2894	4.8	56.52	30	2.23	1.58	0.00	0.00	0.71
**PS5	970	12°	7018	6.0	84.95	40	13.83	8.73	0.09	0.14	0.63
*PS6	1065	12°	4929	5.0	81.37	80	4.18	7.62	0.25	0.09	1.82
PS7	1080	17°	9180	3.6	135.37	20	1.37	4.50	0.33	0.11	3.29
PS8	1145	14°	7300	3.2	497.72	10	2.62	12.37	0.93	0.31	4.72
PS9	1110	20°	3481	3.6	68.30	10	0.43	2.84	0.14	0.08	6.58
Mt Cindoa											
PS1	1110	23°	4474	3.7	379.69	0	7.52	20.74	1.42	0.00	2.76
PS2	1160	23°	15960	4.0	176.26	0	2.01	3.98	0.36	0.16	1.98
Parc Rivière Bleue											
PS1	180	11°	6718	3.9	153.14	10	1.28	3.83	0.48	0.11	3.00
PS2	250	21°	5831	5.1	65.38	30	4.95	4.97	0.19	0.03	1.00

trees were sparse (PS4). Highest % organic carbon values tended to occur at sites with low pH, and both sites at Mt Cindoa had high values. Interestingly, nickel occurred in soil at all sites except at Mt Cindoa, and PS4 at Pic Ningua generally had the lowest concentrations of exchangeable bases. The Mg/Ca quotients were in a similar range to those recorded on ultrabasic mountains in Malaysia and the Philippines, and therefore were also of potentially toxic chemistry (Leakey and Proctor 1987, Thomas and Proctor 1997). Also, calcium-poor soils might be a problem for breeding female birds (e.g., for egg formation) if calcium-rich material like snail shells are unavailable (Graveland and Drent 1997).

5.3.4 Type and availability of potential food supplies for kagus at Pic Ningua

A wide range of taxa made up the 171,900 animals I captured in pitfall traps at Pic Ningua over the 112 weeks of data collection there (Table 5-3). Scincidae were the only non-arthropod animals captured. Amphipoda were the most numerous organisms, followed by Gryllidae, Scarabaeinae/Hybosoridae and Araneae. These four categories accounted for over 85% of all animals captured.

There was strong seasonality in numbers for many of the 28 taxa in Figure 5-8, for example Amphipoda, Carabidae, Dermaptera, Melolonthinae, Orthoptera and Scarabaeinae/Hybosoridae. Numbers of animals for these taxa were highest in traps in the wet season, and lowest in the driest months (September-October) of the dry season. Similar but moderate seasonality occurred for Chilopoda, Araneae, Curculionoidea, Phasmatoidea, Other adults (Isopoda and Neuroptera) and Athoracophoridae. Coleoptera larvae also showed a seasonal distribution similar to most adult Coleoptera. In contrast, Diptera larvae were mostly present after March up until late August, but Diptera adults were most common in the wet season.

Table 5-3. Total numbers and percentages of animals for taxa recorded in pitfall traps (n = 90) and faecal samples (n = 249) collected at Pic Ningua from 25/1/93 to 19/3/95 (two faecal samples collected on 21/3/95 are included). Numbers of animals in faecal samples are adjusted to numbers per 10 g (section 5.2.14). A '----' indicates no taxa were recorded. Percent data do not add up to 100 because of rounding.

Taxa	**Pitfall traps**		**Faecal samples**		**F / P**
	No.	**%**	**No.**	**%**	**% ratio**
Amphipoda	108,103	62.89	90.46	2.64	0.04
Arachnida					
Acari	148	0.09	----	----	
Amblypygi	3	0.002	presence only		
Araneae	6,535	3.80	142.35	4.15	1.1
Pseudoscorpion	7	0.004	----	----	
Triaeononychiidae	20	0.01	presence only		
Blattidae	1,632	0.95	255.45	7.45	7.8
Chilopoda	341	0.20	133.07	3.88	19.4
Coleoptera					
Bhyrridae	1	0.001	----	----	
Carabidae	1,612	0.94	207.74	6.06	6.4
Cerambycidae	19	0.01	36.58	1.07	107.0
Chrysomelidae	54	0.03	10.20	0.30	10.0
Cleroidea	136	0.08	----	----	
Curculionoidea	493	0.29	147.40	4.30	14.8
Elateridae	55	0.03	0.37	0.01	0.3
Lampyridae	1	0.001	----	----	
Lucanidae/Passalidae	3	0.002	20.29	0.59	295.0
Melolonthinae	272	0.16	167.17	4.88	30.5
Scarabaeoidea larvae	----	----	264.17	7.70	
Unknown Coleoptera	63	0.04	----	----	
Other Coleopt. larvae	359	0.21	261.14	7.62	36.3
Pselaphidae	37	0.02	----	----	
Scarabaeinae/Hybosorid.	14,883	8.66	31.09	0.91	0.1
Staphylinidae	926	0.54	38.63	1.13	2.1
Tenebrionoidea	267	0.16	5.25	0.15	0.9
Dermaptera	929	0.54	98.46	2.87	5.3
Diplopoda	1,146	0.67	presence only		

Table 5-3 continued next page.

Table 5-3 continued.

Diptera					
Adult	1,626	0.95	----	----	
Other Diptera larvae	593	0.35	787.81	22.98	65.7
Tipulidae larvae	94	0.05	320.41	9.34	186.8
Tipulidae pupae	3	0.002	presence only		
Gastropoda					
Snails	439	0.26	presence only		
Athoracophoridae	73	0.04	----	----	
Hemiptera					
Coccoidea	555	0.32	----	----	
Homoptera/ Heteroptera nymphs	1,918	1.12	46.83	1.37	1.2
Reduviidae	6	0.003	10.69	0.31	103.3
Hymenoptera					
Other adults	2,641	1.54	----	----	
Apoidea	24	0.01	0.49	0.01	1.0
Formicidae	2,951	1.72	47.44	1.38	0.8
Pompilidae	114	0.07	0.39	0.01	0.1
Isopoda	3,058	1.78	5.67	0.17	0.1
Lepidoptera					
Adult	520	0.30	----	----	
Larvae	1,411	0.82	----	----	
Neuroptera					
Adult	1	0.001	----	----	
Larvae	7	0.004	1.01	0.03	7.5
Oligochaeta	149	0.09	only chaetae recorded		
Orthoptera					
Gryllidae	17,015	9.90	156.15	4.55	0.5
Stenopelmatidae	10	0.01	6.42	0.19	19.0
Tetrigoidea	165	0.10	12.87	0.38	3.8
Phasmatoidea	158	0.09	29.41	0.86	9.6
Scincidae	123	0.07	presence only		
Thysanura	108	0.06	----	----	
Turbellaria	93	0.05	----	----	
Unidentified adults	----	----	18.92	0.55	
Unidentified larvae	----	----	74.66	2.18	
	171,900	100.00	3,428.99	100.00	

Figure 5-8. Graphs showing the temporal distribution of animals captured in pitfall traps at three study areas (Pic Ningua, Mt Cindoa and Parc Rivière Bleue) or recorded in kagu faeces (at Pic Ningua and Mt Cindoa). Pitfall trap data are always graphed in bar format (Pic Ningua: intervals 1-56; Mt Cindoa: intervals 19-55; Parc Rivière Bleue: intervals 26-56). Faecal data (Pic Ningua: intervals 1-49 and 51-56; Mt Cindoa: intervals 19-31, 33, 35-41, 43, 45-49 and 51-55) are graphed in line format or as bars [presence data for Diplopoda, Gastropoda (snails), Other Arachnida, Scincidae and Tipulidae pupae]. Lines graphing faecal data are continuous for ease of viewing, but no error bars are present where data were not collected. Presence data for the five taxa are mean occurrences, for example a 50% value indicates that a taxon was present in half the samples. Animals in Other adults category (Isopoda and Neuroptera) were virtually all Isopoda. The legend for each page is located above the top graph. For pitfall trap data, n = 9 at Pic Ningua and n = 2 at the other two study areas. Sample sizes for faecal data are in Figure 5-14. Error bars on lines ± 1 s.e., and on bars = 1 s.e.. A list of the graphed taxa in order of appearance follows, along with Spearman correlation coefficients for the association between the pitfall trap and faecal data at Pic Ningua. ('*' = $p < 0.05$, n = 55; '----' = no data).

Taxa	Correlation coefficient
Amphipoda	-0.19
Araneae	-0.09
Blattidae	-0.69*
Chilopoda	-0.17
Carabidae	0.65*
Curculionoidea	0.01
Dermaptera	-0.17
Tipulidae pupae	----
Diptera	----
Diplopoda	0.18
Snails	0.28*
Hemiptera	-0.18
Hymenoptera	-0.01
Lepidoptera larvae	----
Lepidoptera	----
Other Arachnida	-0.00
Coleoptera larvae	-0.27*
Diptera larvae	0.07
Melolonthinae	0.62*
Other Coleoptera	0.29*
Oligochaeta	-0.20
Scincidae	0.02
Orthoptera	0.14
Phasmatoidea	0.01
Scarabaeinae/Hybosoridae	0.24
Other adults	-0.22
Athoracophoridae	----
Turbellaria	----
Thysanura	----
Unidentified adults	----
Unidentified larvae	----

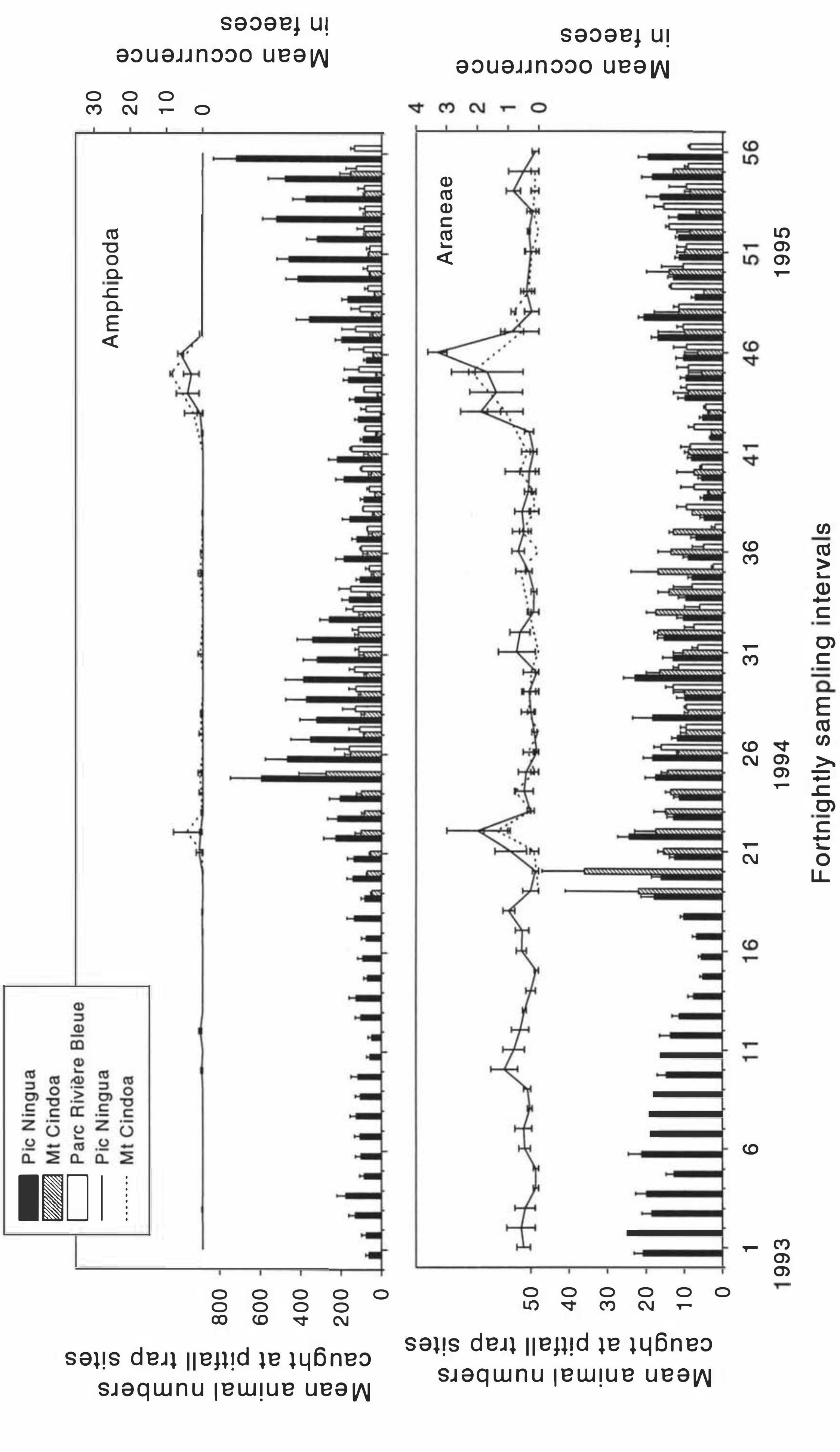
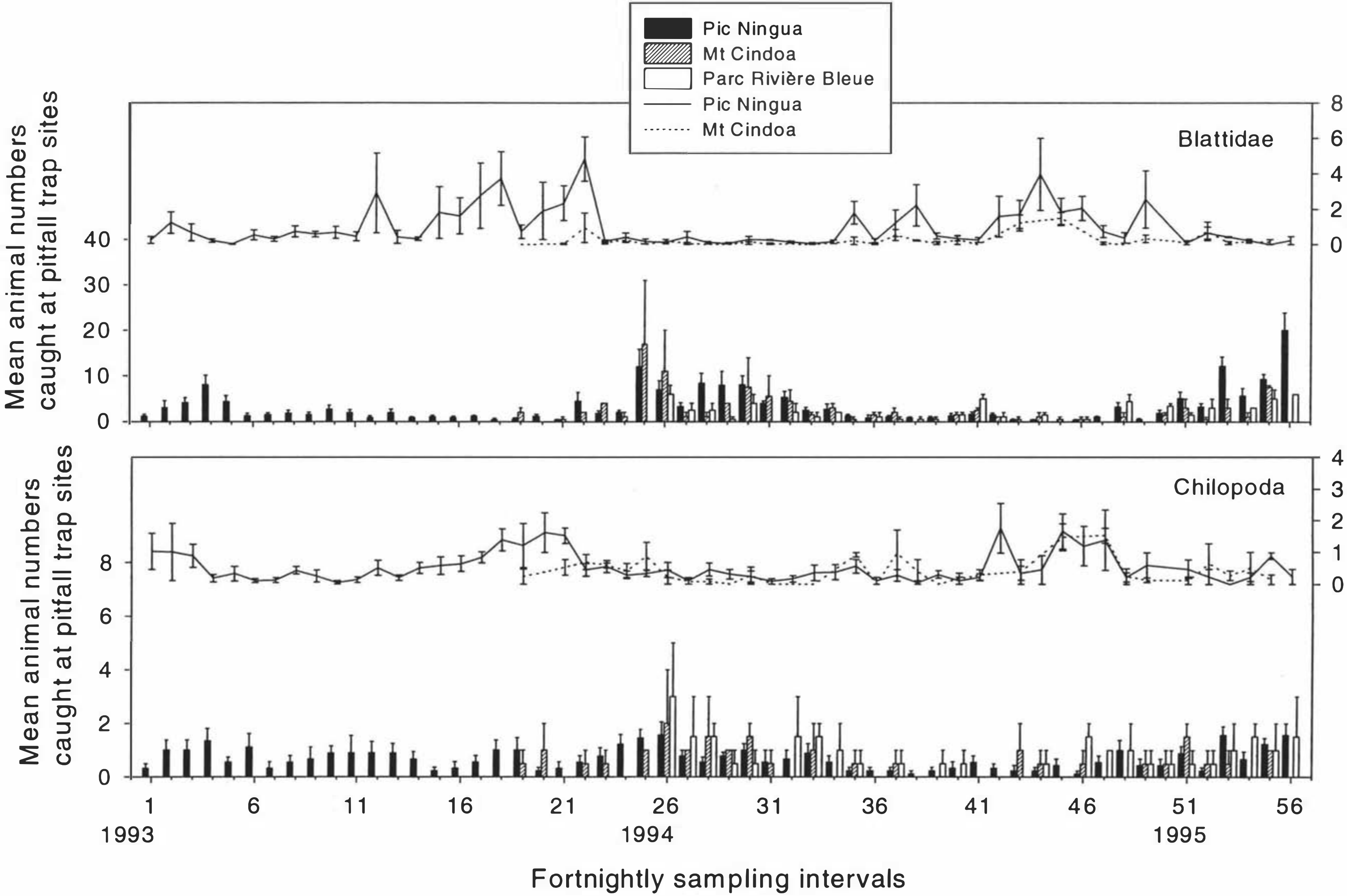

Pic Ningua
Mt Cindoa
Parc Rivière Bleue
Pic Ningua
Mt Cindoa
Amphipoda
Araneae
Mean animal numbers caught at pitfall trap sites
Mean occurrence in faeces
800
600
400
200
0
30
20
10
0
50
40
30
20
10
0
4
3
2
1
0
1
6
11
16
21
26
31
36
41
46
51
56
1993
1994
1995
Fortnightly sampling intervals

Figure 5-8 continued.



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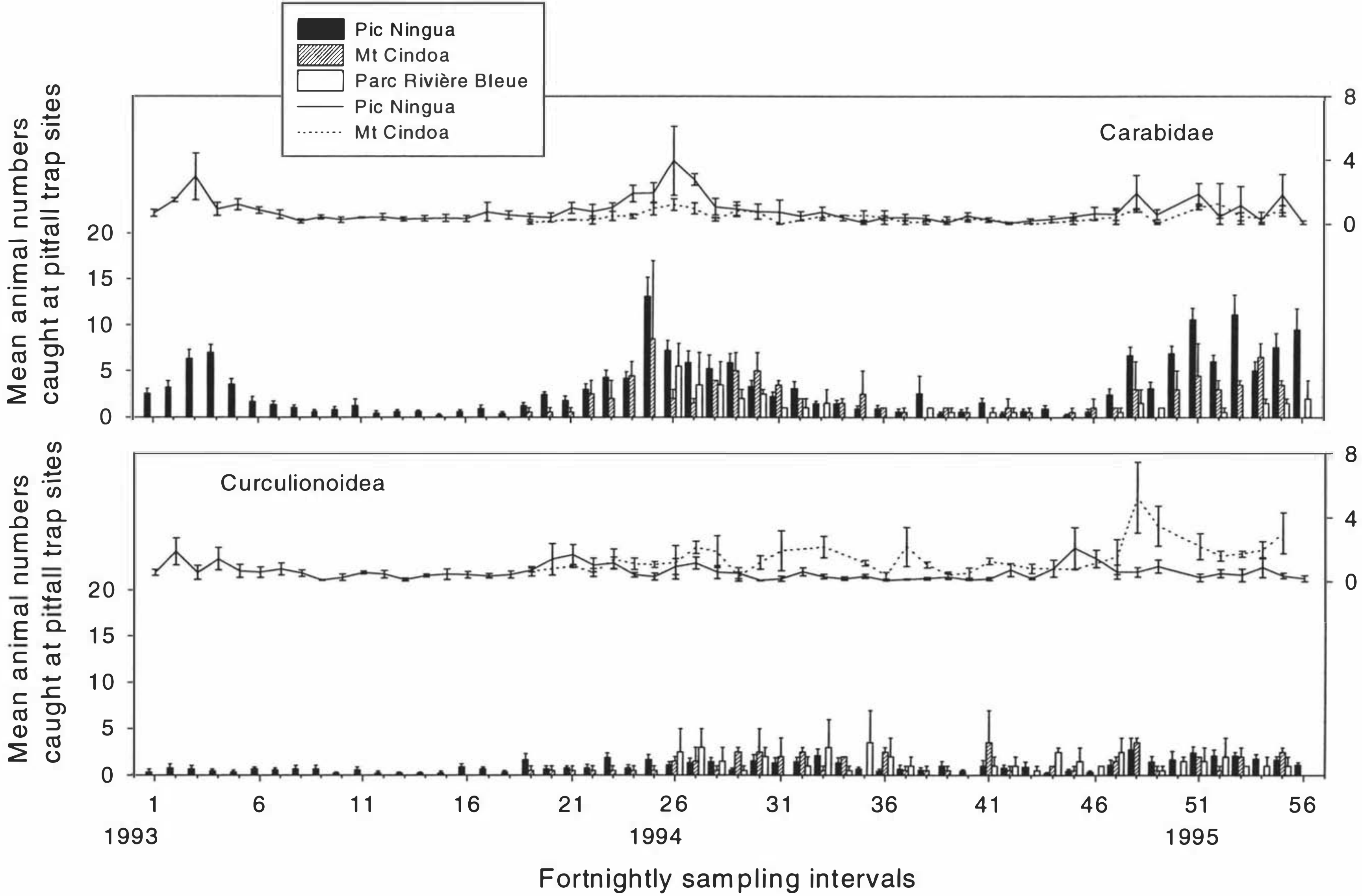

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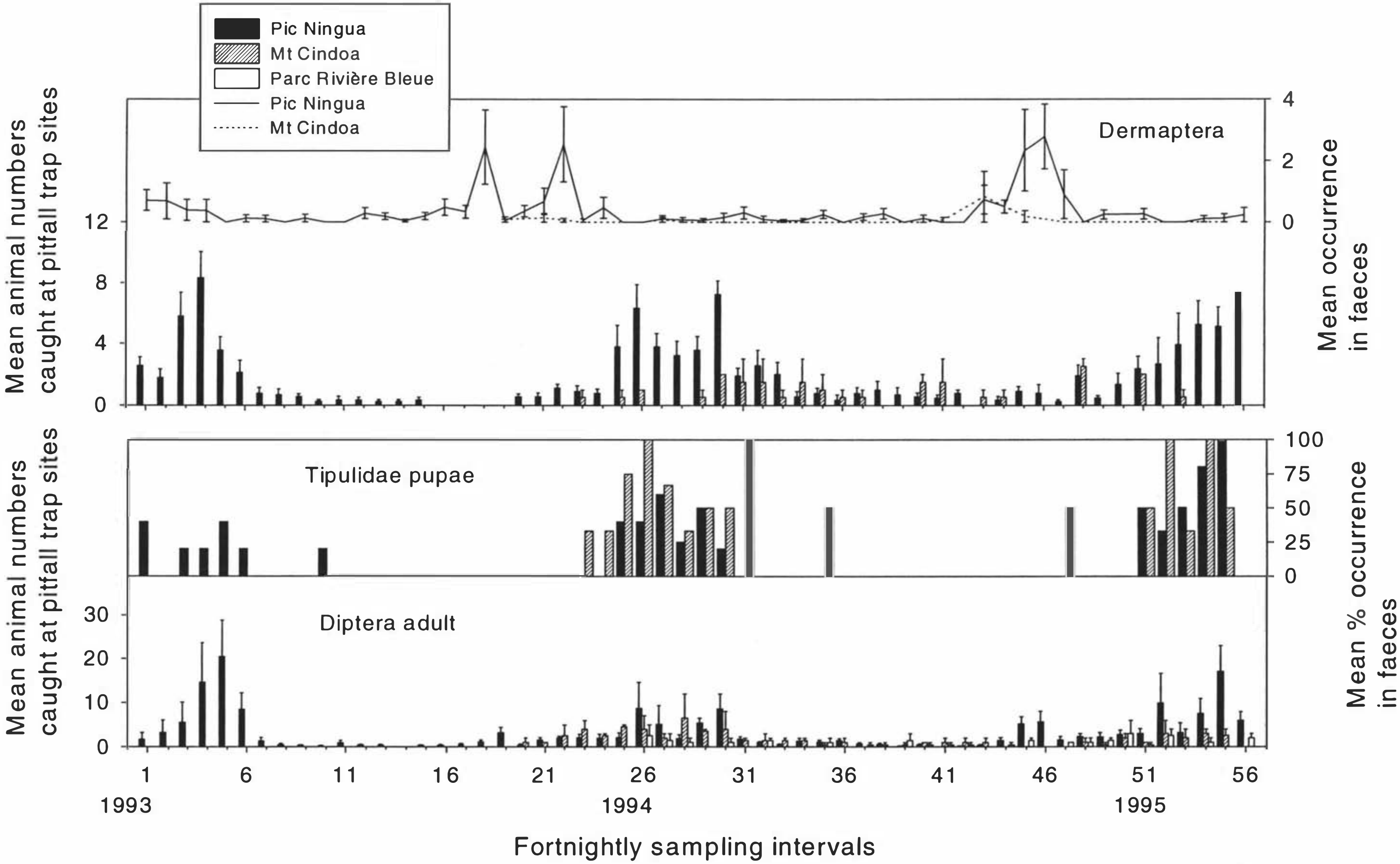

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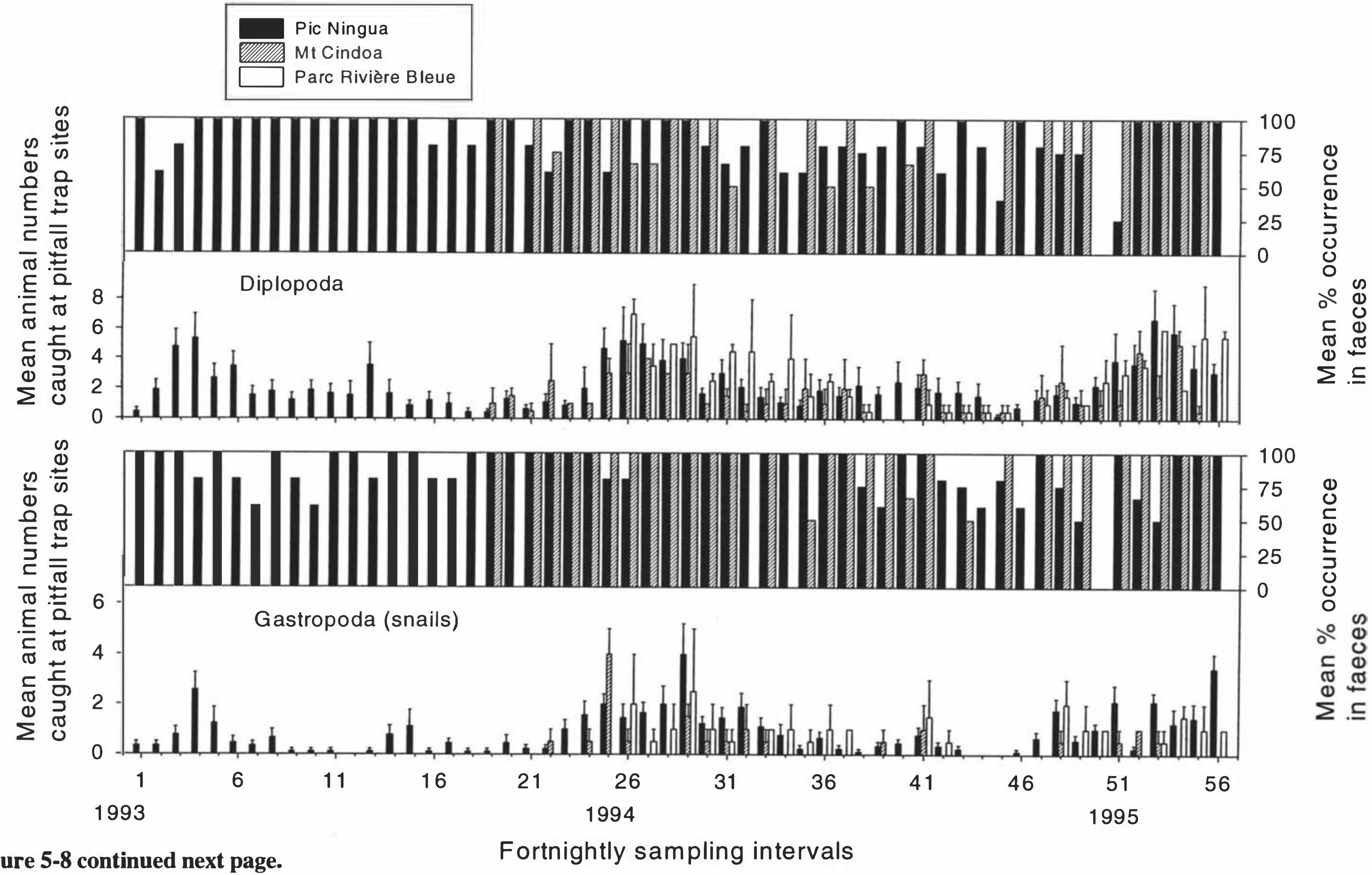

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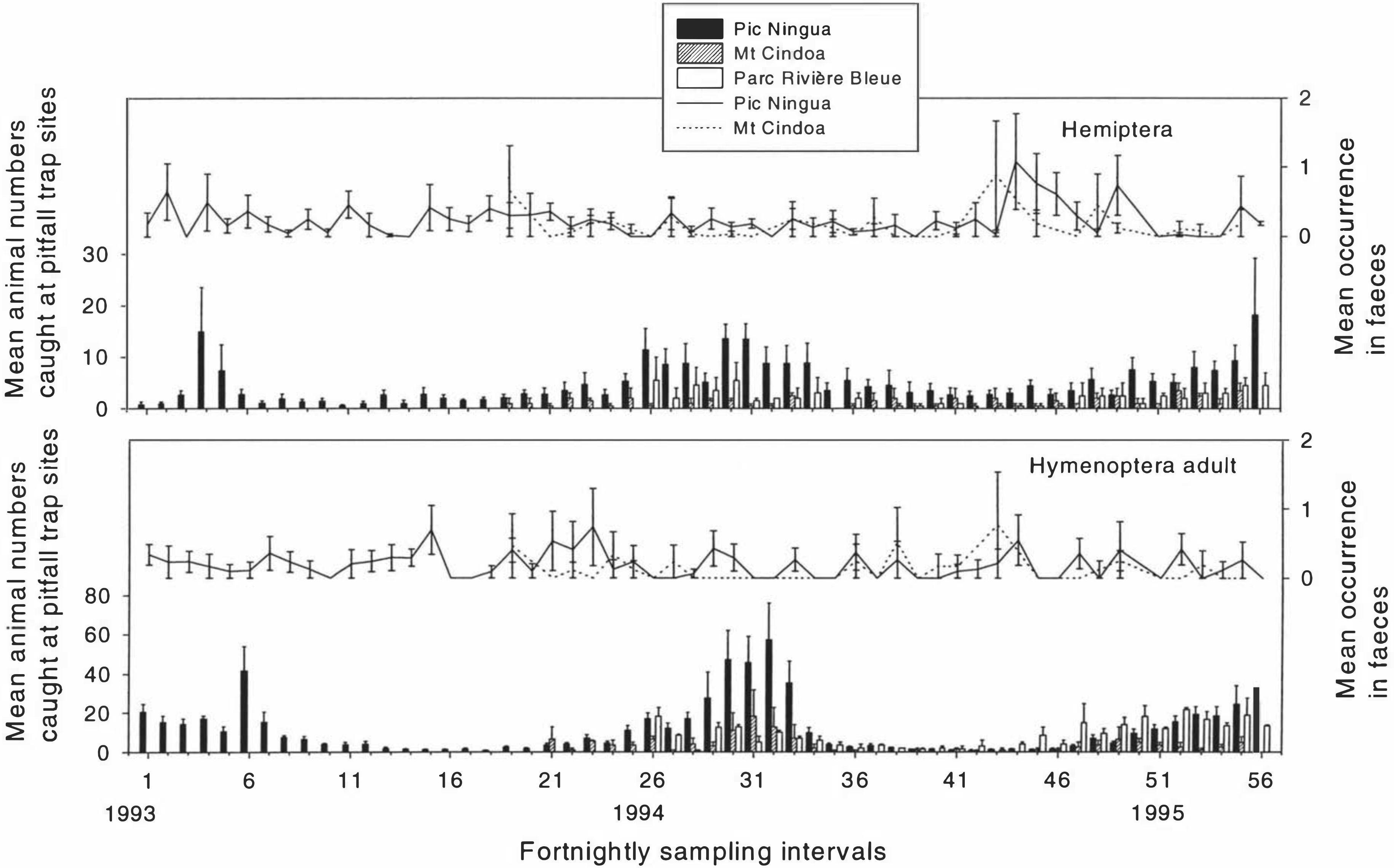

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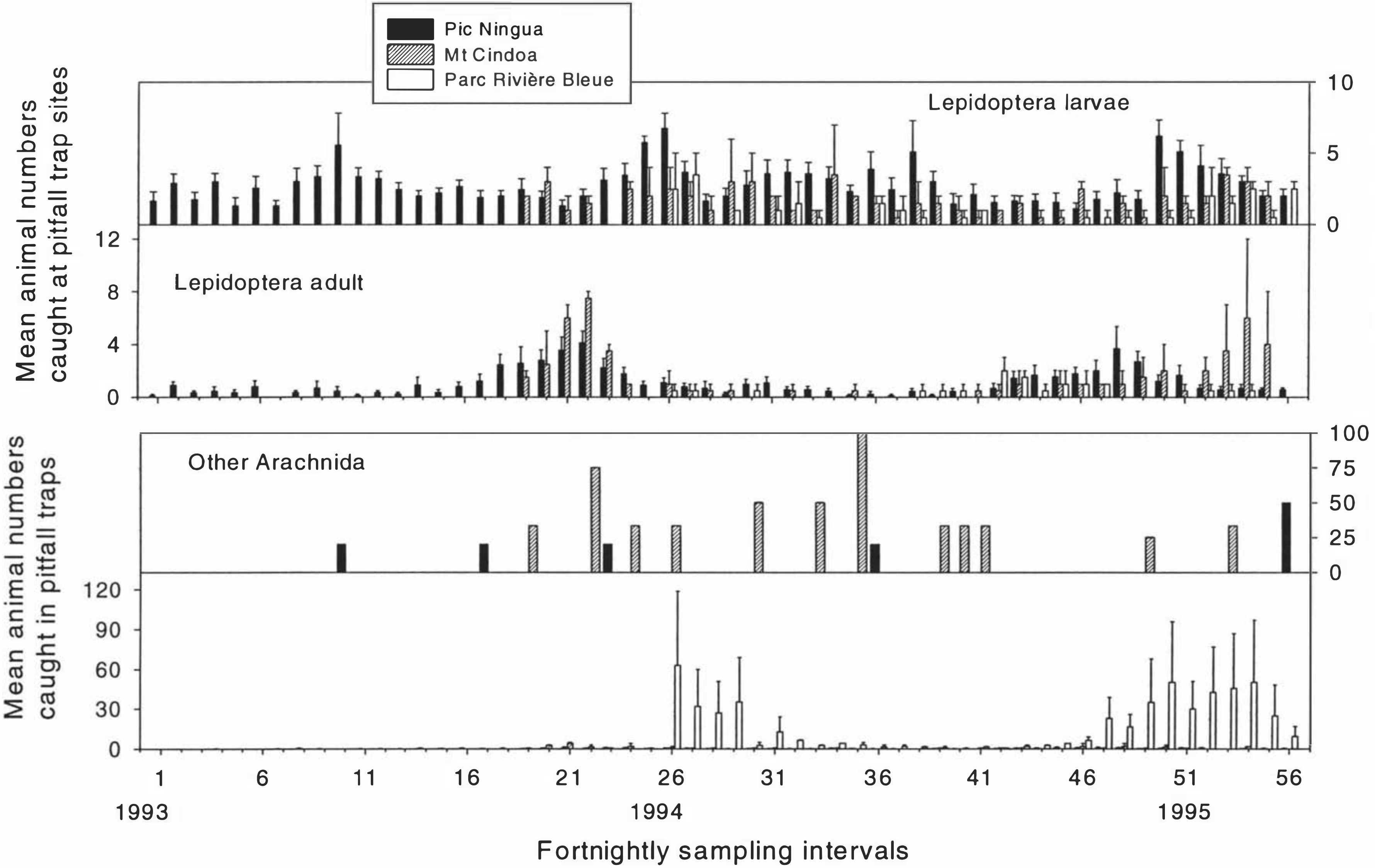

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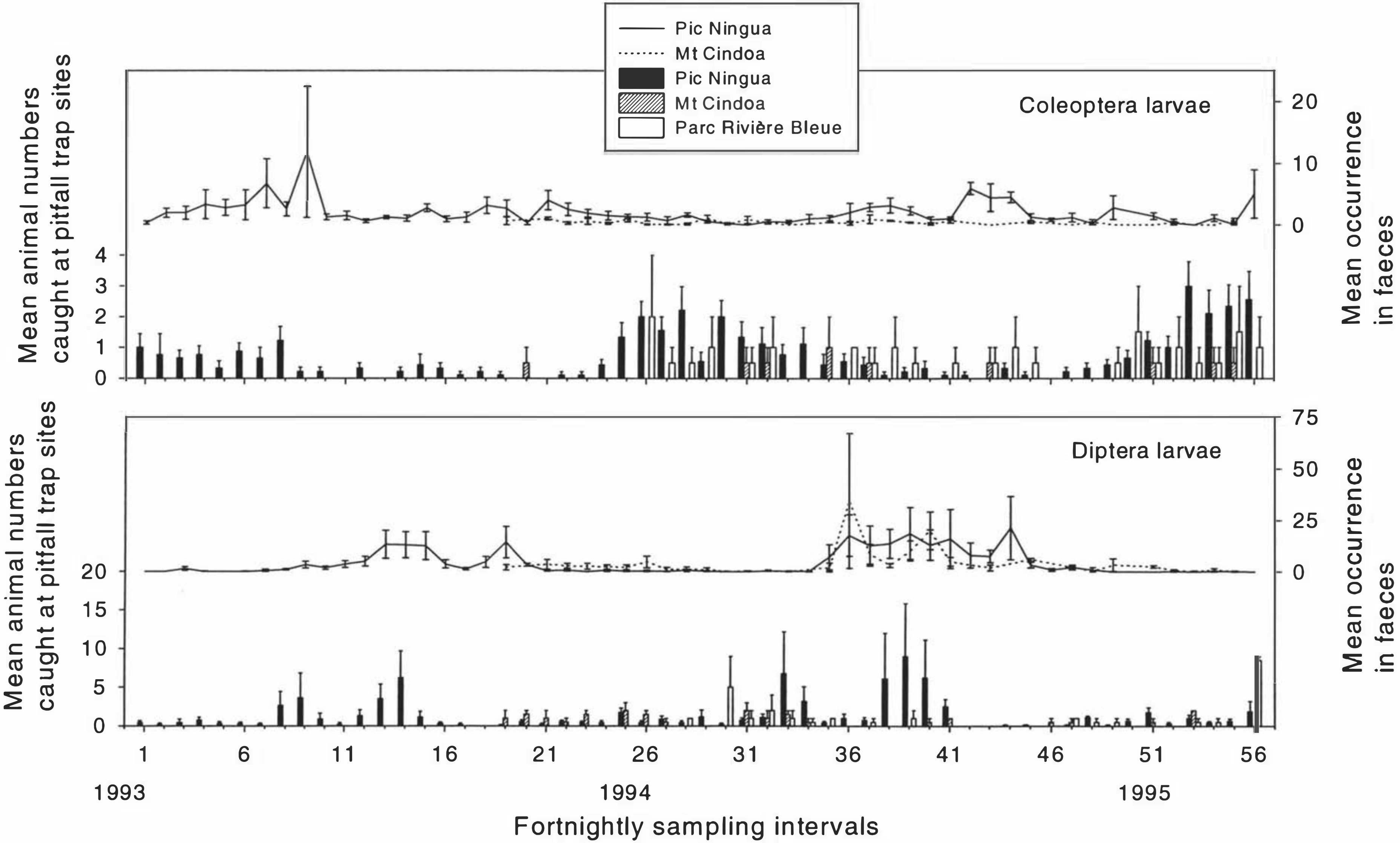

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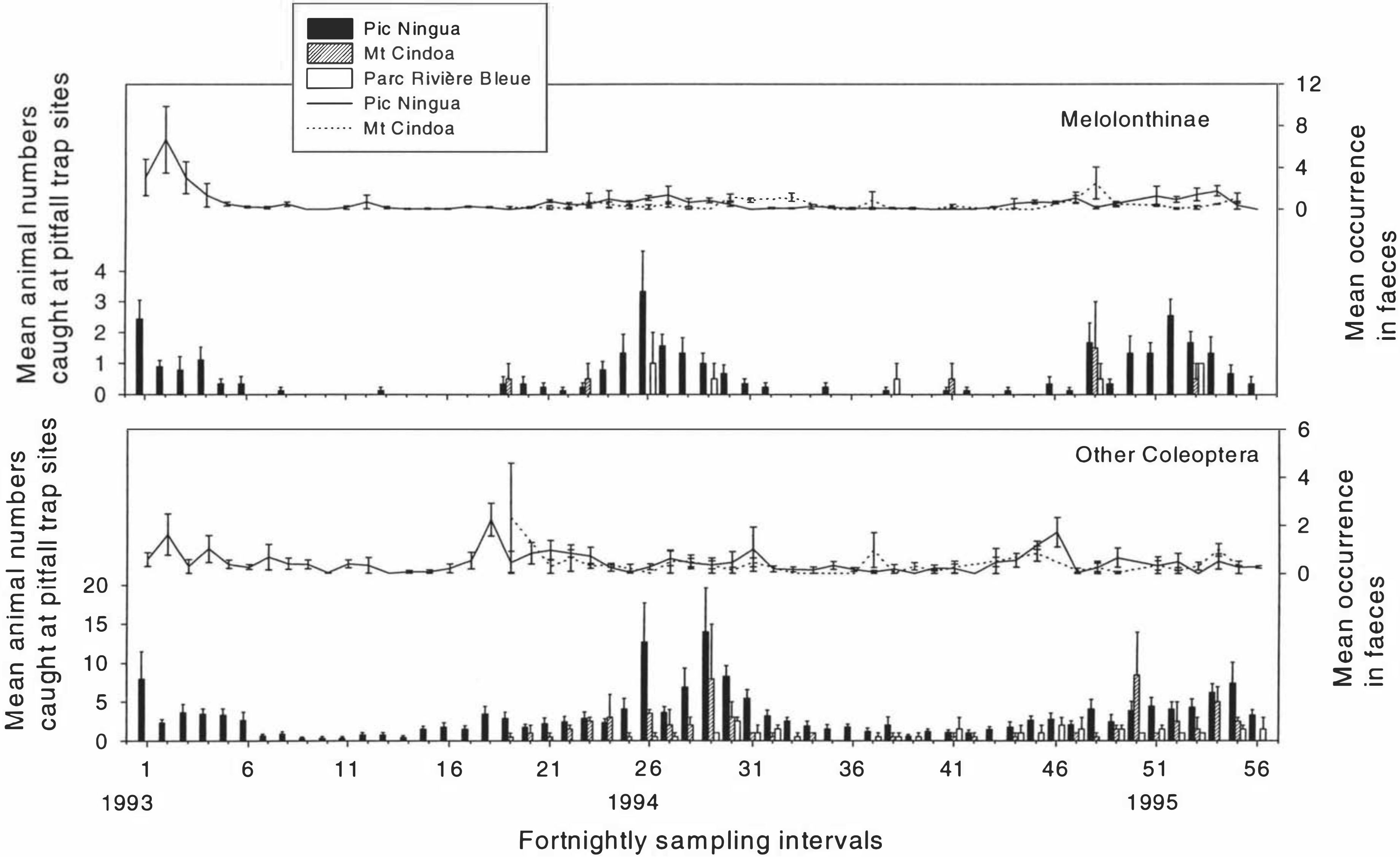

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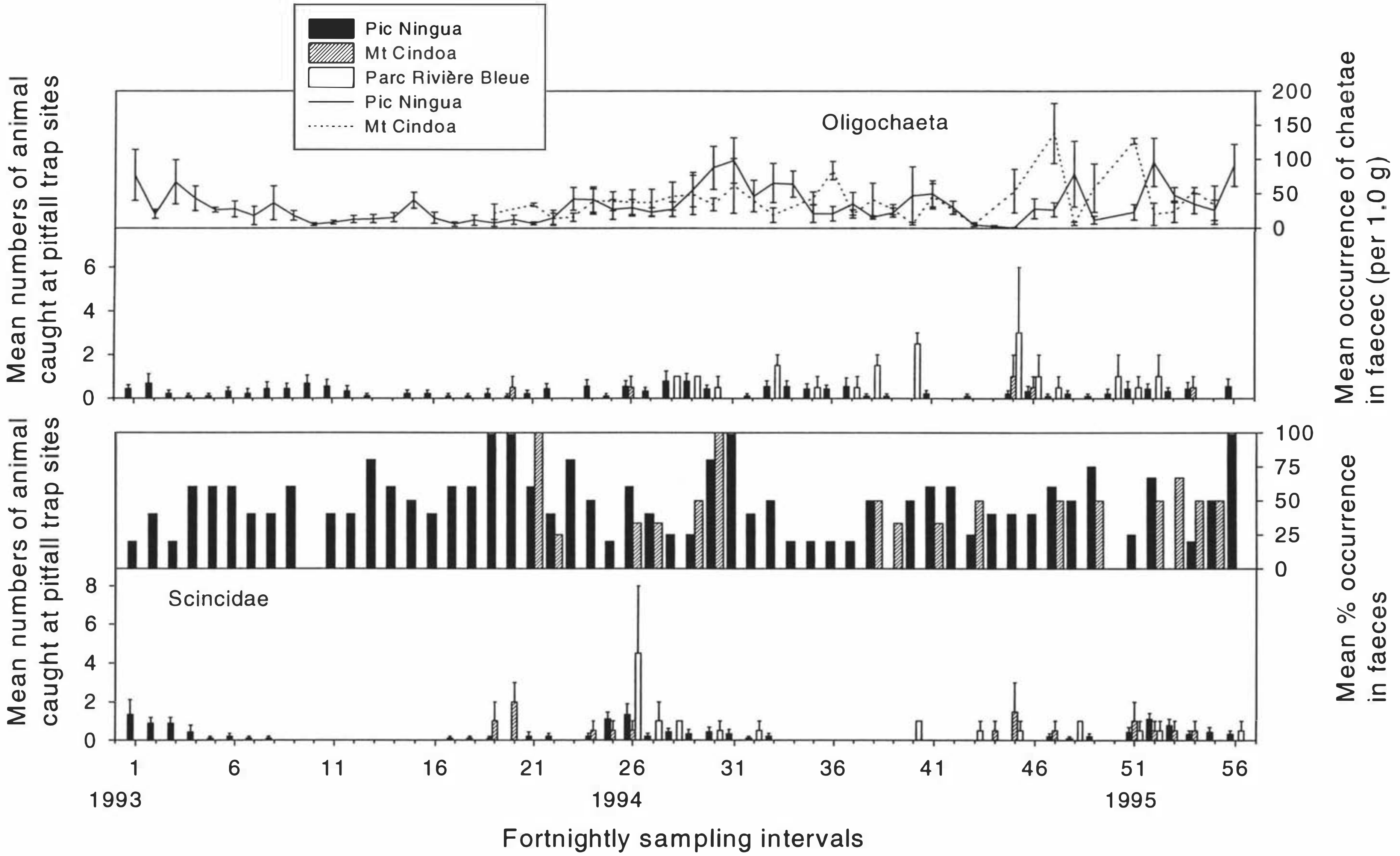

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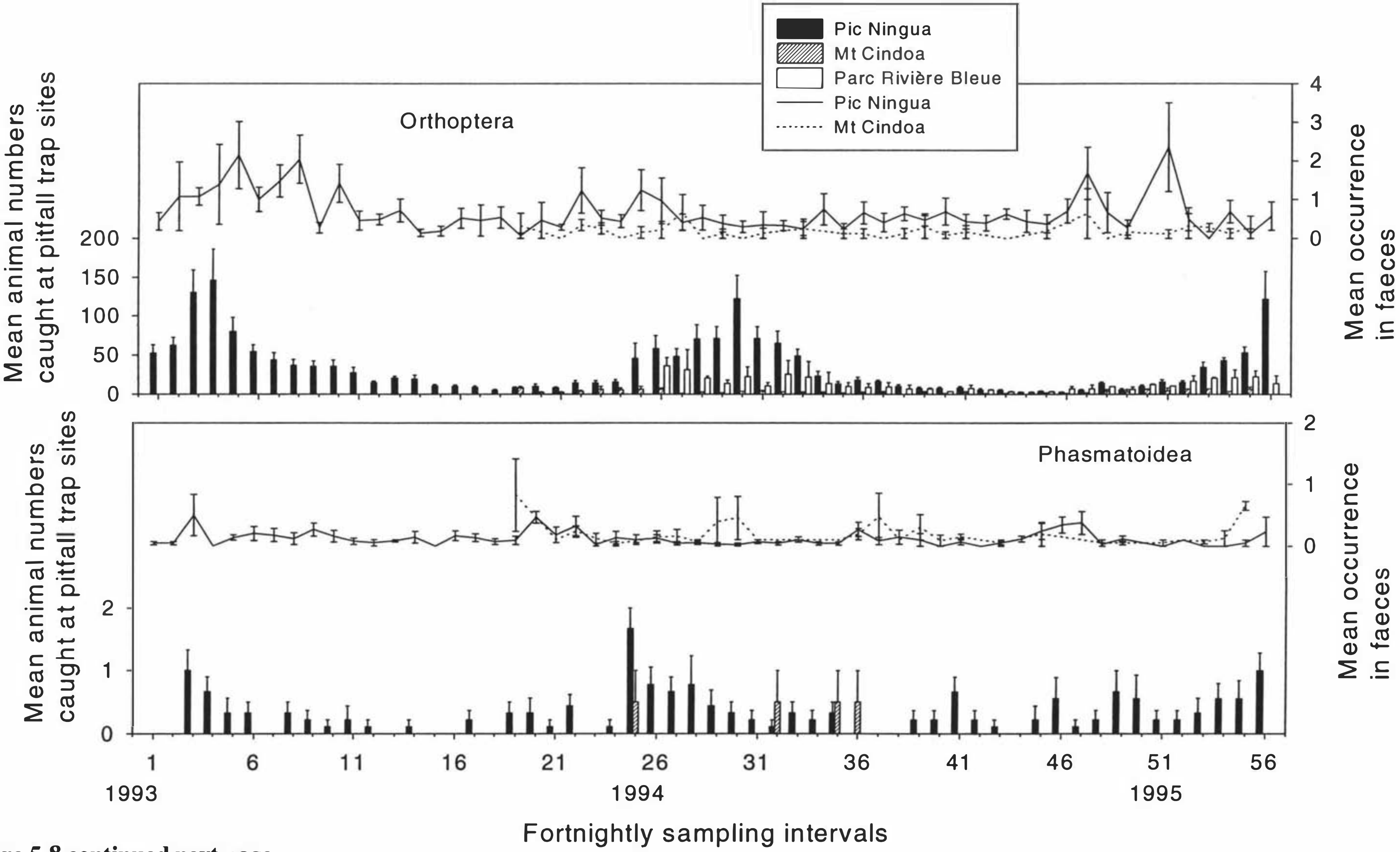

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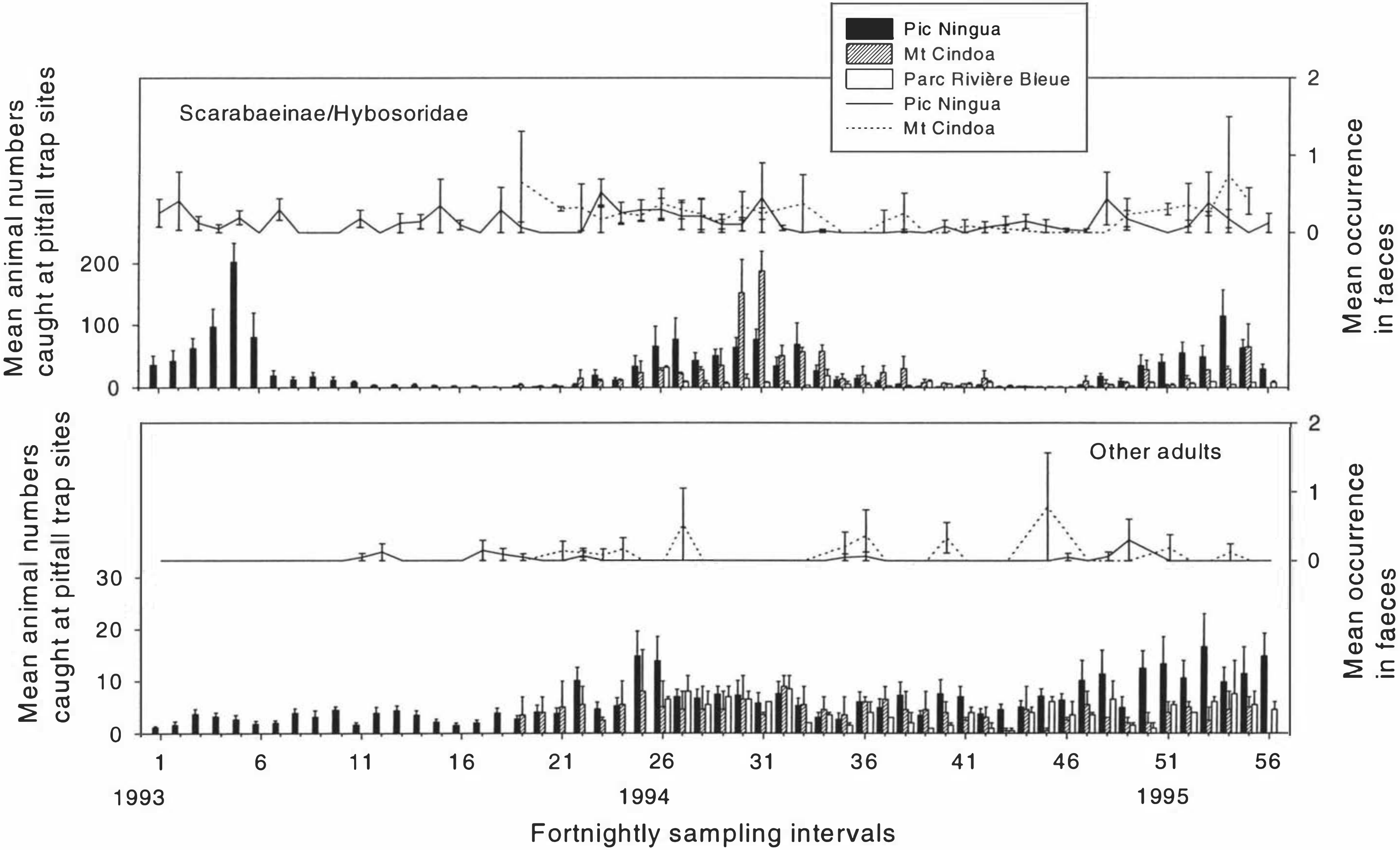

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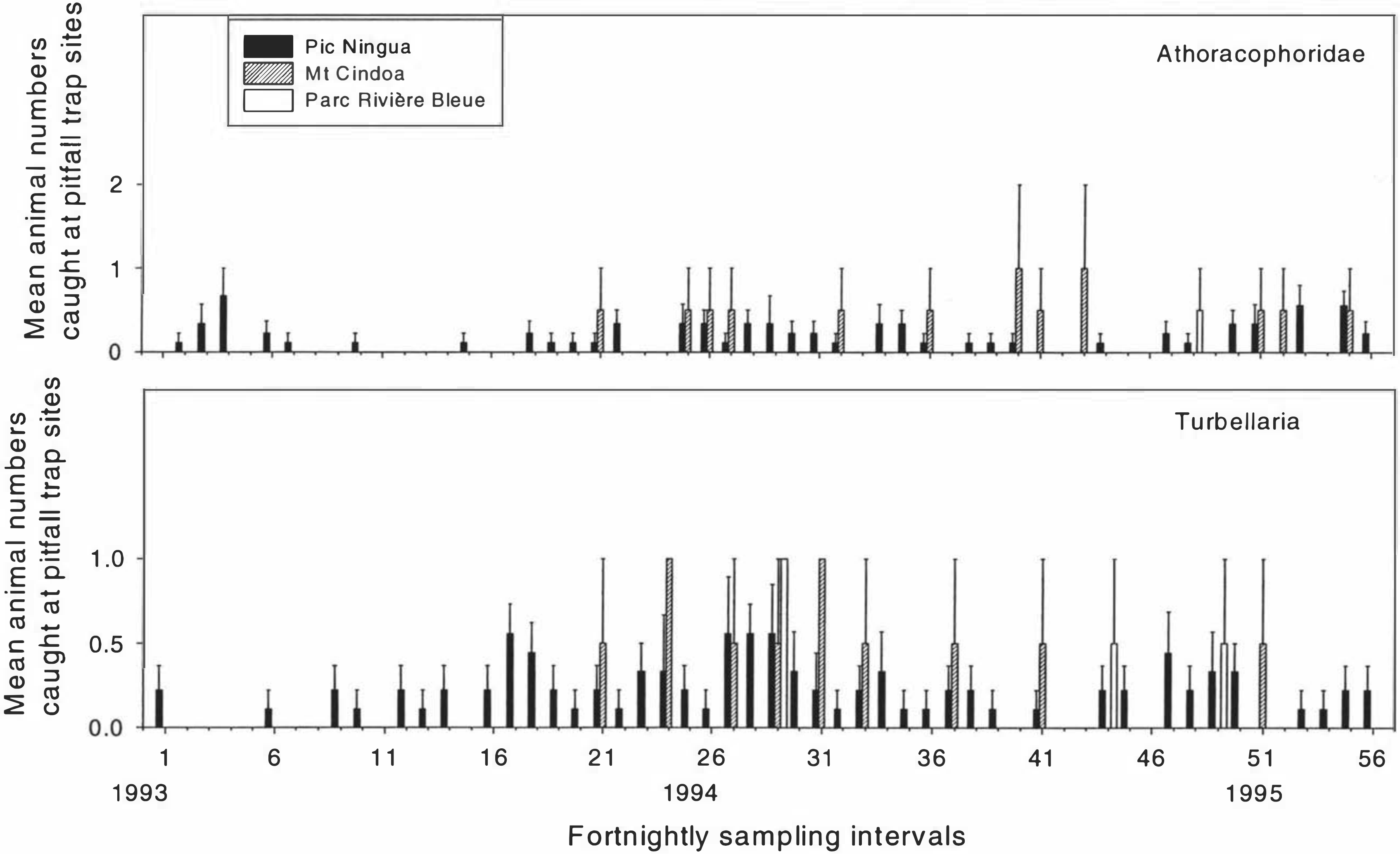

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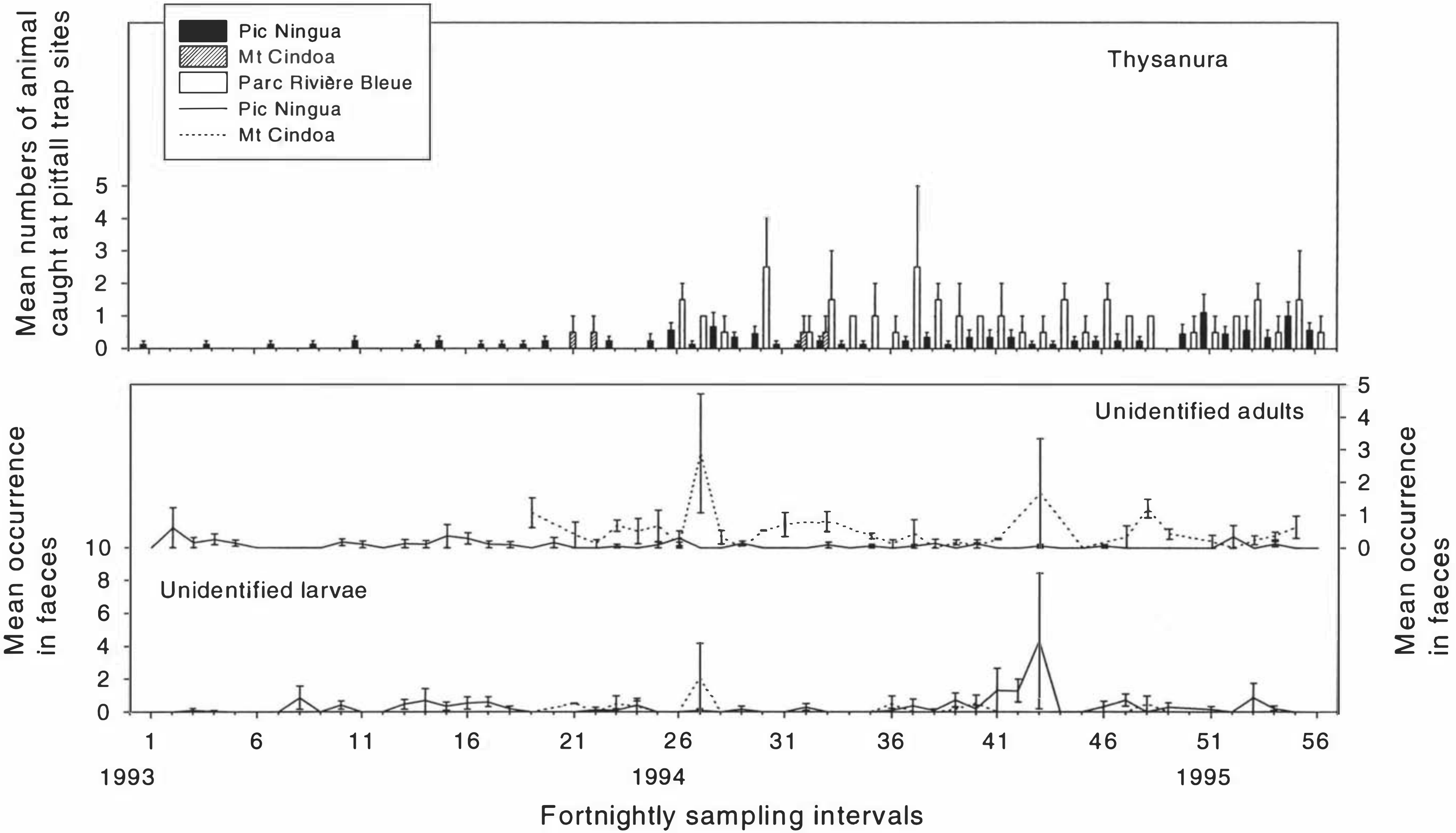


Variation in total animal abundance and dryweight biomass in pitfall traps showed similar strong seasonality between years (intervals 1-26 and 27-52) (Fig. 5-9). Mean animal abundance and dryweight biomass in pitfall traps were not significantly different between years (intervals 1-26 and 27-52) (Repeated measures ANOVA; Table 5-4), however the pattern of variation over time for biomass and abundance varied differently between years (Repeated measures ANOVA: Interval x Year interactions; Table 5-4).

Table 5-4. Results of repeated measures ANOVA analyses for two tests on each of two log-transformed dependent variables: animal numbers and dryweight biomass collected in pitfall traps. Test one makes a comparison between the three study areas (Pic Ningua, Mt Cindoa and Parc Rivière Bleue; intervals 26 to 55), and test two a comparison between years (intervals 1-26 and 27-52) at Pic Ningua. Column 6 gives the Huynh-Feldt adjusted-F values (see section 3.2.9). Data are in Figure 5-9.

Source	d.f.	MS	F	p > F	p > F (H-F adj.)
Dependent variable: Log animal numbers in pitfall traps					
Area	2	29.2737	8.63	0.0066	------
Interval	29	2.1009	20.75	------	0.0001
Interval x Area	58	0.2334	2.30	------	0.0061
Year	1	9.9663	1.88	0.1895	------
Interval	25	5.3668	60.69	------	0.0001
Interval x Year	25	0.7073	8.00	------	0.0001
Dependent variable: Log animal dryweight biomass in pitfall traps					
Area	2	22.0618	12.28	0.0020	------
Interval	29	4.3411	30.60	------	0.0001
Interval x Area	58	0.2759	1.95	------	0.0049
Year	1	0.3311	0.16	0.6980	------
Interval	25	10.3098	89.06	------	0.0001
Interval x Year	25	0.7380	6.38	------	0.0001

Although Amphipoda, Araneae, Orthoptera and Scarabaeinae/Hybosoridae made up over 85% of animal numbers in pitfall traps, they contributed 67.52% to total dryweight biomass (Table 5-5). Blattidae, Carabidae, snails and Scincidae also

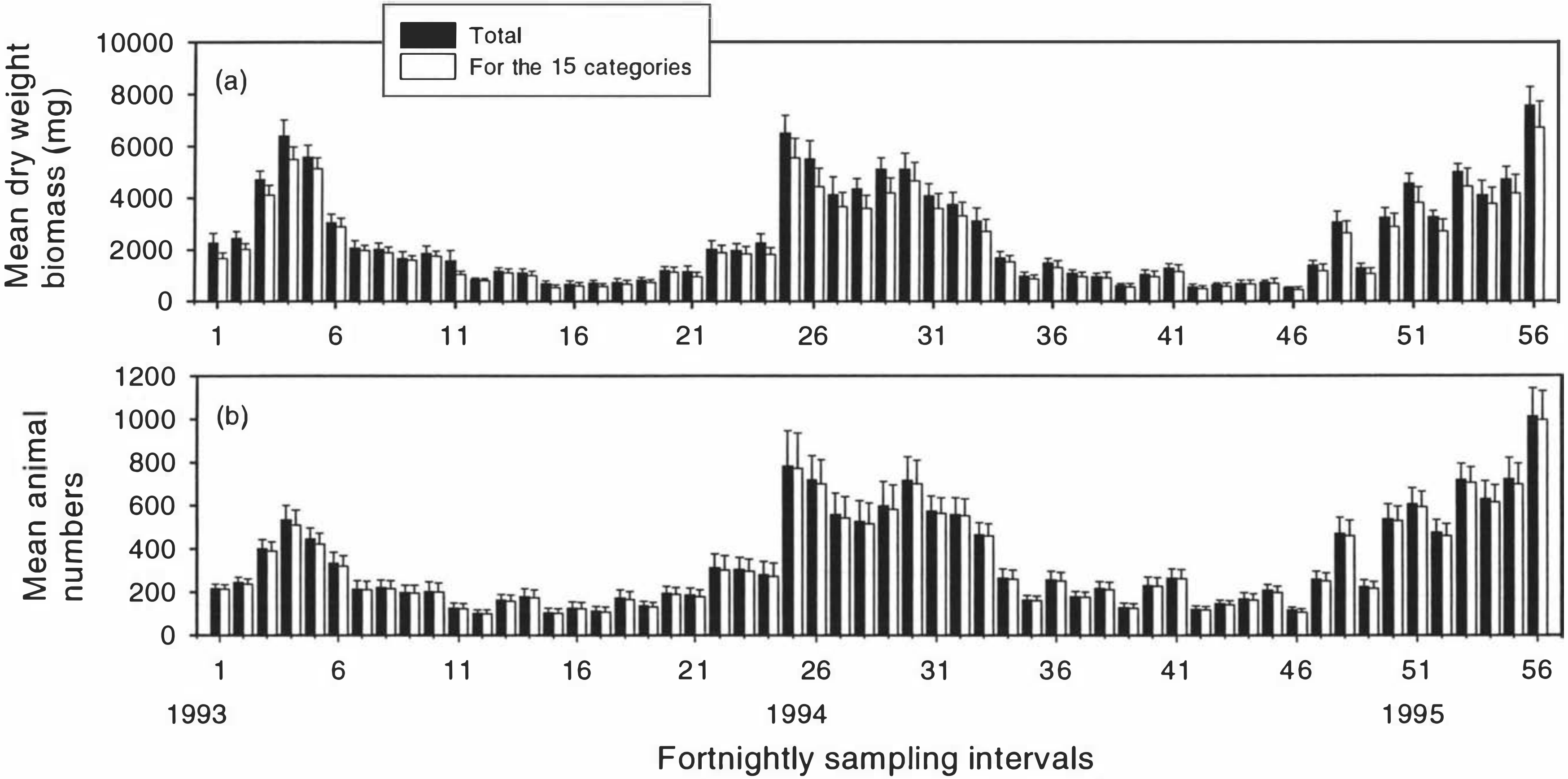


Figure 5-9. Mean animal dryweight biomass (a) and numbers (b) captured in pitfall traps at Pic Ningua. Black bars give total numbers and biomass, and unfilled bars the numbers and biomass for the 15 categories (Appendix X, section 5.2.14) (n= 9 for all bars; error bars = 1 s.e.).

contributed important amounts of biomass, with the highest percentage for Carabidae (9.76%). Scincidae had the highest dryweight biomass per individual animal (a conservative estimate of individual biomass, section 5.2.7). The next four taxa in order were snails, Oligochaeta, Carabidae and Athoracophoridae. Of these five categories, I quantified only Carabidae in kagu faeces (Table 5-3).

Table 5-5. Total animal numbers and estimated dryweight biomass (mg) for the 28 taxa in 90 pitfall traps at Pic Ningua (graphed in Fig. 5-8) from 25/1/93 to 19/3/95 (intervals 1-56). Percentages are in brackets. All taxa are adults unless larvae are specified. Taxa are ranked by their dryweight/abundance ratio (column 4).

Category	**Total numbers** (%)	**Total dryweight biomass (mg)** (%)	**dryweight/ abundance ratio**
Scincidae	123 (0.07)	43,050.00 (3.39)	350.0
Gastropoda (snails)	439 (0.26)	69,568.83 (5.49)	158.5
Oligochaeta	149 (0.09)	15,034.76 (1.19)	100.9
Carabidae	1,612 (0.94)	123,725.84 (9.76)	76.8
Athoracophoridae	73 (0.04)	4,478.42 (0.35)	61.4
Blattidae	1,632 (0.95)	57,737.37 (4.55)	35.4
Phasmatoidea	158 (0.09)	5,086.31 (0.40)	32.2
Melolonthinae	272 (0.16)	6,718.22 (0.53)	24.7
Chilopoda	341 (0.20)	6,586.31 (0.52)	19.3
Orthoptera	17,190 (10.00)	284,669.25 (22.45)	16.6
Diplopoda	1,146 (0.67)	14,543.74 (1.15)	12.7
Scarabaeinae/Hybosorid.	4,883 (8.66)	153,035.49 (12.07)	10.3
Araneae	6,535 (3.80)	60,213.39 (4.75)	9.2
Lepidoptera	520 (0.30)	3,782.01 (0.30)	7.3
Diptera larvae	690 (0.40)	3,831.41 (0.30)	5.6
Turbellaria	93 (0.05)	508.90 (0.04)	5.5
Dermaptera	929 (0.54)	4,944.92 (0.39)	5.3
Other Coleoptera	1,562 (0.91)	7,550.83 (0.60)	4.8
Other adults	3,066 (1.78)	14,022.66 (1.11)	4.6
Diptera	1,626 (0.91)	7,120.78 (0.56)	4.4
Thysanura	108 (0.06)	419.04 (0.03)	3.9
Hemiptera	2,479 (1.44)	8,495.36 (0.67)	3.4
Amphipoda	108,103 (62.89)	358,276.70 (28.25)	3.3
Coleoptera larvae	359 (0.21)	869.00 (0.07)	2.4
Hymenoptera	5,730 (3.33)	10,479.55 (0.83)	1.8
Lepidoptera larvae	1,411 (0.82)	2,499.50 (0.20)	1.8
Curculionoidea	493 (0.29)	861.22 (0.07)	1.8
Other Arachnida	178 (0.10)	183.09 (0.01)	1.0
	171,900	1,268,292.64	

Amphipoda almost always contributed the highest percent occurrence of animal numbers of the 15 categories in each interval (Appendix X), the exception being in intervals 2, 3 and 5 when numbers of either Orthoptera or Scarabaeinae/Hybosoridae were greater. In fact, for the first three months of data collection Amphipoda were at their lowest relative numbers. When I examined dryweight biomass, Amphipoda played a less dominant role, usually showing a strongly negative relationship with biomass of Orthoptera when these species were common during the wet season. In general, percentage contribution of Amphipoda to numbers and biomass tended to be greater outside periods of hot, wet weather when numbers of other taxa were relatively low.

The total numbers of morphological species in intervals in pitfall traps at Pic Ningua (Fig. 5-10) varied similarly and closely with mean animal numbers in the traps (Fig. 5-9b) (Spearman correlation coefficient, $r = 0.88$, $p < 0.0001$, $n = 56$). This indicates that diversity as well as abundance increased in the wet season. The distribution of morphological species in intervals also covaried more closely with minimum temperature than rainfall in forest (Spearman correlation coefficients, $r = 0.86$ and $r = 0.54$, $p < 0.0001$, $n = 54$ and $n = 56$, respectively).

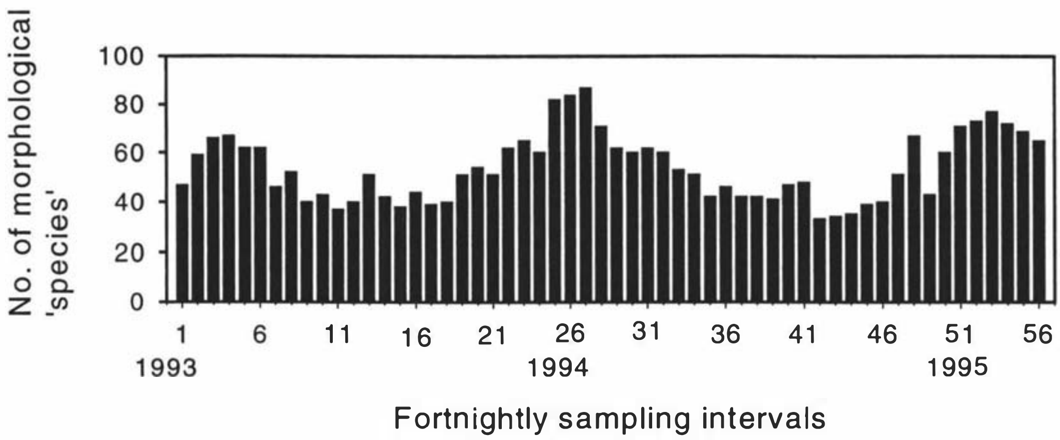


Figure 5-10. Numbers of morphological species in taxa captured in intervals in all pitfall traps (n = 90) at Pic Ningua. See section 5.2.14 for additional details and the taxa used.

My pitfall trapping methods quantified temporal variation and the relative differences in the numbers of soil and litter taxa but not their densities. I used data from two studies on ultrabasic peaks in Malaysia (Leakey and Proctor 1987) and the Philippines (Thomas and Proctor 1997) to obtain an indication of what the densities at my study areas might be (Table 5-6).

Table 5-6. Comparison of densities of certain taxa in the soil (top 15 cm) and litter in rainforest on ultrabasic peaks in Malaysia (Gunung Silam; data from Leakey and Proctor 1987) and the Philippines (Mt Giting-Giting; data from Thomas and Proctor 1997). The data below at each area (columns 2 and 3) for each taxa are means of several sites at various altitudes on the peaks. Data from Malaysia were collected from 20/7 to 10/9 in the drier season when 754 mm of rain fell at the study site, and those from the Philippines collected from 2/8 to 24/9 in the wet season when 408 mm fell. Column 4 gives the mean of columns 2 and 3 (I rounded values upwards).

Taxa	**Malaysia (No. per m^2)**	**Philippines (No. per m^2)**	**Mean**
Amphipoda	0	70	35
Araneae	31	40	36
Blattidae	13	18	16
Chilopoda	30	64	47
Coleoptera adults	96	69	83
Dermaptera	17	13	15
Diplopoda	25	29	27
Gastropoda	10	8	9
Hemiptera	11	15	13
Isopoda	28	64	46
Larvae	34	117	76
Oligochaeta	69	342	206
Orthoptera	1	6	4
Phasmatoidea	1	2	2
Total	385	864	625

5.3.5 Comparison of pitfall trap data between the three study areas

The seasonality of abundance for taxa in pitfall traps at Pic Ningua was also evident at the other two study areas, where mean numbers of animals captured were generally fewer (Fig. 5-8). Almost all the 28 taxa in Figure 5-8 were captured at all three study areas. Exceptions were Dermaptera and Phasmatoidea which were not captured at

Parc Rivière Bleue, although kagus ate these taxa at the Parc (Létocart 1989). Major differences between the study areas were that large Diplopoda (commonly over 900 mg dryweight) and Scorpiones were captured at Parc Rivière Bleue, but only small species of the former (commonly 100-150 mg) and none of the latter were captured at Pic Ningua and Mt Cindoa. The large millipedes, which kagus eat (Y. Létocart pers. comm., Hunt 1996b) and are probably highly toxic (Williams *et al.* 1997), made up a significant amount of the dryweight biomass in pitfall traps at the Parc during certain intervals (26-28, 48, 51 and 53) in the wet season, as the higher ratio of biomass to animal numbers at those times indicates (Fig. 5-11). Few Melolonthinae adults were caught at Mt Cindoa and Parc Rivière Bleue, and few Athoracophoridae and Turbellaria at Parc Rivière Bleue.

Mean numbers of animals in pitfall traps showed stronger seasonality at Pic Ningua (Fig. 5-9b) compared to the other two study areas (Fig. 5-11b), as the greater contrast between peaks and troughs at Pic Ningua indicates. Mean numbers of animals in intervals though between all three areas were significantly correlated (Spearman correlation coefficients: Pic Ningua and Mt Cindoa, $r = 0.79$, $n = 37$; Pic Ningua and Parc Rivière Bleue, $r = 0.77$, $n = 30$; Mt Cindoa and Parc Rivière Bleue, $r = 0.67$, $n = 30$; all tests $p < 0.0001$). At Pic Ningua and Mt Cindoa, the ratio of dryweight biomass to animal numbers in intervals was relatively constant (partly due to averaging biomass for categories with high numbers of animals, for example Amphipoda), but less so at Parc Rivière Bleue (Figs. 5-9 and 5-11). High biomass at the Parc in some wet season intervals was mostly due to the occurrence of large Diplopoda (see above), and higher numbers of Scincidae captured when the traps were first set (interval 26).

The wet-season-peak/dry-season-low ratios for mean animal numbers and dryweight biomass (between intervals 27 and 55) at Parc Rivière Bleue were 2.5:1 and 8.5:1, respectively, at Mt Cindoa 15.5:1 and 17.0:1, and at Pic Ningua 6.0:1 and 10.5:1.

When compared over intervals 28 to 55, mean animal abundance and dryweight biomass were significantly different between the three study areas (Repeated measures ANOVA; Table 5-4). The pattern of variation for these two variables over time also varied significantly between the study areas (Repeated measures ANOVA: Interval x Area interactions; Table 5-4).

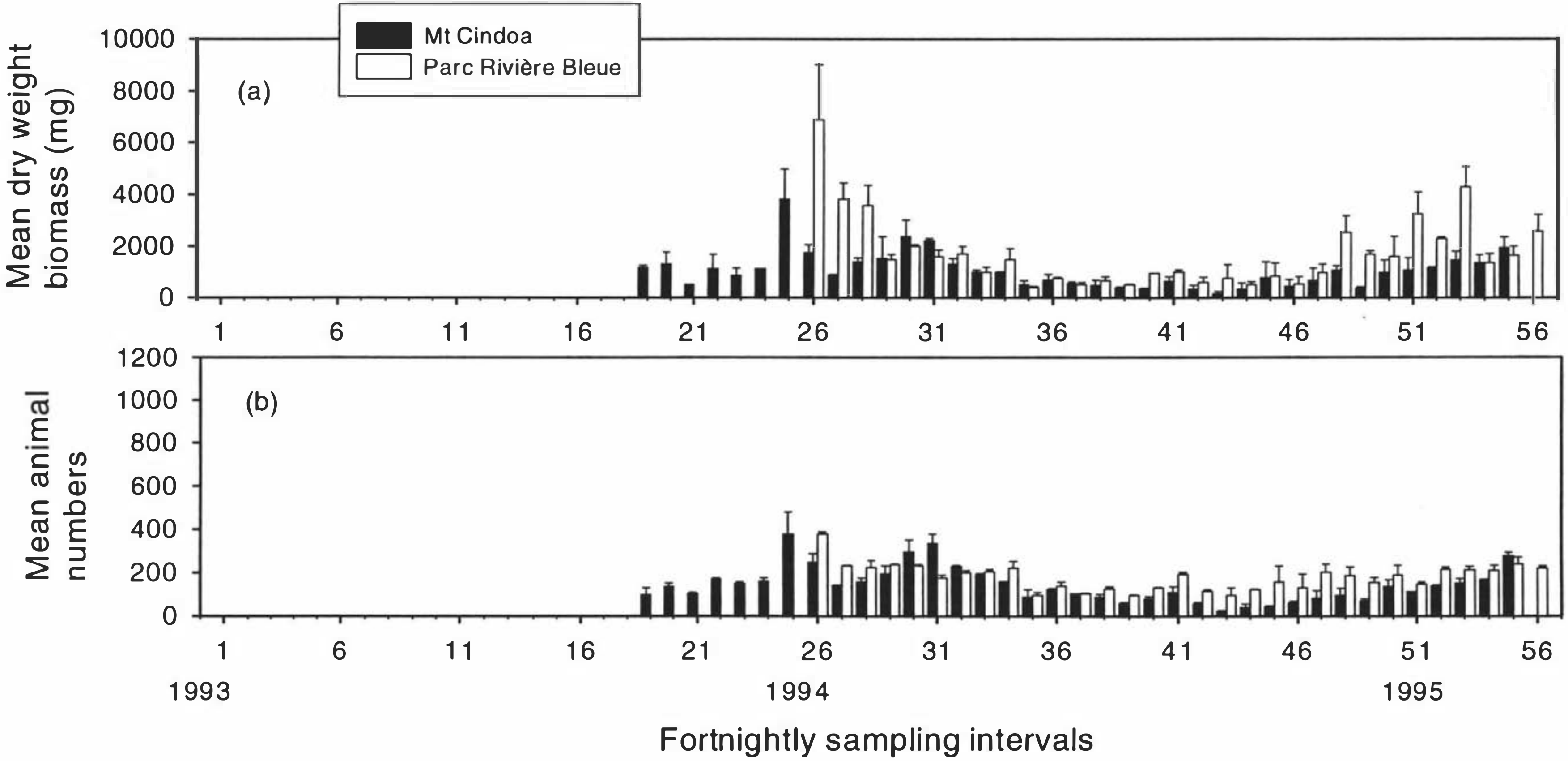


Figure 5-11. Mean animal dryweight biomass (a) and numbers (b) captured in pitfall traps at Mt Cindoa (black bars; intervals 19-55) and Parc Rivière Bleue (unfilled bars: intervals 26-56) (n = 2 for all bars, error bars = 1 s.e.).

5.3.6 Litter searches and worm activity

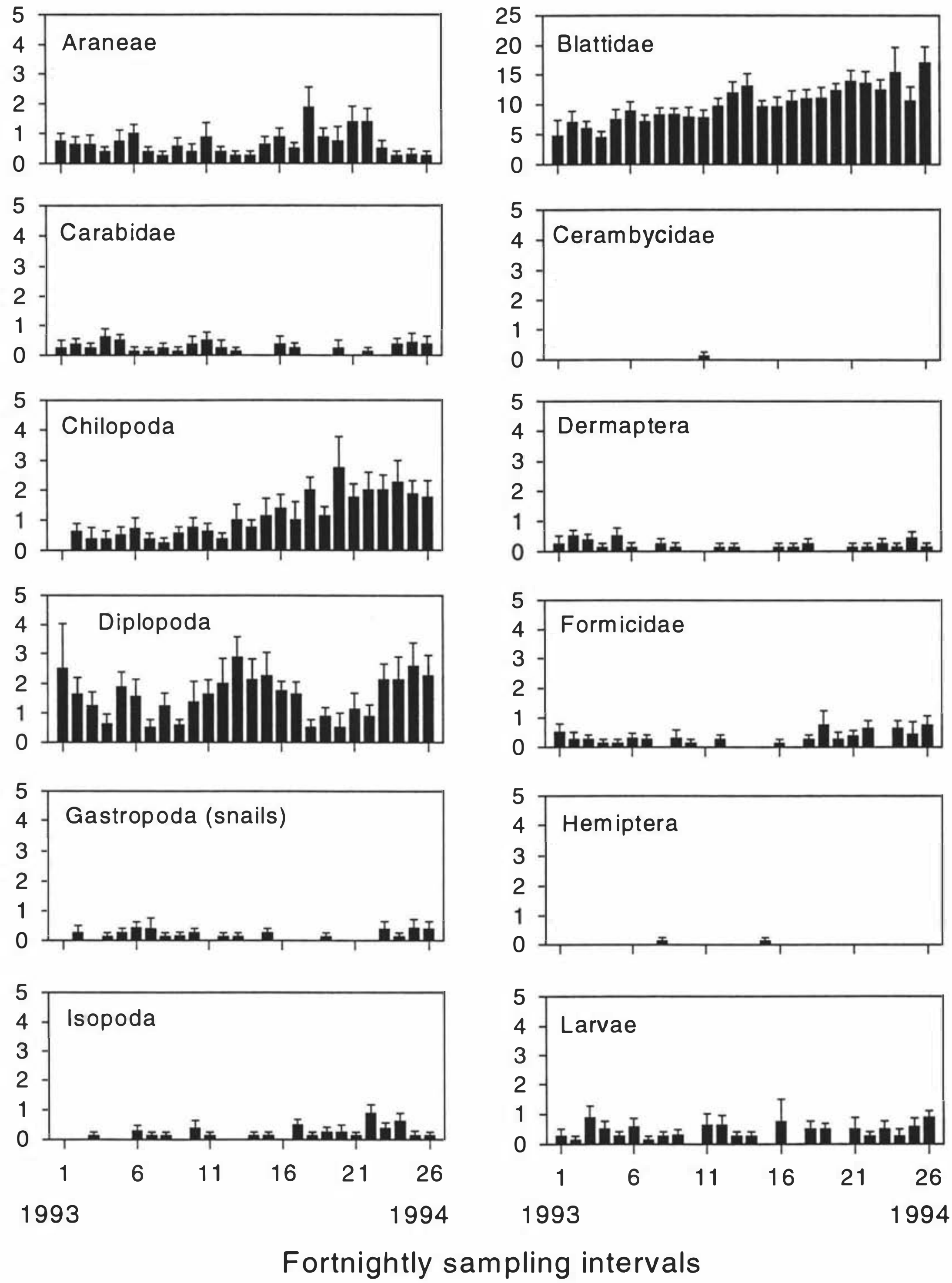
I searched the litter for a total of 98.5 hrs around pitfall trap sites at Pic Ningua capturing 3,396 animals and observing 89 lizards (Fig. 5-12). I captured and saw a wide variety of animals, and all the categories in Figure 5-12 were present in the pitfall trap samples. However, the traps contained taxa that I did not capture. Those particularly important to kagu diet (section 5.3.7) were large nocturnal Carabidae, Curculionoidea, and Tipulidae larvae and pupae. Larvae I caught were virtually all Coleoptera (Staphylinidae and Elateridae) and Lepidoptera, and I caught one Diptera larva. Blattidae were the commonest larger-sized invertebrates I saw in the litter (other than Amphipoda and Orthoptera which I did not attempt to capture, section 5.2.9). Also relatively common were Chilopoda and Diplopoda, followed by Araneae, Oligochaeta and Athoracophoridae. I detected no distinct trend for lower presence of Blattidae, Scincidae and Athoracophoridae in the dry season as occurred in pitfall trap samples. Distributions for Araneae, Carabidae, Dermaptera, Formicidae, Diplopoda, Melolonthinae and Oligochaeta tended to be similar to respective data in the trap samples. I also tended to catch increasing numbers of Blattidae and Chilopoda over the litter search period, but this trend was absent from other categories, suggesting it was probably not caused by improved captures rates by increased searching experience.

Mean numbers of wormcasts at Pic Ningua in 1994 (Fig. 5-13) had a similar distribution to many taxa in pitfall traps over the same period (Fig. 5-8) as their frequency declined from high values over the wet season to lowest ones (no casts were recorded in interval 46) in the driest period of the dry season (Fig. 5-13). A similar trend was seen in Oligochaeta captured in pitfall traps (Fig. 5-8).

5.3.7 Kagu diet

Kagus fed on a wide range of the prey types living in and around the forest floor (Table 5-3), including most of the taxa that occurred in pitfall traps. The larger-sized taxa that I did not find in faeces (Coccoidea : Margarodidae, Diptera and Lepidoptera adults, Athoracophoridae and Turbellaria) lacked hard body parts and/or were probably difficult for birds to capture (e.g., Diptera adults). Other taxa in Table 5-3 not recorded in faeces were probably rarely available for kagu (e.g., Bhyrridae,

Figure 5-12. Graphs of the 25 taxa captured or seen (Scincidae) in litter searches around pitfall trap sites at Pic Ningua in intervals 1-26. Lucanidae and Margarodidae (Coccoidea) are shown on the same graph. 'Larvae' were Coleoptera except one Diptera larva in interval 16. No data were collected for Scincidae in intervals 1 and 2. Sample sizes for bars were n = 8 except in intervals 6, 9 and 25 (n = 7), and 1 and 20 (n = 4) (error bars = 1 s.e.).



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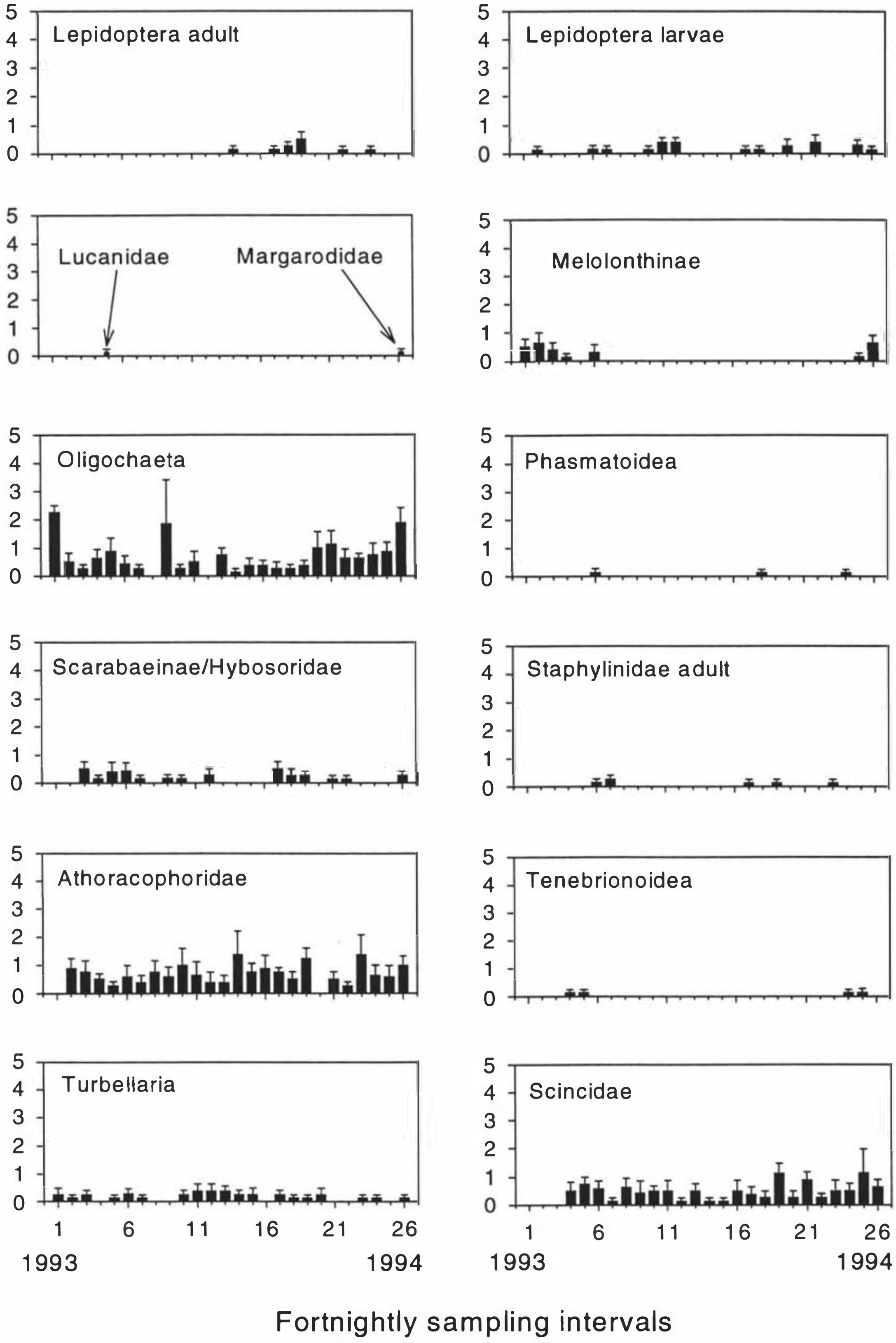


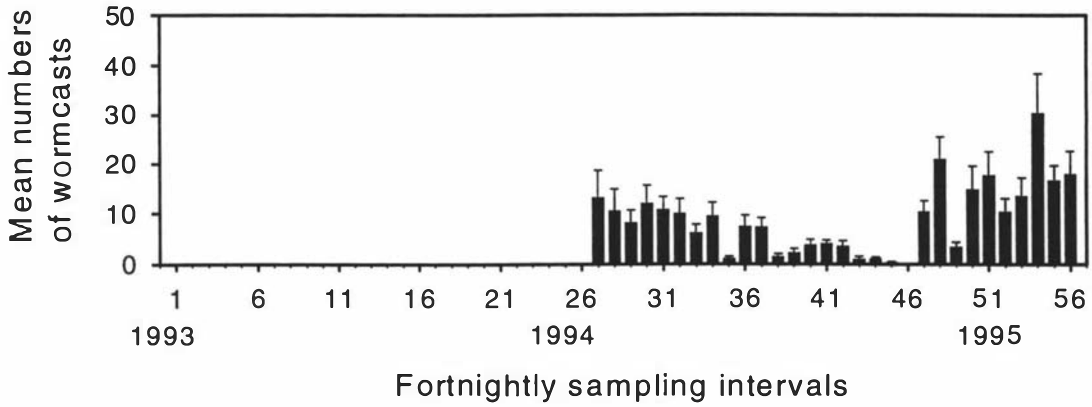


Figure 5-13. Mean numbers of wormcasts counted at eight pitfall trap sites (on approximately 3.50 m^2 at each site, section 5.2.10) at Pic Ningua in intervals 27-56 (error bars = 1 s.e.).

Lampyridae), soft bodied (Acari, Coccoidea other than Margarodidae and Athoracophoridae), too small for birds to fed on (Acari, Pseudoscorpiones), or a combination of these factors. It was also possible that some unidentified adults in faeces may have been present in pitfall traps but I was unable to identify them. The only kagu prey category not found in pitfall traps were soil-dwelling Scarabaeoidea larvae. Many taxa were rare in faeces and pitfall traps: Amblypygi, Apoidea, Chrysomelidae, Elateridae, Neuroptera larvae, Reduviidae, Pompilidae, Stenopelmatidae, Tenebrionoidea, Tetrigoidea and Triaeononychiidae. Interestingly, kagu also ate wood-dwelling Coleoptera larvae indicating that birds probably also searched in wood. I found these larvae in 16 faecal samples collected at Pic Ningua (n = 14) and Mt Cindoa (n = 2), mostly in the dry season between May and August. I also found small amounts of vegetation (pieces of leaves and wood) in faecal samples, most likely ingested incidentally (Létocart 1989) or from contamination of the faecal sample itself (section 5.2.1). I also found small (*c.* 1 mm long) banana-shaped seed-like objects in several faecal samples, and although they could not be confirmed as seeds this was probably the case (H. Outred pers. comm.).

Large ratios in Table 5-3 (column 6) suggested either that kagus were highly selective in eating these taxa or the trap samples greatly underestimated their availability. The latter was likely for soil-dwelling larvae like Scarabaeoidea and taxa which might only descend rarely to the forest floor like certain Coleoptera (e.g., Chrysomelidae) and Hemiptera. Small ratios (< 1.0) suggested that kagus avoided these taxa, could not easily capture them or they were not available to kagus during the day. Low ratios occurred for taxa caught in relatively large numbers in traps (Amphipoda, Isopoda, Gryllidae and Scarabaeinae/Hybosoridae), and for Pompilidae which feed on spiders on the forest floor (Moeed and Meads 1985). Although I did not record Lepidoptera larvae in faeces, many unidentified larvae may have been these animals.

Four significant positive correlations existed between distributions of prey in faeces and animals in pitfall traps at Pic Ningua (Carabidae, snails, Melolonthinae, and Other Coleoptera), and two negative ones (Blattidae and Coleoptera larvae) (legend to Fig. 5-8). All these six taxa were more abundant in the wet season in pitfall traps. Birds also tended to capture more Araneae, Diptera larvae, Hemiptera, Other Coleoptera and Phasmatoidea in the dry season. Kagus fed on large numbers of Diptera larvae in the dry season (Fig. 5-8), and these animals accounted for over 30% of the total prey numbers recorded in faeces at both Pic Ningua and Mt Cindoa (Table 5-7). Mean percent occurrence of Diplopoda and snails in faeces was usually well over 50% throughout the year, but averaged around 50% for Scincidae, similarly year round. The frequency of worm chaetae in faeces at Pic Ningua (Fig. 5-8) appeared closely related to rainfall, and was lowest (none recorded) in interval 45 in the driest period of the study. Numbers of wormcasts at pitfall trap sites (Fig. 5-13) and worm chaetae in faeces in the same intervals in 1994 were significantly correlated (Spearman correlation coefficient, $r = 0.81$, $p < 0.0001$, $n = 29$).

Total numbers of prey in kagu faeces at Pic Ningua (Fig. 5-14a) was significantly negatively correlated with total numbers of animals in pitfall traps there (Fig. 5-9b) (Spearman correlation coefficient, $r = -0.71$, $p < 0.0001$, $n = 55$). Kagus ate more prey items in the dry season, mostly due to the high numbers of larvae they fed on. When I removed larvae, numbers of prey items in faeces dropped considerably, but still tended to be quite high over the driest months (September/October) in each year (especially in 1994). Thus, kagus continued to feed on larger numbers of (quantifiable) prey at these times compared to the wet season, but these were not larvae. However, no significant correlation existed between prey numbers in faeces and animals in pitfall traps when I removed larvae (Spearman correlation coefficient, r = -0.14, ns, n = 55). Prey numbers in kagu faeces at Mt Cindoa (Fig. 5-14b) exhibited a similar distribution to prey numbers at Pic Ningua, but birds at Mt Cindoa tended to eat fewer larvae between intervals 36 and 46.

Table 5-7. Total numbers of animals (based on a 10 g faecal sample, section 5.2.3) recorded in kagu faecal samples at both Pic Ningua (n = 249) and Mt Cindoa (n = 79) for each of the 19 taxa quantified in kagu faeces in Figure 5-8. Taxa are ranked in descending order by abundance at Pic Ningua. Percentages do not add to 100 because of rounding.

Category	**Pic Ningua**		**Mt Cindoa**	
	No.	**%**	**No.**	**%**
Diptera larvae	1,108.22	32.32	326.38	36.69
Coleoptera larvae	525.31	15.32	31.70	3.56
Blattidae	255.45	7.45	22.06	2.48
Carabidae	204.09	5.95	38.52	4.33
Orthoptera	175.44	5.12	14.66	1.65
Melolonthinae	167.17	4.88	31.84	3.58
Curculionoidea	147.40	4.30	114.98	12.93
Araneae	142.35	4.15	36.50	4.10
Chilopoda	133.07	3.88	33.11	3.72
Other Coleoptera	114.97	3.35	29.19	3.28
Dermaptera	98.46	2.87	3.77	0.42
Amphipoda	90.46	2.64	90.74	10.20
Unidentified larvae	74.66	2.18	13.78	1.55
Hemiptera	57.52	1.68	11.15	1.25
Hymenoptera	48.32	1.41	9.94	1.12
Scarabaeinae/Hybosoridae	31.09	0.91	17.85	2.01
Phasmatoidea	29.41	0.86	14.52	1.63
Unidentified adult	18.92	0.55	39.75	4.47
Other adults	6.68	0.19	9.02	1.01
Totals	3,428.99	100.00	889.46	100.00

Kagus ate larvae throughout the year, but their percent occurrence in faeces at Pic Ningua was strongly seasonal (Appendix X), especially in 1994. Percent occurrence of larvae generally rose considerably in May and remained high until conditions became dry in late September. The next most prevalent diet category over this period was Blattidae. Larvae were usually the dominant prey category in faeces, with either Carabidae, Curculionoidea or Melolonthinae taking that role when kagus were eating

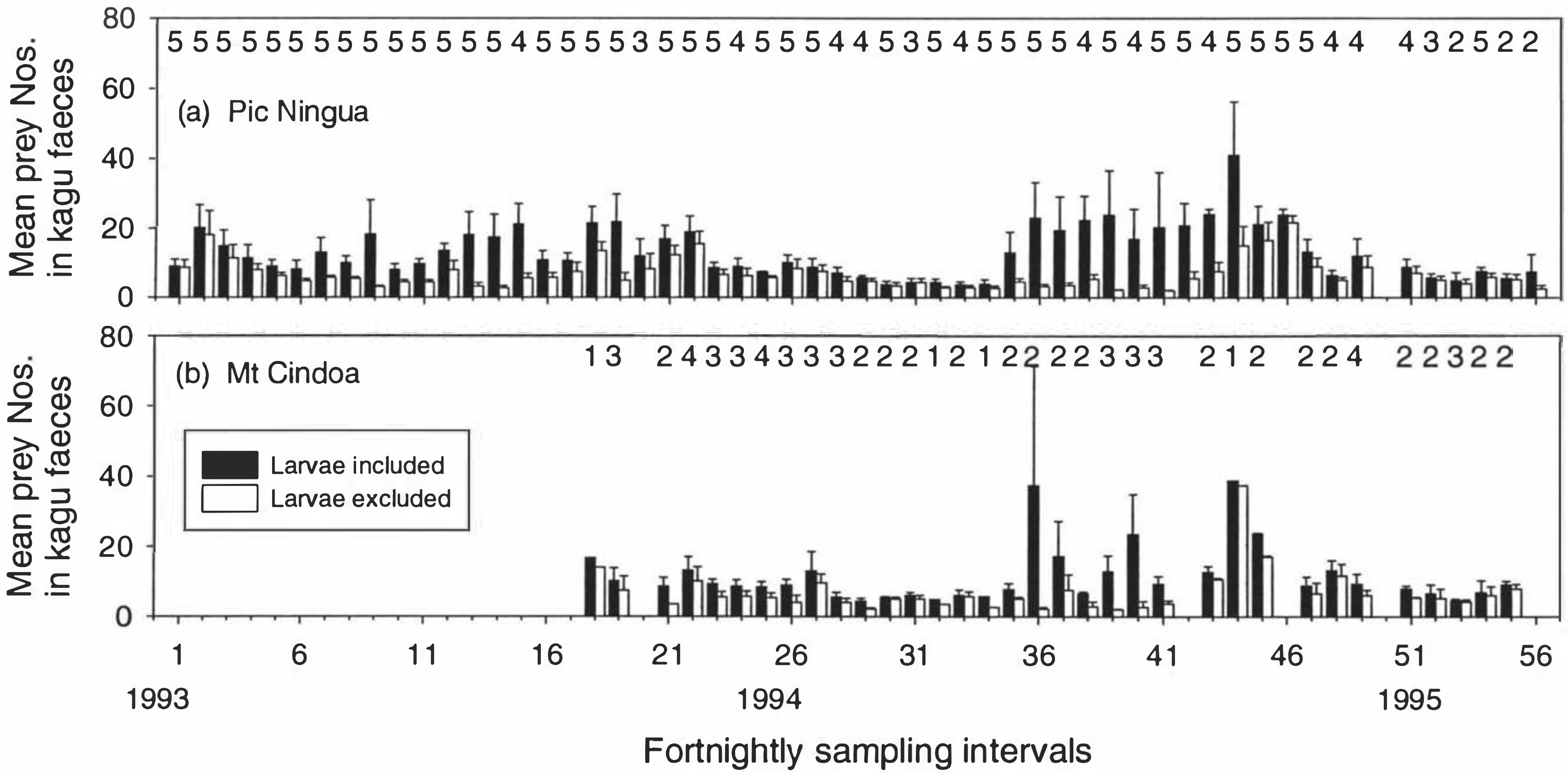


Figure 5-14. Mean numbers of animals (adjusted to values per 10 g) recorded in kagu faeces at Pic Ningua (a) and Mt Cindoa (b). Data are given for all animals (black bars) and with larvae excluded (unfilled bars). Samples sizes (numbers of faecal samples from different birds) are along the top of the graphs (error bars = 1 s.e.).

low numbers of larvae. Birds ate Carabidae, Melolonthinae and Orthoptera most frequently in warm, wet conditions, but tended to eat Carabidae and Melolonthinae at relatively higher frequencies in the early wet season and Orthoptera in the later stages. Kagus ate substantially more Amphipoda in very dry conditions, especially from late September to late October 1994 at Pic Ningua and Mt Cindoa.

Kagus at Pic Ningua and Mt Cindoa ate the same taxa (Fig. 5-8), however the percentage contribution of the different taxa to kagu diet at the two areas varied (Table 5-7). Diptera larvae had the highest percentage at both areas, but birds at Mt Cindoa ate, for example, relatively more Amphipoda and Curculionoidea and fewer Blattidae, Coleoptera larvae and Orthoptera than did birds at Pic Ningua. These differences may be related to the less well developed soil/litter layer environment at Mt Cindoa and the apparently lower abundance of fauna that lived there.

Kagus preyed on ten taxa in Table 5-3 that I did not find in litter searches. These were either rare in pitfall traps and faecal samples (Amblypygi, Apoidea, Elateridae, Neuroptera larvae, Triaenonychiidae), probably difficult to catch (Pompilidae) or may have been found in other locations (Chrysomelidae, Curculionoidea, Reduviidae, Tipulidae pupae). Those taxa that I found in litter searches but were not recorded in kagu faeces (Table 5-3) were either soft-bodied (Lepidoptera adults, Margarodidae, Athoracophoridae and Turbellaria) or perhaps unidentified prey in faeces (Lepidoptera larvae). Although I only found one Margarodidae in litter searches, they were not uncommon in pitfall traps at Pic Ningua in the wet season. Interestingly, the litter search data were a better indication of the presence of Scincidae in kagu diet than the pitfall traps, which might also indicate that birds were eating Athoracophoridae year round as well as I found these animals in nearly all intervals.

Because of the relatively large numbers of Amphipoda, Orthoptera and Scarabaeinae/Hybosoridae in pitfall traps, the distribution of mean animal abundance in the traps may not have well indicated the distribution of overall kagu prey abundance because these taxa were not that common in kagu faeces. To check this I tested the correlation between the data set with all taxa present (Fig. 5-9b) and one with these three taxa removed. The two data sets were highly correlated (Spearman correlation coefficient, $r = 0.81$, $p < 0.0001$, $n = 56$).

5.3.8 Homogeneity of kagu diets and pitfall fauna

The general pattern of variation in homogeneity (*H'*, high values indicate increased homogeneity) across the 15 categories in pitfall traps (Fig. 5-15c) was similar to the distribution of total animal numbers caught in the traps (Fig. 5-9b); high values in the wet season, and lowest ones in September/October. Interestingly, homogeneity increased sharply in intervals 19 and 46 which corresponded to the driest periods in each year. This was associated with a decrease in percent occurrence of Amphipoda in pitfall traps (Appendix X) in these two intervals. An overall trend for decreased homogeneity values over the duration of the study was also evident, and this appeared to be because of an overall increased relative abundance of Amphipoda. Percent occurrence of Amphipoda in pitfalls and homogeneity values in intervals were strongly negatively correlated (Spearman correlation coefficient, $r = -0.9719$, $p < 0.0001$, $n = 56$). However, homogeneity did not vary between years (Repeated measures ANOVA; Table 5-8).

Table 5-8. Results of repeated measures ANOVA analysis comparing homogeneity of pitfall trap fauna across 15 categories at Pic Ningua between years (intervals 1-26 and 27-52). Column 6 gives the Huynh-Feldt adjusted-F values (see section 3.2.9). Data are in Figure 5-15c.

Source	d.f.	MS	F	p > F	p > F (H-F adj.)
Dependent variable: Homogeneity of pitfall trap fauna across 15 categories					
Year	1	4.9815	2.23	0.1546	------
Interval	25	0.5055	9.60	------	0.0001
Interval x Year	25	0.0980	1.86	------	0.0548

Variation in diet homogeneity across the 15 categories at Pic Ningua showed the same seasonal pattern in both years of the study (Fig. 5-15a). Values were mostly high except for the cool and damp months of the dry season (June-August). Highest homogeneity was recorded in interval 46 in late October 1994, the driest period of the study, just before the first substantial rain fell for many weeks in interval 47. Removal of larvae from the data resulted in more even homogeneity over the study period as low values in June-August disappeared (Fig. 5-15b).

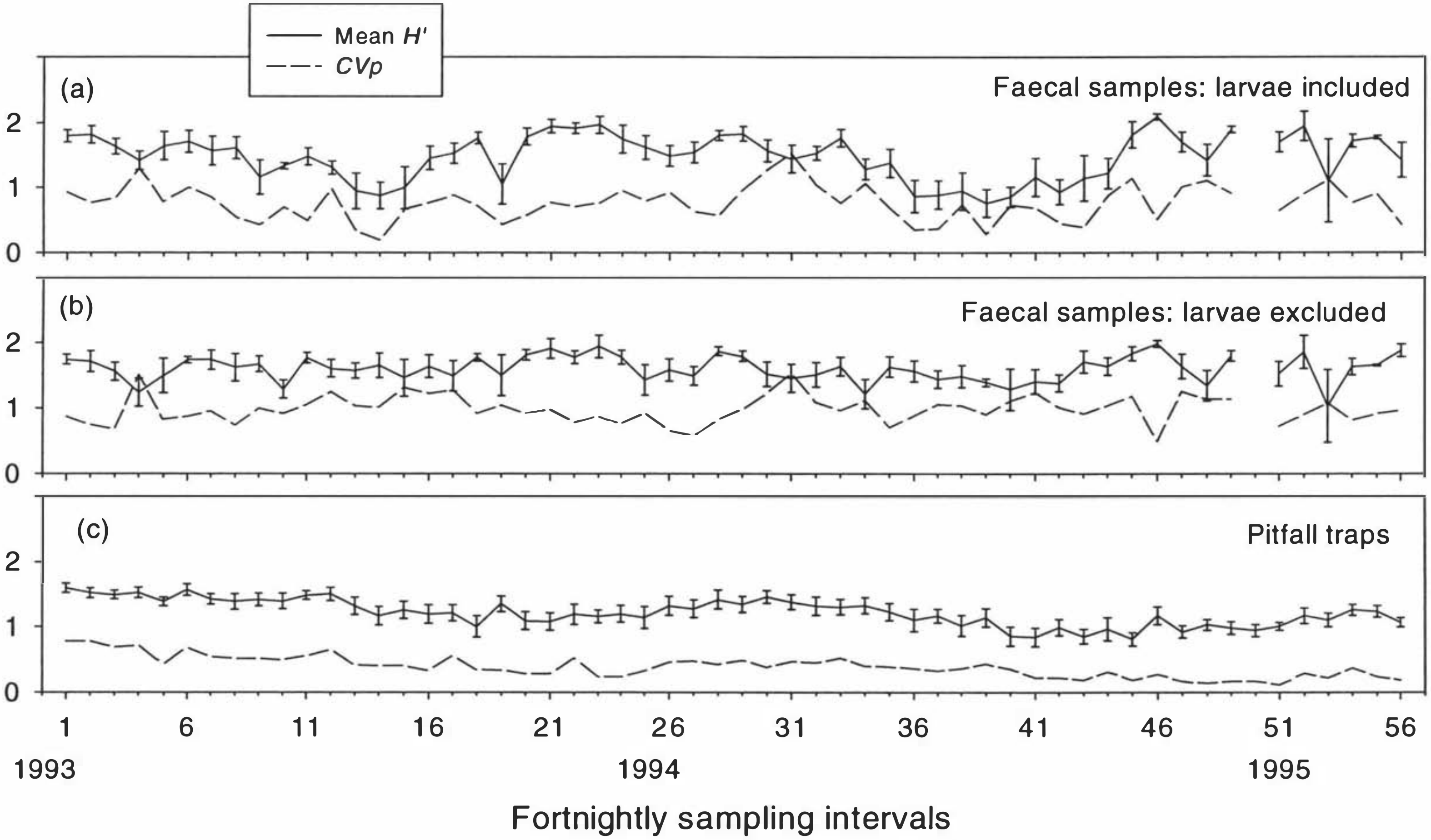


Figure 5-15. Homogeneity values (*H'* for Shannon's diversity index, continuous lines) and a coefficient of variation (*CVp*, dashed lines) for percent occurrence of numbers of animals in 15 categories in faecal samples with (a) and without (b) larvae and pitfall traps (c) at Pic Ningua (Appendix X). Descriptions of *H'* and *CVp* are in section 5.2.14. There were no faecal data for interval 50. Sample sizes for faecal data are in Figure 5-14a, and n = 9 for all pitfall trap data (all error bars ± 1 s.e.).

Variation among individual birds (*CVp*, high values indicate increased variation) in the use of each of the 15 prey categories was generally positively associated with diet homogeneity when larvae were included in the data (Fig. 5-15a). This suggested that greater homogeneity was achieved by increased diet variation among individuals, but at times of lowest homogeneity individual diets were very similar. The most obvious exception was for interval 46 when the highest homogeneity value was associated with a low *CVp* value, in extremely dry conditions. When I removed larvae from the data, *CVp* values tended to be negatively associated with homogeneity values, suggesting that when birds were eating large numbers of larvae their diets differed considerably in the other hard-bodied prey they used. *CVp* values when larvae were removed were lowest in interval 46. Thus it appeared that the diets (only hard-bodied prey) of individual kagus were most similar in the dry season when birds were eating large numbers of larvae or when conditions were very dry.

I also compared variation in homogeneity over the study period between diet and pitfall trap data (Fig. 5-16). With larvae included, homogeneity between the two data sets was very similar over the 1993 and 1994 wet seasons and the dry seasons up until around September when larvae in birds' diets declined considerably. From October up to the first heavy rains of the wet season, diet homogeneity was generally much higher than occurred in pitfall traps. Similar patterns also existed in the data when larvae were excluded.

5.3.9 Correspondence analyses on kagu diet and pitfall trap data

The first two dimensions explained 78.88% of the inertia (or variance) (Table 5-9, Fig. 5-17) for the association between the 15 categories and intervals for pitfall trap data. Dimension one explained 61.99%, making the association between intervals and categories quite strongly one-dimensional. From the percent occurrence data graphed in Appendix X and the squared cosines (which indicate contribution to the inertia) for the row and column points (Appendix XI), dimension one positioned intervals and categories based mostly on the negative relationship in relative abundance of Amphipoda with Orthoptera and Scarabaeinae/Hybosoridae (Fig. 5-17a,b). The latter two categories were relatively more abundant in intervals in the early period of my study when Amphipoda abundance was relatively low. Dimension two was less easy to interpret. Percent occurrence graphs and squared cosines

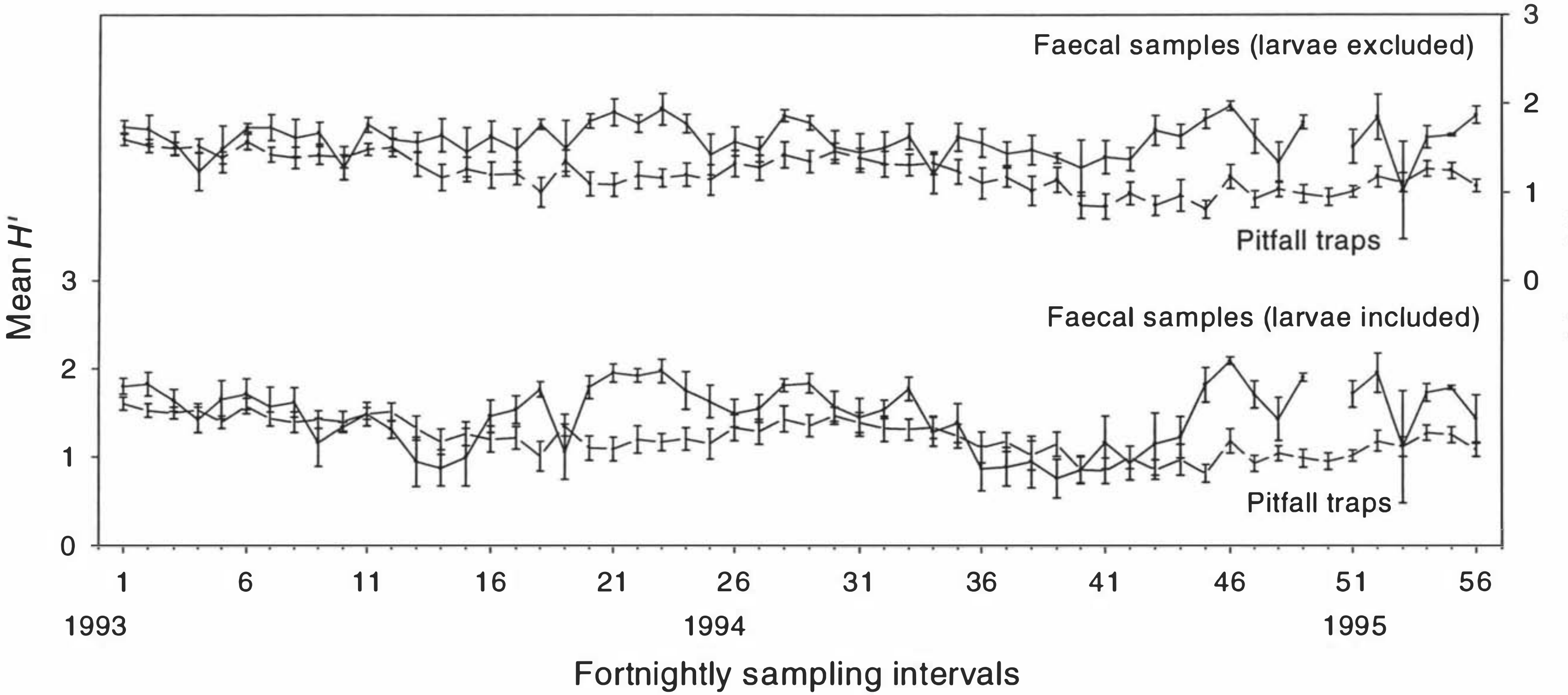


Figure 5-16. Plots of homogeneity values (Shannon's *H'*) taken from Figure 5-15. Homogeneity values for faecal data (continuous lines) with and without larvae are graphed separately with homogeneity values for pitfall traps at Pic Ningua (dashed lines). See legend to Figure 5-15 for additional graph details.

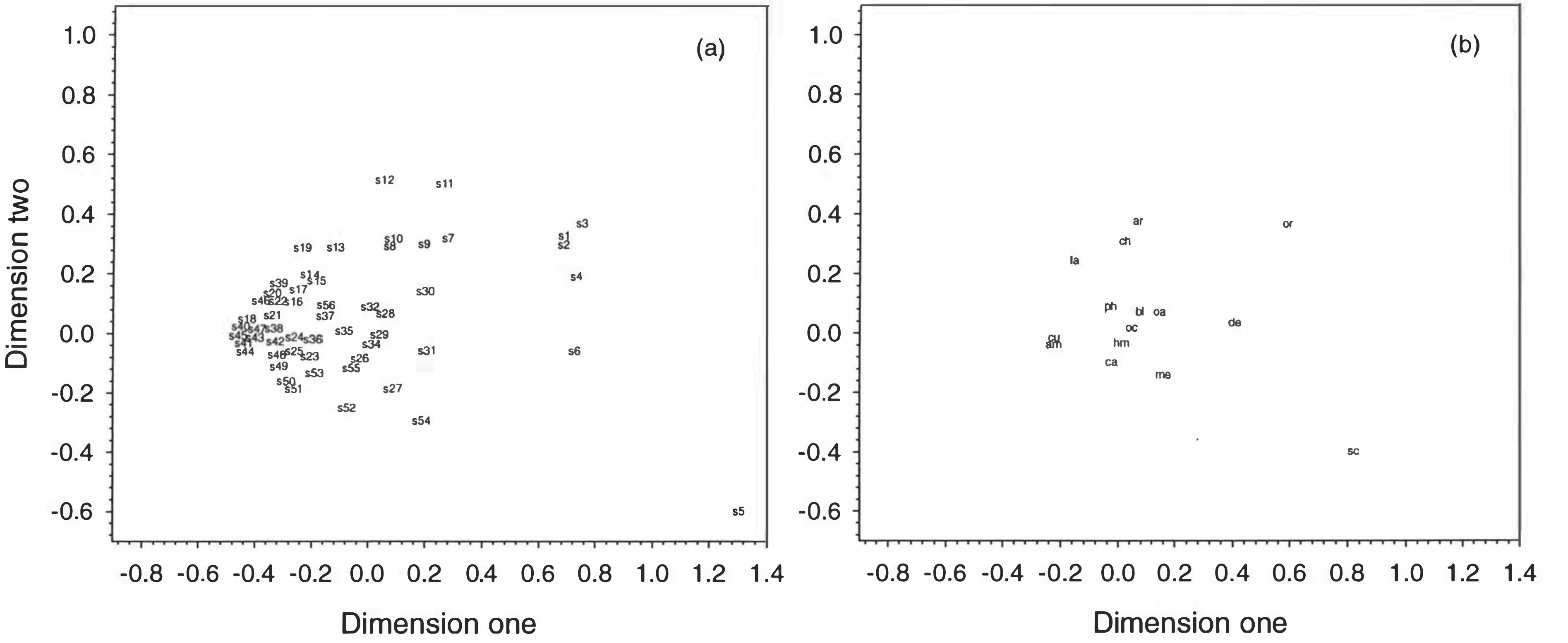


Figure 5-17. Plots of dimension one against dimension two for correspondence analysis on pitfall trap data at Pic Ningua. Plot (a) shows the positions of intervals (symbols s1-s56), and plot (b) the positions of the 15 categories. Categories are indicated by symbols: 'am' = Amphipoda, 'ar' = Araneae, 'bl' = Blattidae, 'ca' = Carabidae, 'ch' = Chilopoda, 'cu' = Curculionoidea, 'de' = Dermaptera, 'hm' = Hemiptera, 'la' = Larvae, 'me' = Melolonthinae, 'oa' = Other adults, 'oc' = Other Coleoptera, 'or' Orthoptera, 'ph' = Phasmatoidea, 'sc' = Scarabaeinae/Hybosoridae. I moved symbols of some intervals on plot (a) to avoid overlapping.

(Appendices X and XI) indicated that it mostly represented the negative relationship of Araneae, Chilopoda and Orthoptera to Scarabaeinae/Hybosoridae. Thus the association between the 15 categories in intervals appeared to be explained by both seasonal and year-to-year variation.

Table 5-9. Inertia and chi-square decomposition for the first five dimensions for correspondence analyses on diet and pitfall trap data at Pic Ningua. Rows were intervals and columns the 15 categories in Appendix X. Data were numbers of animals in each category not percent occurrence as was graphed in Appendix X.

Dimension	Principal inertias	Chi-square	Percent of chi-square
Pitfall trap data			
1	0.1316	2,447.80	61.99
2	0.0358	666.88	16.89
3	0.0144	267.89	6.78
4	0.0098	182.58	4.62
5	0.0085	158.79	4.02
Diet data			
1	0.3469	252.80	40.67
2	0.1967	143.33	23.06
3	0.0697	50.79	8.17
4	0.0647	47.16	7.59
5	0.0434	31.65	5.09

The first two dimensions for diet data explained slightly less inertia (66.67%) than those for pitfall trap data, and were more equal in the amount each explained (Table 5-9). Thus the association was more two-dimensional, as is indicated in Figure 5-18a where the pattern in the spread of the plotted intervals tended to be triangular. From the percent occurrence graphs (Appendix X) and the squared cosines for the row and column points (Appendix XI), dimension one positioned intervals and categories based mostly on the negative relationship between the relative abundance of larvae and all other categories, especially Carabidae, Curculionoidea and Melolonthinae (Fig. 5-18a,b). Larvae were eaten in relatively large numbers in intervals tightly grouped towards the lower left-hand corner of Figure 5-18a. This seemed to

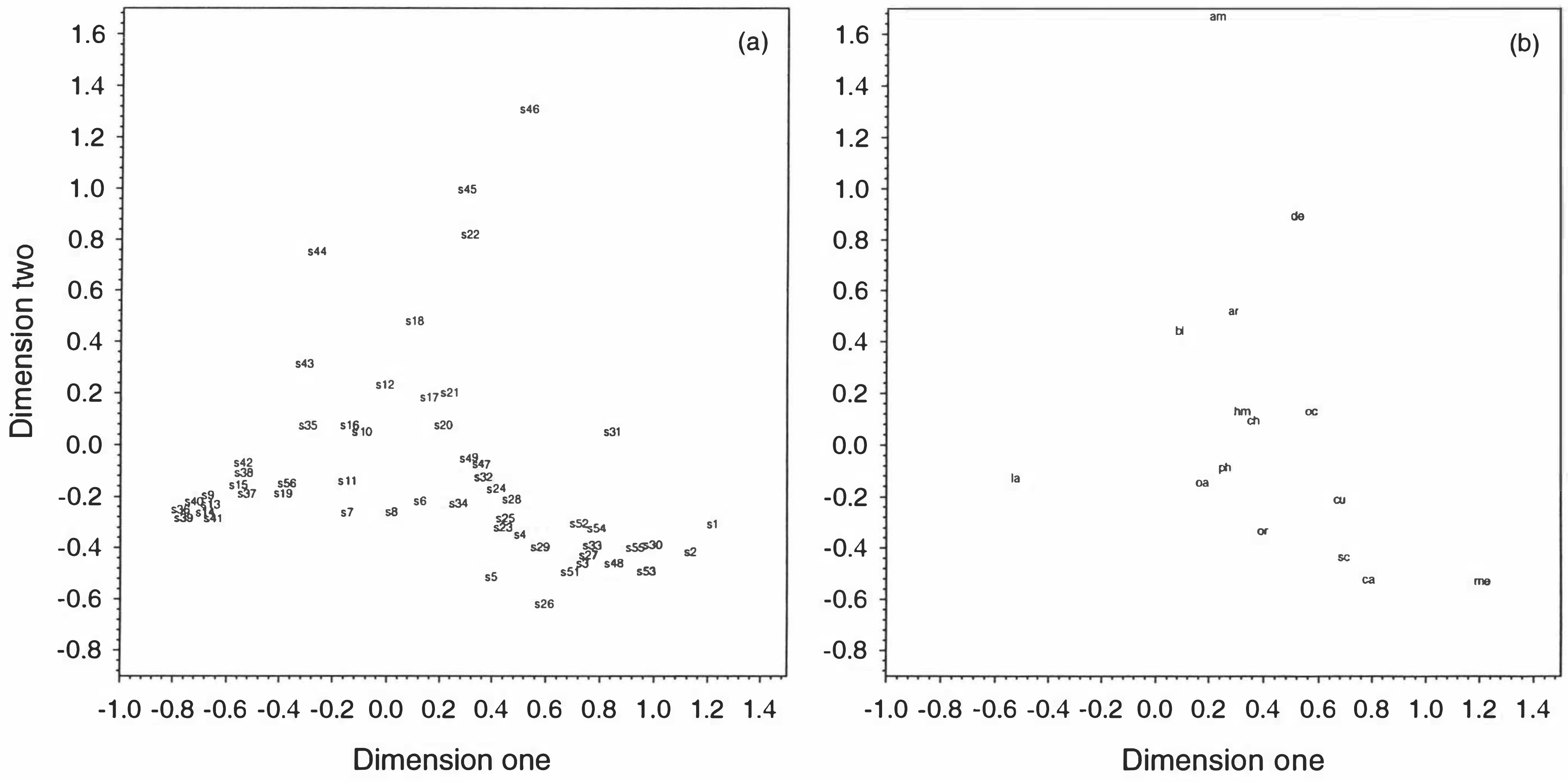


Figure 5-18. Plots of dimension one against dimension two for correspondence analysis on diet data at Pic Ningua. Plot (a) shows the positions of intervals (symbols s1-s49, s51-s56), and plot (b) the positions of the 15 categories. See legend to Figure 5-17 for the key to the symbols on plot (b). I moved symbols of some intervals on plot (a) to avoid overlapping.

distinguish kagu diets in the early dry season from those at other times as birds ate larvae in relatively greater numbers in the former period. Dimension two explained 26.48% of the inertia (Table 5-9). From the percent occurrence graphs and squared cosines (Appendices X and XI), this dimension represented the negative relationship between Amphipoda, Araneae, Blattidae and Dermaptera and other prey categories (Fig. 5-18b). Thus dimension two seems to distinguish kagus' diets in very dry conditions from those at other times.

Results of the correspondence analyses above suggested that variation between intervals in pitfall trap fauna and kagu prey might be under a strong seasonal influence. This might have been a consequence of combining all taxa together, therefore I checked the strength of the associations between the abundance of animals in intervals for the taxa in pitfall traps and faecal samples at Pic Ningua (Fig. 5-8) with both rainfall and minimum temperature (Table 5-10). For pitfall traps, 23 of the correlations with minimum temperature were significant, and 20 with rainfall. For many taxa, the coefficients were considerably higher for minimum temperature than rainfall, notable exceptions were for Diplopoda, Diptera larvae and Athoracophoridae. For faecal data, there were 11 significant correlations with rainfall and 14 with minimum temperature. As with the trap data, most strong correlations (Blattidae, Carabidae, Diptera larvae, Melolonthinae and Tipulidae pupae) were with minimum temperature. Blattidae had a strong negative association with rainfall. In contrast to the pitfall trap data, there were many negative correlations between taxa in faecal samples and the two weather variables, which indicated that kagus ate these taxa more in the dry season, but most were more abundant in traps in the wet season. These included Amphipoda, Araneae, Blattidae, Chilopoda, Dermaptera, Hemiptera and Coleoptera larvae.

Table 5-10. Spearman correlation coefficients between taxa in pitfall traps and faecal samples (Fig. 5-8), and rainfall (Fig. 3-3) and minimum temperature (Fig. 3-8) in forest at Pic Ningua. Data for all taxa in pitfall traps were numbers of animals, but were percent data (Diplopoda, snails, Other Arachnida, Scincidae, and Tipulidae pupae) or numbers of chaetae (Oligochaeta) for some taxa in faecal samples. '*' = p < 0.05 (sample sizes, or numbers of intervals, are in brackets beneath each variable name). A '----' indicates no taxa were recorded.

Analysis	**Pitfall traps**		**Faecal samples**	
Variable	**Rainfall**	**Minimum temperature**	**Rainfall**	**Minimum temperature**
N	**(56)**	**(54)**	**(55)**	**(54)**
Amphipoda	0.45*	0.58*	-0.40*	-0.36*
Athoracophoridae	0.49*	0.43*	----	----
Araneae	0.33*	0.69*	-0.42*	-0.34*
Blattidae	0.64*	0.82*	-0.56*	-0.61*
Carabidae	0.52*	0.86*	0.29*	0.67*
Chilopoda	0.34*	0.61*	-0.33*	-0.21
Coleoptera larvae	0.45*	0.71*	-0.23	-0.32*
Curculionoidea	0.12	0.43*	-0.15	0.21
Dermaptera	0.43*	0.81*	-0.26	-0.20
Diplopoda	0.54*	0.53*	0.07	0.15
Diptera	0.16	0.71*	----	----
Diptera larvae	0.47*	0.09	-0.31*	-0.77*
Gastropoda (snails)	0.67*	0.69*	0.22	0.14
Hemiptera	0.38*	0.51*	-0.30*	-0.22
Hymenoptera	0.39*	0.88*	-0.01	-0.03
Lepidoptera	-0.25	0.03	----	----
Lepidoptera larvae	0.13	0.32*	----	----
Melolonthinae	0.26*	0.79*	0.04	0.56*
Oligochaeta	-0.03	0.27*	0.42*	0.51*
Orthoptera	0.57*	0.78*	0.25	0.14
Other adults	0.30*	0.38*	-0.23	-0.25
Other Arachnida	-0.21	-0.09	-0.07	-0.11
Other Coleoptera	0.26*	0.72*	-0.23	0.10
Phasmatoidea	0.28*	0.48*	0.10	-0.20
Scarabaeinae/Hybosorid.	0.44*	0.85*	0.21	0.31*
Scincidae	0.35*	0.59*	-0.08	0.02
Thysanura	0.19	0.19	----	----
Tipulidae pupae	----	----	0.40*	0.75*
Turbellaria	-0.08	0.05	----	----
Unidentified animals	----	----	0.11	0.02
Unidentified larvae	----	----	-0.00	-0.35*

5.3.10 Effects of feral pig foraging on kagu food supplies at Pic Ningua

Only pitfall trap sites at Pic Ningua received noticeable damage from pig rooting (Table 5-2). Pitfall trap sites PS1, PS3 and PS5 were frequently disturbed by pigs (Table 5-11). PS5 was the most disturbed site and much of the ground was turned over, but pig rooting there ceased from interval 42. PS4 and PS6 were moderately disturbed in intervals 29-56, and PS2, PS7, PS8 and PS9 little or not disturbed.

Table 5-11. Numbers of individual pitfall traps at pitfall trap sites at Pic Ningua with fresh pig rooting within 1 m radius in intervals 29-56. I recorded damage each fortnight when I emptied the traps. Pig exclosures were erected around five of the ten traps at pitfall trap sites PS1, PS3, PS5, and PS6 (section 5.2.8).

Interval	**Trap sites**								
	N1	**N2**	**N3**	**N4**	**N5**	**N6**	**N7**	**N8**	**N9**
29					5				
30			2	1	2				
31	2			1	5				
32				3	3				
33					5				
34			1	1					
35	2		2	1	4				
36						2			
37			2			1			
38									
39	2		3		2				
40			2						
41									
42			1		4				1
43				1		1			
44	2		1	1					
45			1						
46									
47			2						
48	3								
49			2						
50	2		2						
51									
52	2					1			
53			2						
54			2	2		3			
55	1								
56			2						

When I compared sites little or not pig disturbed (PS2, PS7, PS8 and PS9) with those highly disturbed (PS1, PS3 and PS5), animal abundance and dryweight biomass in traps were generally less at the latter sites (Fig. 5-19). These differences were statistically significant (Repeated measures ANOVA; Table 5-12). The pattern of variation over time for animal abundance was the same at disturbed and undisturbed sites, but varied significantly for dryweight biomass (Repeated measures ANOVA: Interval x Pig disturbance interactions; Table 5-12). Homogeneity did not vary between sites with high and little or no pig disturbance (Repeated measures ANOVA; Table 5-12). The pattern of variation in homogeneity over time also did not vary between sites with different levels of pig disturbance (Repeated measures ANOVA: Interval x Pig disturbance interaction; Table 5-12).

Table 5-12. Results of repeated measures ANOVA analyses comparing (log-transformed) animal numbers and dryweight biomass collected in pitfall traps at Pic Ningua, and homogeneity across 15 categories, between sites little or not (PS2, PS7, PS8 and PS9) and highly (PS1, PS3 and PS5) pig disturbed. Column 6 gives the Huynh-Feldt adjusted-F values (see section 3.2.9). Data are in Figures 5-15c and 5-19.

Source	**d.f.**	**MS**	**F**	**p > F**	**p > F (H-F adj.)**
Dependent variable: Log animal numbers in pitfall traps					
Pig disturbance	1	36.8482	7.44	0.0414	------
Interval	55	3.2003	35.41	------	0.0001
Interval x Pig dist.	55	0.1511	1.67	------	0.1223
Dependent variable: Log animal dryweight biomass in pitfall traps					
Pig disturbance	1	19.1559	25.38	0.0040	------
Interval	55	4.8700	46.60	------	0.0001
Interval x Pig dist.	55	0.2197	2.10	------	0.0130
Dependent variable: Homogeneity in pitfall traps					
Pig disturbance	1	11.0061	3.93	0.1041	------
Interval	55	0.3036	6.12	------	0.0001
Interval x Pig dist.	55	0.0681	1.37	------	0.1733

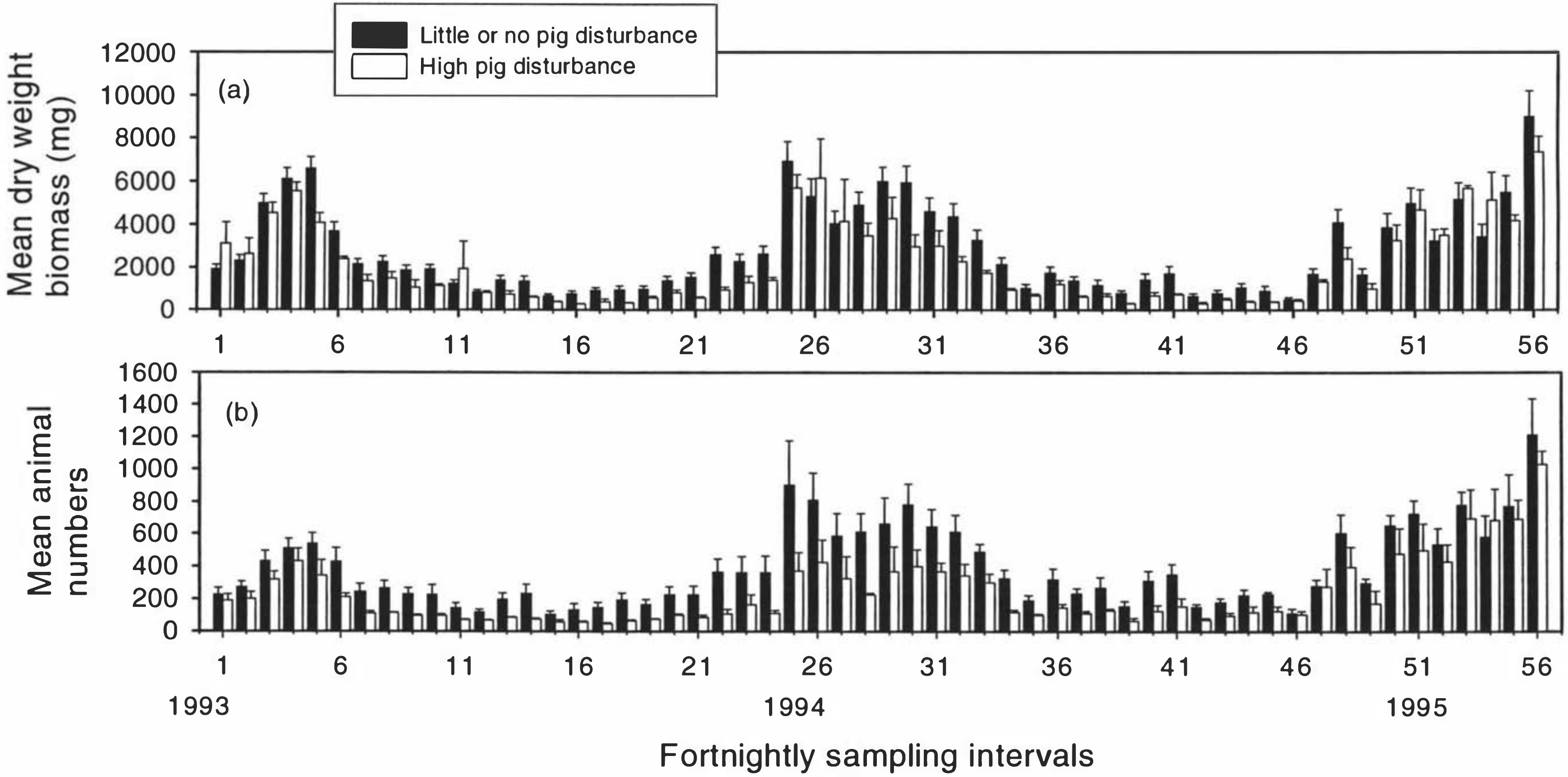


Figure 5-19. Comparison of mean total animal dryweight biomass (a) and numbers (b) captured in pitfall traps at Pic Ningua between sites with high (PS1, PS3 and PS5; unfilled bars) and little or no (PS2, PS7, PS8 and PS9; black bars) pig rooting disturbance (error bars = 1 s.e.).

I collected 53 individual feral pig faecal samples over a period of approximately six months (29/8/94-5/3/95) in forest at Pic Ningua. I found invertebrate parts in all the samples, which I separated into 16 taxa and one class of unidentified animals (Fig. 5-20). Percent occurrence of these taxa in the 53 samples ranged from 72% for Scarabaeoidea larvae to 2% for Formicidae and Other Coleoptera. The frequency of the 17 categories per sample ranged from one to nine (mean = 4.09, s.d. = 1.93, n = 53).

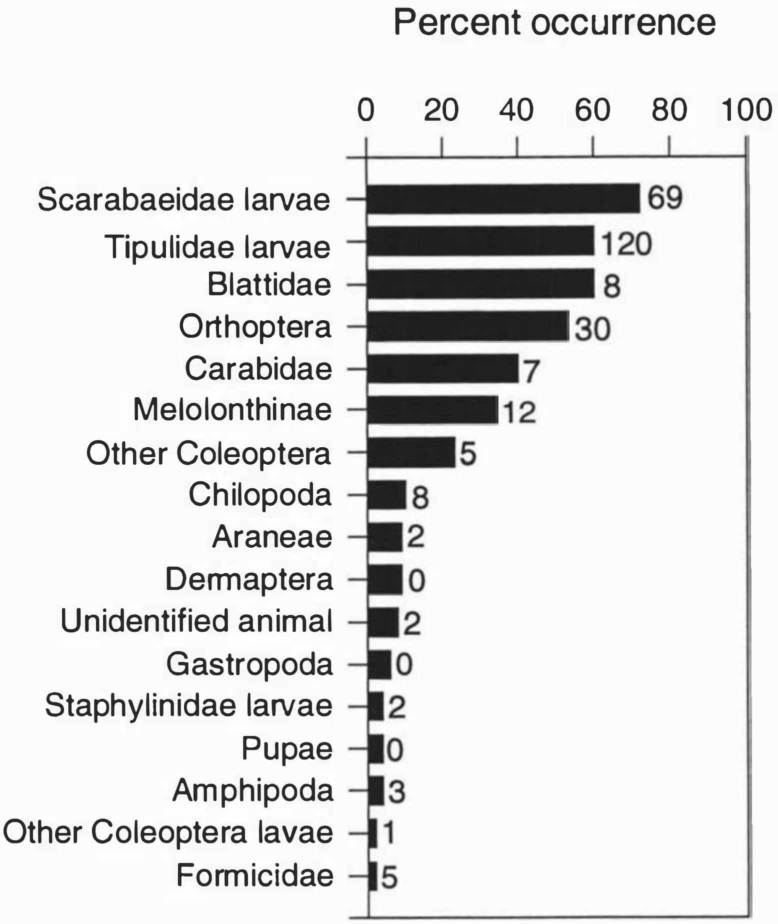


Figure 5-20. Percent occurrence of taxa identified and unidentified in 53 feral pig faecal samples collected in forest at Pic Ningua. Numbers next to the bars give the total numbers of individuals quantified for each taxa. A '0' value indicates taxa that were present but could not be quantified.

5.4 Discussion

5.4.1 Abundance of soil and litter animals

My results at Pic Ningua were consistent with other studies in tropical rainforests that showed seasonal and year-to-year variation in insect abundance (Wolda 1988). I found strong seasonal variation in the numbers of animals captured in pitfall traps and their associated dryweight biomass over a 26 month period. Mean numbers and dryweight biomass of animals captured did not vary between years, suggesting that overall levels of food supplies for kagus might be very similar each year. Year-to-year variation in availability of individual taxa is probably common in tropical forests (Wolda 1978b, Wolda and Fisk 1981). The different patterns of variation in total animal numbers and biomass between years at Pic Ningua was probably strongly influenced by the changing relative abundance of Amphipoda (the most numerous taxon). Nevertheless, similar strong seasonal patterns of variation in animal abundance and dryweight biomass in 1993 and 1994, indicated that the seasonality in potential kagu food supplies on the peak probably occurred annually. Animal abundance and biomass in pitfall traps at all three study areas peaked during hot, wet conditions associated with tropical depressions or cyclones, and was lowest in the driest period (September and October) of the dry season. This was consistent with other studies in tropical rainforests, and kagu foraging behaviour at Parc Rivière Bleue (section 5.1). The only taxa in pitfall traps (Fig. 5-8) showing a distinct negative seasonal trend (i.e. wet-season-low/dry-season-peak) was Diptera larvae, whose numbers tended to peak in the early dry season.

El Niño can seriously effect food supplies and reproduction for sea and land birds (Barber and Chávez 1986, Hall *et al.* 1988, Grant and Grant 1996). The seasonality I found may have been strengthened by the El Niño event influencing the southwest Pacific during my study (section 1.3), that was associated with generally drier and cooler weather in New Caledonia. The lowest animal abundance when conditions were dry and/or cold indicated that this might have been the case. Dry conditions can also affect insect abundance in the following wet season (Wolda 1978), thus the extremely dry spell in October 1994 might have reduced the abundance of some taxa in the 1994/95 wet season. However, if this occurred it was not evident at Pic Ningua, as animal abundance there tended to be higher in the wet season of 1994/95 compared to 1993/94. Abundance at Mt Cindoa though, tended to be lower in the

1994/95 wet season compared to the 1993/94 one. The dry conditions in October 1994 may have had a greater effect on subsequent abundance because of the normally wetter climate there.

Other evidence suggested that the seasonality I observed recurred each year at Pic Ningua regardless of the prevailing climatic conditions. First, the strong associations between air temperature and the abundance of many taxa in pitfall traps suggested this, together with the fact that long-term air temperature records at Thio did not differ greatly from the temperatures recorded there in 1993 and 1994 (Fig. 3-9). Second, although weather at Pic Ningua in 1993 and 1994 was probably drier than average, long-term records at Thio showed the same strong annual variation in rainfall that I recorded during my study. Last, Frith and Frith (1985) investigated seasonality in insect abundance (using light and malaise traps) at *c.* 875 m in an east coast Australian tropical forest at a slightly lower latitude (19°S) than Pic Ningua from 1978 to 1981 over three wet seasons. The seasonal variation in climate at their study site was very similar to that at Pic Ningua, but it received considerably more rainfall in the wet season. They found strong seasonality in insect abundance; numbers peaked in the wet season and were generally lowest in the colder months of the dry season (June-August). They also found that the seasonality in abundance was similar between years.

Few data exist to enable a comparison of soil and litter animal abundance at my study sites to that elsewhere in tropical and temperate regions because such studies are rare and collection methods differed. However, Leakey and Proctor (1987) and Thomas and Proctor (1997) found ‘substantial’ arthropod populations still occurred on potentially toxic ultrabasic soils at their study sites. Moeed and Meads (1985) pitfall trapped over 14 months at four sites ranging from 150 m to 800 m a.s.l. in different forest types near Wellington, New Zealand. Mean air temperatures ranged from approximately 6°C to 15°C at 150 m a.s.l. at their study site (it was unclear whether this was inside or outside forest). I used virtually the same pitfall trapping methods that they used (10 individual traps at each site, and each trap approximately 100 mm^2 in trapping area) thus a direct comparison was possible. They captured (excluding Acari and Collembola) an average of 7,633 animals at each site over 14 months, whereas I captured an average of 9,550 animals at each of my nine pitfall trap sites at Pic Ningua over 13 months. Thus my results also suggest that ultrabasic soils can support considerable numbers of soil and litter arthropods. A comparison of the average numbers of certain taxa captured per site between data from Pic Ningua and those in Moeed and Meads's study was also interesting (numbers are rounded): Amphipoda, 6,006 and 2,285, respectively; Araneae, 363 and 627; Blattidae, 91 and 33; Carabidae, 90 and 123; Chilopoda, 19 and 13; Dermaptera, 52 and 1; Diplopoda, 64 and 262; Hemiptera, 138 and 164; and Orthoptera, 955 and 288. Moeed and Meads's also presented seasonal data. The mean total numbers of 12 taxa (Blattidae, Dermaptera, Orthoptera, Phasmatoidea, Hemiptera, Thysanura, Coleoptera, Amphipoda, Isopoda, Chilopoda, Diplopoda and Araneae) captured at their four sites in each season were: winter (June-August), 509 animals; spring (September-November), 857; summer (December-February), 1,509; and Autumn (March-May), 1,583. Thus abundance tended to peak in autumn which was later than at Pic Ningua.

There were similarities between temporal variation in both minimum air temperature and rainfall with that of animal abundance in pitfall traps at Pic Ningua. Correspondence analysis suggested that variation between intervals across 15 taxa was largely explained by the negative relationship between relative abundance of Amphipoda, and Orthoptera and dung beetles. These three taxa were more strongly correlated with minimum temperature than with rainfall. This, and the generally stronger correlations between taxa in pitfall traps and minimum temperature than between taxa and rainfall, suggested that temperature might be a better predictor of changing animal abundance at Pic Ningua than rainfall. This would contrast with most other studies in tropical rainforests with seasonal climates that generally suggested rainfall was the main climatic factor associated with variation of insect abundance (e.g., Frith and Frith 1985).

The same seasonal pattern of animal abundance in pitfall traps at Pic Ningua also occurred at Mt Cindoa and Parc Rivière Bleue, although abundance (particularly of Amphipoda) was significantly lower at the latter two areas. This difference may have been partly influenced by my lower sampling intensity at those areas. Annual variation was weaker at Parc Rivière Bleue as indicated by the lower wet season/dry season ratios there for abundance and dryweight biomass, and that mean animal numbers in pitfall traps in the dry season in some intervals (e.g., 41, 47 and 48) were often similar to numbers in intervals in the wet season. The greater evenness in abundance at the Parc compared to the high altitude areas was less likely to be an artefact of lower sampling intensity and may have been related to the milder, but still seasonal (Fig. 5-6), climate at lower altitude. Seasonal variation of air temperature at Parc Rivière Bleue was just as great as that I recorded at the high altitude areas, but generally several degrees warmer. The wet season/dry season ratios at Pic Ningua and Mt Cindoa were higher than at Parc Rivière Bleue, which is consistent with higher ratios found in more temperate and harsh climates (Bell 1985). Although animal abundance and dryweight biomass at Mt Cindoa were lower than at Pic Ningua, ratios at the former area were higher suggesting that conditions there may be less favourable for soil and litter fauna. This could explain why kagus at Mt Cindoa tended to have lower bodyweights that birds at Pic Ningua (sections 3.3.3 and 3.3.11). Lower mean biomass at Parc Rivière Bleue compared to Pic Ningua is consistent with studies that show higher biomass of soil and/or litter invertebrates at intermediate altitudes on tropical mountains, possibly because of more favourable microclimates in that habitat (Leakey and Proctor 1987, Olson 1994). This might be expected when other data show mid-altitude peaks in flying insect biomass and species richness in the tropics (Janzen 1980).

Variation in the abundance of different taxa between pitfall trap sites at Pic Ningua was relatively low as indicated by the generally small error bars in Figure 5-8, and the small *CVp* values (Fig. 5-15c) calculated on percent occurrence data. This is probably an indication that the soil and litter environment in the forest understorey is relatively spatially homogenous and physically buffered (Sherry 1984).

Although relative abundance of Amphipoda in pitfall traps at Pic Ningua tended to increase over time, this did not appear to mean a decline in other prey for kagus. There was no corresponding trend for a reduction in numbers of the various taxa that birds preyed on (Fig. 5-8). On the contrary, numbers of certain taxa tended to increase in 1994 compared to 1993, for example Blattidae, Carabidae, Coleoptera larvae, Curculionoidea, Hemiptera and Melolonthinae. Also, mean kagu bodyweights in 1994 did not reach the lowest mean weight recorded in 1993. This seemed to suggest that conditions for soil and litter fauna improved over the period of my study on the peak, and differences in kagu bodyweight variation between years was probably more related to changing environmental conditions rather than a consequence of birds' larger home ranges.

My pitfall trapping probably provided a biased picture of the community of litter-inhabiting fauna (section 5.2.9). This seemed to be especially so in cooler months.

For example, although Blattidae captured in traps in 1993 showed the usual seasonal distribution, this was not the case for these animals that I captured in litter searches. Also, I saw Scincidae in most intervals when I carried out litter searches, but they were virtually absent in traps over the coldest dry season months. Scincidae remains occurred in faecal samples over the dry season indicating that although these animals were apparently less active, kagu were still capturing them. Therefore the increased diversity and abundance in warmer months may have resulted in part from increased activity by fauna present year round (e.g., Scincidae) or the increased probability that they would fall into the traps. Other animals like Melolonthinae adults were mostly only present over summer after emerging from the larval stage.

5.4.2 Effects of pig rooting on kagu food supplies

My results show the potential for feral pigs to compete indirectly (by damage to the forest understorey) and/or directly (by eating kagu prey) with kagus for food supplies. Pig-disturbed pitfall trap sites were associated with lower animal numbers and dryweight biomass, therefore pig rooting probably indirectly reduces at least some prey for kagus in highly disturbed areas. Prey likely affected would be litter dwelling species because forest litter was scarce in disturbed areas. It was interesting that the pattern of variation over time between sites little and highly disturbed by pigs was only different for dryweight biomass. Figure 5-19 seems to indicate that the reason for this was the higher biomass at disturbed sites in intervals in both the 1994 ($n = 2$) and 1995 ($n = 3$) wet seasons (higher animal numbers at disturbed than undisturbed sites only occurred once, in interval 54). This appeared to be largely due to the capture of more large mobile Carabidae beetles at the disturbed sites (data not presented in the thesis). Therefore pig rooting might not stop more mobile animals like beetles using disturbed areas. Homogeneity in pitfalls was not different between disturbed and undisturbed sites, which also suggests that the main effect of pig rooting might be to reduce rather than alter composition of the soil and litter fauna. However, I did not investigate the effect of night versus day on the presence of soil and litter fauna between disturbed and undisturbed sites. As with the Carabidae, animals may use or travel over disturbed areas more at night between undisturbed areas, thus making disturbed areas poor foraging sites for kagus during the day.

All the taxa I identified in feral pig faeces at Pic Ningua were also eaten by kagus on the peak, therefore pigs could also compete directly with kagus for prey. The potential for competition was highlighted by the fact that (1) the six taxa at highest frequency in pig faeces were also the six taxa eaten in the highest numbers by kagus at Pic Ningua (Table 5-7); and (2) the high frequency (from 34%-72%) of these six taxa in pig faeces. It was also interesting that I did not find Curculionoidea parts in pig faeces when they were common in kagu faeces, which suggests that kagus might find these animals on substrate above the forest floor (mainly tiny Curculionoidea fell into pitfall traps at Pic Ningua, section 5.2.3).

Thompson and Challies (1988) found that invertebrates composed only 2.7% of the diet of feral pigs in podocarp-tawa forests in New Zealand. However, they only collected material in a 4.0 mm sieve, and nearly all the invertebrate parts that I found would have passed through this mesh size. Thus the pigs' diets may have consisted of a considerably higher percentage of invertebrates than their study suggested.

5.4.3 Kagu diet and its relationship to food availability and abundance

Kagu diet at Pic Ningua and Mt Cindoa was considerably more diverse than that described by Létocart (1989). New taxa I recorded eaten by birds were Amphipoda, Amblypygi, Apoidea, Blattidae, Carabidae, Cerambycidae, Chilopoda, Chrysomelidae, Diptera larvae (not Tipulidae), Formicidae, Isopoda, Neuroptera larvae, Orthoptera, Pompilidae, Reduviidae, Staphylinidae and Triaeononychiidae. Except for Triaeononychiidae, all these taxa were captured in pitfall traps at the Parc, in my study or by Létocart (1989) (Apoidea), thus kagus may also eat them there.

The close similarity between the range of taxa used by kagus and those captured in pitfall traps at Pic Ningua indicates that birds were generalist predators of forest floor fauna when overall dietary composition was considered. This relationship would probably be closer than I showed if soft-bodied prey that were probably eaten by kagus (e.g., Athoracophoridae, Turbellaria) were included. Given that kagu prey were relatively evenly dispersed in forest and birds ate a wide range of prey, the movements of birds after the dog attacks may not have greatly affected their diets. Also, the diets of birds at Pic Ningua and Mt Cindoa were very similar, where birds at the latter area generally moved in small home ranges.

I only measured animal abundance rather than quality of food supplies (e.g., lipid and protein content), but the former is probably a good indicator of the resources available for reproduction. First, biomass of total invertebrate prey is probably an accurate indicator of its energy content (Brodmann *et al.* 1997 cited in Brodmann and Bollmann 1997). The close relationship between kagu bodyweight and dryweight biomass tended to support this. Second, energy content may be more important than nutrients (excluding Calcium for egg-shell formation) or protein for reproductive success (Brodmann and Bollmann 1997).

Létocart (1989) observed that kagus foraged more or less continuously during daylight hours (section 1.4), therefore birds could be under considerable selection to forage efficiently to meet their energy needs. This might be especially so at Pic Ningua and Mt Cindoa during periods when (non-breeding) birds experienced continual bodyweight decline for many weeks in the dry season when food supplies also appeared to be scarce. At these times, natural selection should favour individual strategies for maximising net energy intake over time (Catterall 1985). Kagus should therefore show appropriate shifts in diet selectivity in response to changing environmental and physiological conditions, besides that related to seasonal changes in their food resources. The similar year-to-year variation in dietary homogeneity suggested that kagu diets were strongly influenced by seasonal changes in their food supplies.

Taxa in pitfall traps and kagu faeces were not directly comparable (e.g., ground-dwelling larvae were rare in pitfalls). Nevertheless, correspondence analyses suggested non-random use of prey by kagus might be occurring because the associations between time and the 15 taxa in pitfall trap and diet samples differed markedly. The diet analysis identified three broad temporal diet differences that were associated with environmental conditions. These differences were associated with (1) warm and wet; (2) cool and damp; and (3) cool and dry conditions. I next examine each of these three main diet differences in turn to see if kagus foraged selectively as theory predicted to maximise their net energy intake over time in response to changing energy needs and levels of food supplies.

Theory predicted that common prey in kagu diet when food was diverse and plentiful (clearly in the wet season when kagu bodyweights were also high) would be preferred prey if it was not super-abundant, and their frequency in kagu diet should closely match their availability. From correlations between faecal and pitfall trap samples in intervals for taxa that I quantified (legend to Fig. 5-8), and the relative percent occurrence of prey used in the wet season (Appendix X), Carabidae, Melolonthinae and Curculionoidea (all Coleoptera) met the above conditions for preferred kagu prey. That the former two taxa are nocturnal, all three were rare in my litter searches, and the latter two (especially larger Curculionoidea) rare in pitfall traps, indicates that kagus sought out these animals. Also, that Coleoptera are often common prey for birds (e.g., Reid *et al.* 1982, Amat 1986, Beauchamp 1987, Colbourne and Powlesland 1988, Galbraith *et al.* 1993, Shaffer and Laporte 1994, Itämies *et al.* 1996) suggests they are highly profitable prey. My litter searches though, were not carried out at dawn and dusk when nocturnal prey like large Carabidae and Melolonthinae may have been more active. There was circumstantial evidence that certain soft-bodied prey (Oligochaeta, Athoracophoridae) or those hard-bodied prey that were difficult to quantify (Diplopoda, snails, Scincidae and Tipulidae pupae) might also be preferred prey. First, the combination of high bodyweights and low total prey numbers in faecal samples in the wet season indicated this. Second, some of the above prey, at least, were likely to have been highly profitable because they were often large items (e.g., snails, Oligochaeta, Scincidae, and Athoracophoridae). Last, the presence of these taxa was generally higher in pitfall trap and/or faecal samples in the wet season (Fig. 5-8). Earthworms, when available, may constitute a large part of kagu diet (Létocart 1989), which would not be surprising given that kagus foraged in soil and earthworms are known to be highly profitable for many bird species. For example, New Zealand kiwis *Apteryx* spp. (Colbourne and Powlesland 1988) and common Snipe *Gallinago* sp. (Lofaldli *et al.* 1992, Green *et al.* 1990) have a high occurrence of earthworms in their diets. Thus in warm, wet weather when most kagu prey were more abundant, it seemed that birds had diet preferences, and possibly selected larger and/or more profitable prey. At Pic Ningua, Amphipoda were absent in kagu faeces collected in the wet season when these animals were by far the most abundant potential prey. This suggests that Amphipoda, at least, were outside the 'optimal prey set' for kagus in the wet season (Krebs 1991).

In the early dry season, homogeneity across the 15 prey categories was lowest as kagus fed on relatively large numbers of larvae. Although there may have been a positive relationship between larvae availability and their numbers in faeces, larvae were not the only potential prey in the soil and litter. Three, not necessarily mutually exclusive, explanations might account for the high numbers of larvae eaten by kagus:

(1) birds targeted larvae because they were more profitable; (2) they 'encountered' them more often; and (3) larvae were eaten in larger numbers because they were spatially clumped. I suggest that kagus used larvae non-randomly for three reasons. First, as with large nocturnal Carabidae, larvae were concealed (in soil and wood) or probably difficult to find in the litter (I found only one Diptera larva in litter searches), which suggested that birds sought them out. Second, the combination of low homogeneity across prey categories and low variation (i.e. low *CVp* values) between the diets of individual kagus when they were eating high numbers of larvae indicated that birds were feeding similarly. Although the availability of many litter-dwelling taxa was far lower outside the wet season, animals like Amphipoda, Araneae, Blattidae, and Chilopoda were still present. These relatively mobile animals, though, may have been difficult for kagus to catch in damp conditions (see below). Last, larvae may have been the most profitable prey for birds trying to minimise bodyweight decline in the early dry season. Larvae in general are high in lipids and other necessary compounds (carbohydrates and protein) which are required for the metamorphosis to the adult insect stage (Kilby 1963, Gilbert 1967). Lipids are a highly efficient energy source for birds because they are quickly assimilated (Blem 1990), and Sprenkle and Blem (1984) showed in captive eastern house finches *Passer domesticus* that foods high in lipids provided better cold tolerance because they increased survival. However, Wansink and Tinbergen (1994) found no relationship between the fat content of food in the diet of captive great tits *Parus major* and ambient temperatures. Wild great tits appeared to eat more fat rich food (nuts) on colder winter days (Balen 1980), but alternative prey (insects) may have been less available then (Wansink and Tinbergen 1994). Although kagus in the early dry season were losing bodyweight, birds might have still foraged efficiently when larvae were common to minimise their net energy loss over time by avoiding certain prey (e.g., Amphipoda).

In the drier periods of the late dry season, kagus' diets changed from larvae-dominated ones to those composed of mostly litter-inhabiting prey (Amphipoda, Araneae, Blattidae, Chilopoda and Dermaptera). Birds also ate more Hemiptera at these times. Birds tended to eat more of the above six taxa when they were least abundant in pitfalls, however the only significant negative correlation between their abundance and use was for Blattidae. Blattidae, for example, were reasonably large prey items and were also eaten in considerable numbers by kagus. Therefore it was not clear why they were not eaten at higher frequency in the wet season when they were captured more in pitfall traps. This could mean that size might not be a good indicator of prey profitability for some taxa. If the six taxa were less preferred prey in the wet season, then their value would have increased in dry conditions when more preferred prey were much less available or absent (e.g., large Carabidae, larvae, Melolonthinae and Oligochaeta). Alternatively, the above six taxa may have been less available in wetter conditions (e.g., more difficult to capture). Circumstantial evidence for this was that all the above six taxa in kagu diet were negatively correlated (all significantly except for Dermaptera) with rainfall. Amphipoda, for example, tend to congregate in damp patches under litter in dry conditions (Beauchamp 1987, pers. obs.), therefore birds may have been able to fed on relatively greater numbers of them because of their highly clumped distribution. The increased use of Amphipoda by kagus in late September and October 1994, in association with very dry conditions and lowest bodyweights, strongly suggested that food and profitable prey were very scarce and birds were forced to eat least profitable prey. In very dry conditions, Amphipoda became relatively more common as soil animals became less available and many litter-dwelling ones probably seek refuge in inaccessible damper locations as indicated by the lower homogeneity values in pitfalls at these times. Thus Amphipoda became part of the 'optimal prey set' for kagus in these conditions, and the high dietary homogeneity and low dietary variation between individuals in interval 46 (the driest interval of the study) appeared to result from low selectivity when food availability was extremely low.

Food shortage cannot be inferred from falling bodyweights alone (Bednekoff and Houston 1994). That there was a food shortage for kagus during much of the dry season is strongly implied by the close positive association between falling bodyweights and low prey abundance, together with a lack of other factors that could have influenced kagu bodyweight variation (section 3.4.5). From the above discussion, there was considerable evidence that diet variation of kagus was not just related to seasonal changes in prey availability, but birds were using prey non-randomly to forage efficiently to meet their changing energy needs over time. More information however, like the ability of kagus to capture more mobile litter animals (e.g., Amphipoda, Blattidae, Dermaptera and Araneae) in wet conditions, is needed to better interpret kagu diet variation.

That kagus preyed on concealed prey (e.g., large nocturnal Carabidae, soil and wood-dwelling larvae) also raises the question of how birds detected them. Kagus have excellent vision (Pouget 1875), which Létocart (1989) thought was the main method they used to detect prey. However, the detection of concealed prey would seem to require other modalities such as sound, smell, vibration or perhaps learning by experience where prey might be located. Although kagus do not move litter with their feet, some birds clearly attempted to flush prey by using one foot to gently brush dry litter (Hunt 1996b), and might use a similar technique to aid in capturing earthworms (Bartlett 1862). The use of feet to flush hidden or buried prey has mostly been observed in waders and seabirds like piping plovers *Charadrius melodus* (Cairns 1977 cited in Shaffer and Laporte 1994), but has been reported in *Catharus* thrushes who flushed invertebrate prey from mowed grass (Moore and Yong 1990). Flushing animals from litter would tend to rule out kagus' detection of some prey at least by smell.

New Zealand kiwis and wekas *Gallirallus* spp. are the only birds I know of with a very similar foraging niche (soil and litter invertebrates in mainly forest) to kagus, and whose diets have been closely studied. Kiwis are mostly nocturnal and wekas maybe mostly diurnal. When foraging in forest, kiwis and wekas exhibit invertebrate diets remarkably similar to that of kagus (Reid *et al.* 1982, Beauchamp 1987, Colbourne and Powlesland 1988, Colbourne *et al.* 1990). However kagus fed on a wider range of prey than either kiwis or wekas did, so they appeared to be more generalist in the invertebrate prey used than the New Zealand birds. This is not surprising since kiwis foraged more in soil and wekas more in leaf litter, and from their diets kagus appeared to commonly forage in both locations. However, kiwis appear to occasionally eat fruit (Colbourne and Powlesland 1988), and wekas eat fruit, vegetation and carrion (Beauchamp 1987), but there was no evidence that kagus ate these types of foods.

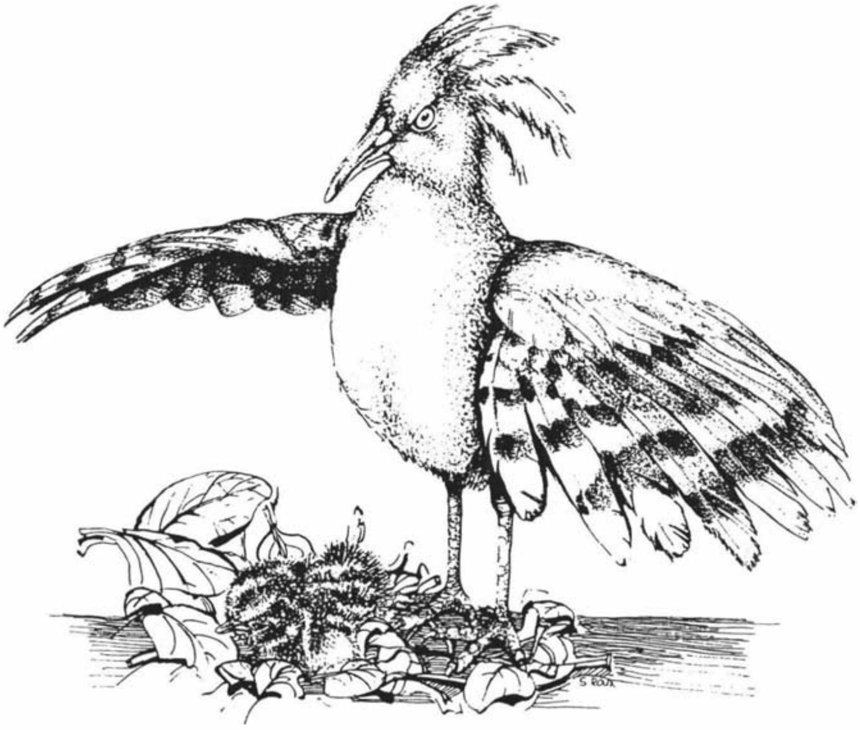
Earthworms, Coleoptera adults and soil-dwelling larvae and/or nymphs (Cicadidae) were major components of kiwis' diets, whereas wekas on Kapiti Island consumed mainly litter-dwelling animals (e.g., Amphipoda, Araneae, Chilopoda, Coleoptera adults, Dermaptera, Diplopoda, snails, Isopods and Orthoptera). Obvious differences between kagu and kiwi diets were that no Scincidae and Blattidae and few ground Orthoptera and Curculionoidea have been reported to be eaten by kiwis, but these species are probably rarer in New Zealand forest litter (see Moeed and Meads 1985, 1987 for data on invertebrate abundance). Unlike kagus and kiwis, wekas on Kapiti Island did not eat soil-dwelling Melolonthinae larvae. Like kagus, kiwis and wekas often foraged continuously when away from their day roosts (Beauchamp 1987, Reid *et al.* 1982). Colbourne *et al.* (1990) suggested that little spotted kiwis *A. australis owenii* showed diet selectivity particularly for soil-dwelling invertebrates but, as with kagus, little information was known about the difficulty or not that birds have in capturing mobile surface-dwelling fauna like Blattidae. Little spotted kiwis and brown kiwis *A. a. mantelli* also preyed on Amphipoda, for example, but rarely (Moeed and Meads 1987, Colbourne and Powlesland 1988). Wekas commonly ate Amphipoda (found in over 99% of weka faeces on Kapiti Island; Beauchamp 1987), especially when conditions were dry and these animals were concentrated in damp areas, as was also the case for kagus. Food supplies for little spotted kiwis and wekas on Kapiti Island appeared to peak over autumn and winter (Colbourne *et al.* 1990, see section 5.4.1), before they bred in spring (Jolly 1989, section 3.4.5), whereas food supplies for kagus peaked earlier in the year.

5.4.4 Parasite eggs in kagu faeces

C. dorsalata eggs in kagus' faeces were more numerous in warm and humid conditions when birds' bodyweights were usually increasing and/or high, and they were eating more prey such as Coleoptera, snails and Oligochaeta. Oligochaeta are commonly external hosts of nematodes for ground feeding birds (Rausch 1983), and may also be for *C. dorsalata* given the strong correlation between earthworm chaetae and egg numbers in kagu faeces and that earthworms are common prey for the birds. Although *C. dorsalata* were more reproductively active at times when kagu food supplies were more abundant, these types of parasites may have a significant effect on unhealthy birds even in the dry season (Hudson *et al.* 1992). Murray *et al.* (1997) found snowshoe hares were more affected by nematodes when food was in short supply, which supported the idea that malnourished animals have reduced resistance to parasitic infections (Crompton 1991). This may have been the case with very thin bird 205 at Mt Cindoa, at a time when food was in short supply there.

6

Temporal relationships between weather, food, and kagu bodyweight, parasites and roosting behaviour



6.1 Introduction

In this chapter I use exploratory analyses to investigate the temporal links between several kagu-related (bodyweight, diet, *Cagourakis dorsalata* egg numbers and roosting behaviour) and environmental (climate, food supplies) factors that I measured in *Chapters 3* and *5* at Pic Ningua.

As I suggested in section 1.5, the kagu's low and relatively invariable annual fecundity might be related to some invariable factor(s) in the environment like annually occurring density-independent food limitation for reproduction. If so, there might be predictable inter-related patterns in other aspects of kagu life style that are closely associated with predictable environmental conditions. Air temperature was probably highly predictable year-to-year. If food supplies and kagu behaviour were closely associated with air temperature, for example, this would suggest they might also be highly predictable year-to-year. There was some evidence for this in *Chapters 3* and *5*. However, the seasonality meant that covariation between variables was often strong making it very difficult to see what the important functional relationships between them were. For example, does temperature alone or in combination with other variables (e.g., rainfall) describe significant amounts of variation in food supplies? Determining the relationship between a dependent and independent variable(s) might allow better interpretation of the data and provide additional clues about causality and/or directions for future research. Although associations between variables do not imply causality, inter-related and predictable patterns in the behaviour of (mostly non-breeding) kagus at Pic Ningua in close association with variation in environmental factors would be support for the idea that the kagu's reproductive output was also linked to environmental conditions.

My specific objective in this chapter is to carry out two types of exploratory analyses on data I presented in earlier chapters to look for possible clues about what might be influencing variation in kagu bodyweight, diet, food supplies and roosting behaviour. These analyses are: (1) correspondence analyses to graphically relate the associations between time and kagu diet and food supplies that I found in *Chapter 5* to other variables that I measured. I plot important variables as supplementary ones on the correspondence plots from *Chapter 5* (Figs. 5-17b and 5-18b); and (2) multiple regression to find significant functional associations (rather than for prediction) between dependent and independent variable(s). I looked at four general relationships over time related to the food limitation hypothesis: between food supplies and climate; between kagu diet and climate, food supplies and parasites; between kagu bodyweight and climate, food supplies and parasites; and between kagu roosting behaviour and climate, food supplies, kagu diet and kagu bodyweight.

6.2 Methods

6.2.1 Analyses and variables used

I carried out correspondence (section 6.2.2) and regression (section 6.2.3) analyses. I used 16 different variables, including a time variable to look for any long-term trends. Fifteen of the variables are presented in the earlier chapters, and I created a new binary one (variable No. 2 below) from an existing variable. The 15 variables, plus the time variable, that I measured in each interval at Pic Ningua are below, and are graphed together in Figure 6-1:

(1) *Animal numbers captured in pitfall traps*

Mean total animal numbers captured in pitfall traps at nine sites in forest (section 5.2.4, Fig. 5-9).

(2) *Direction of kagu bodyweight change*

A binary variable that measured the direction of kagu bodyweight change in each interval ('0' = weight decreasing '1' = weight increasing). I took the values from the bodyweight curve I drew through mostly 8-weekly means for birds (Fig. 3-29a). When it was unclear if bodyweights were decreasing or increasing (at saddles and peaks in the curve), I estimated the direction they might likely be moving in.

(3) *Homogeneity of kagu diet*

Mean diet homogeneity (Shannon's *H'*) across 15 prey categories (Appendix X) in kagu faecal samples (section 5.2.14, Fig. 5-15a).

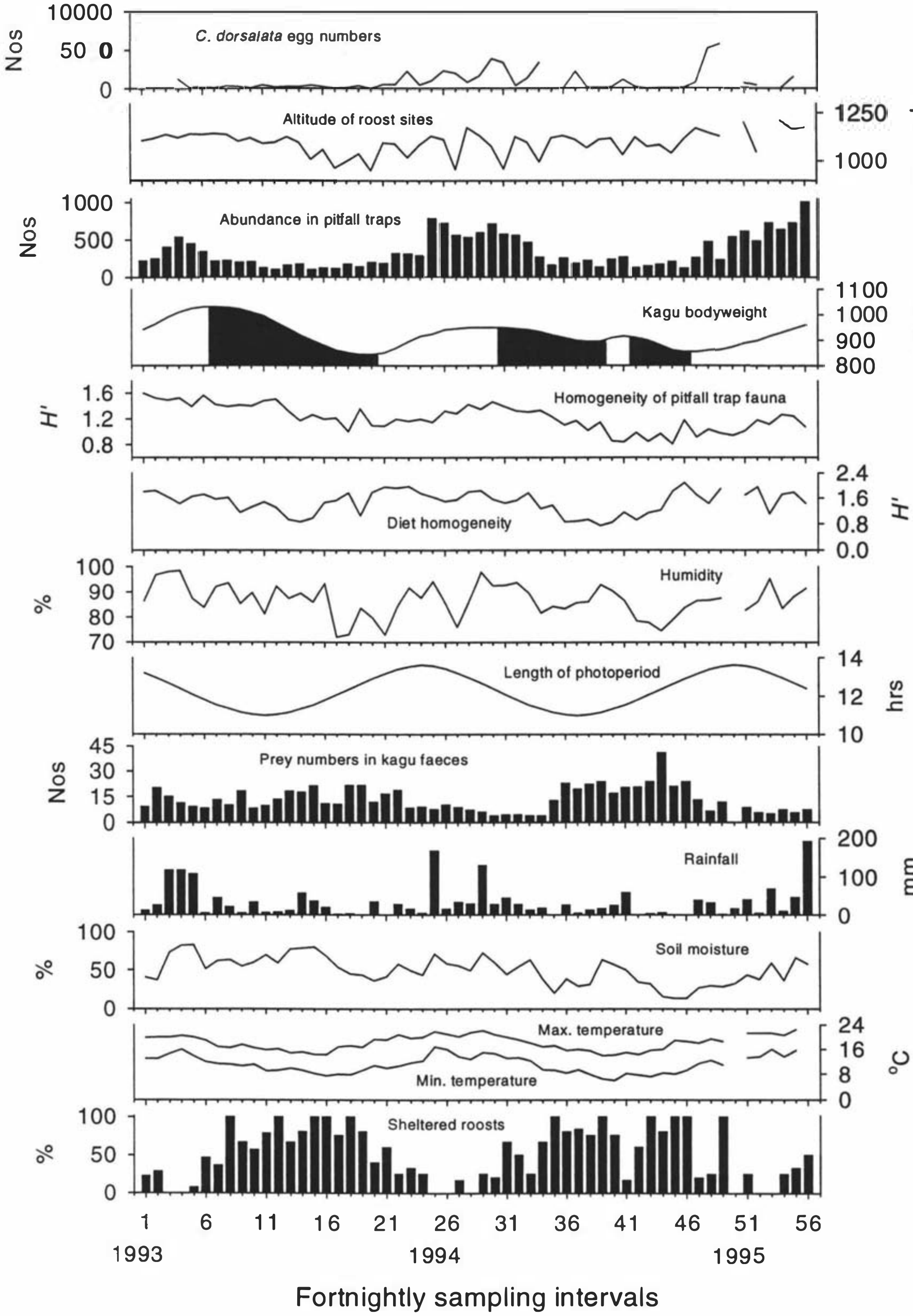
(4) *Homogeneity of pitfall trap fauna*

Mean homogeneity (Shannon's *H'*) across 15 categories (Appendix X) recorded in pitfall trap samples (section 5.2.14, Fig. 5-15c).

(5) *Kagu bodyweight*

Mean kagu bodyweight in each interval taken off the bodyweight curve drawn through mostly 8-weekly means (section 3.2.9, Fig. 3-29a).

Figure 6-1. Graphs of 15 variables used in the analyses. All the data shown are given in greater detail (e.g., errors bars included) in either *Chapters 3* or *5*, and are presented here together for an easy comparison between them. The locations of the data in the previous chapters, along with brief descriptions or the variables, are in section 6.2.1. On the kagu bodyweight graph, shaded regions under the curve indicate the intervals categorised as '0' (decreasing bodyweights) for the binary variable direction of bodyweight change, and unshaded areas the intervals categorised as '1' (increasing bodyweights).



(6) *Prey numbers in kagu faecal samples*

Mean total prey numbers recorded in kagu faecal samples (section 5.2.14, Fig. 5-14a), including unidentified animals.

(7) *Use of sheltered roosts by kagus*

The percent use of sheltered roosts by birds (sections 3.2.8 and Fig. 31a).

(8) *Cagourakis dorsalata egg numbers*

Mean *C. dorsalata* egg numbers in kagu faeces (Fig. 5-7a).

(9) *Altitude of roost sites*

Mean altitude of all (sheltered and unsheltered) roost sites (section 3.2.8, Fig. 3-32).

(10) *Humidity*

Mean percent humidity measured in forest (section 5.2.13 and Fig. 5-3).

(11) *Maximum air temperature*

Mean maximum air temperature in forest (section 3.2.3 and Fig. 3-8).

(12) *Minimum air temperature*

Mean minimum air temperature in forest (section 3.2.3 and Fig. 3-8).

(13) *Length of photoperiod*

The average number of daylight hours (from sunrise to sunset) per day in an interval (section 3.2.3, Fig. 3-6).

(14) *Rainfall*

Mean rainfall in forest (section 3.2.3 and Fig. 3-3).

(15) *Soil moisture*

Mean percent soil moisture at pitfall trap sites in forest (section 5.2.11 and Fig. 5-3).

(16) *Time*

I used the fortnightly sampling intervals (Appendix III) to look for any effects of time on variables.

6.2.2 Correspondence analyses

I plotted supplementary variables (Greenacre 1981) on Figures 5-17b and 5-18b to aid interpretation of dimensions one and two, and to identify important relationships between these variables and the associations between the 15 categories in food supplies and diet over time. I first correlated the row (intervals) co-ordinates for dimensions one and two from the correspondence analyses on pitfall trap and faecal data with 16 variables (after Death 1996) to see which of them was most highly correlated with the co-ordinates. Then I plotted on Figures 5-17b and 5-18b seven (I only used seven variables to avoid over cluttering plots) supplementary variables with high (Spearman) correlation coefficients with one or both axes of the respective plots. For pitfall trap data, I only plotted variables which could be biologically meaningful in explaining variation in these data. Positions of each category were the same as those in Figures 5-17b and 5-18b because supplementary variables do not determine the positions of the 'active' row (intervals) and column (the 15 categories) points (Greenacre 1981). To include the supplementary variables it was necessary to categorise them. I used three categories for each variable other than direction of kagu bodyweight change (already in two categories), and allocated the number of observations (intervals) roughly equally between each category (Table 6-1).

6.2.3 Regression analyses

I carried out separate regression analyses on the temporal changes (between intervals) in seven variables I treated as dependent (Nos. 1-7 in section 6.2.1).

Data in Figure 6-1 were time series and exhibited strong seasonality, which had two important implications. First, seasonal lag effects in the data greater than one interval might be present. For example, air temperature lagged behind length of photoperiod as might be expected. Second, it was possible that a key assumption of regression analysis, that the errors are independent, might be violated because of autocorrelated errors. If this occurred, then the statistical tests of significance of the parameters would not be correct. The bias with autocorrelated errors usually results in a higher significant result than should be the case (SAS Institute 1995), therefore it is important to correct for these errors.

After preliminary attempts to identify lags in the data, it became apparent that it was extremely difficult to know if a lagged relationship between two variables was real or non-sensical. For example, kagu bodyweights lagged behind animal numbers in pitfall traps and temperature (Fig. 6-1). However, the situation was not straightforward. It was possible that bodyweights continued to increase after abundance in the traps began declining because conditions for prey such as Oligochaeta were highly favourable when soils were still wet and temperatures still

Table 6-1. Categories for the 12 variables used as supplementary information on correspondence analyses plots of pitfall trap and kagu faecal data at Pic Ningua. Column 4 gives the number of intervals in each category.

Variable	category	value	N
Animal numbers in pitfalls	low	< 200	19
	moderate	200-399	18
	high	400 +	19
Diet homogeneity (*H*')	low	< 1.4	16
	moderate	1.4-1.69	19
	high	1.7 +	20
Direction of weight change	increasing	'1'	28
	decreasing	'0'	28
Homogeneity of pitfall trap fauna (*H*')	low	< 1.1	16
	moderate	1.1-1.29	18
	high	1.3 +	22
% Humidity	low	< 85	19
	moderate	85-89.9	19
	high	90+	17
Kagu bodyweights (g)	low	< 900	18
	moderate	900-949	22
	high	950 +	16
Length of photoperiod (hrs)	short	< 11.75	18
	moderate	11.75-12.74	18
	long	12.75 +	20
Minimum temperature (°C)	low	< 10	23
	moderate	10-12.9	14
	high	13 +	17
Prey numbers in faeces	low	< 9	21
	moderate	9-16.9	16
	high	17 +	18
% Soil moisture	low	< 40	18
	moderate	40-59.9	22
	high	60 +	16
% Use of sheltered roosts	low	< 30	21
	moderate	30-79.9	17
	high	80 +	17
Time (intervals)	early	< 20	19
	middle	20-37	18
	late	38+	19

reasonably warm. Availability of prey like Oligochaeta would be under-estimated in pitfall traps. Bodyweights probably stayed low for many weeks after temperatures began increasing around late August because conditions became drier and less humid until late October in both years. Bodyweights increased in August 1994 in close association with milder weather and increased numbers of animals in pitfalls, which showed that food supplies and weather conditions could have immediate effects on kagu bodyweights.

Therefore, I did not adjust any of the variables for possible lag effects prior to the regression analyses. Instead, I excluded length of photoperiod, which had an important lag effect on at least some of the other variables (e.g., temperature), and assumed that any lag effects between the remaining variables were taken into account by the fortnightly sampling intervals. There was some evidence to suggest that this may be the case because there was a high degree of correlation between the remaining 15 variables (Table 6-2). Temperature was the variable significantly correlated (often strongly) with the highest number (n = 13) of the other 15 variables, and appeared to represent the seasonality in the data. Neither maximum or minimum temperature was correlated with soil moisture or time, however a close relationship existed between soil moisture and rainfall which was correlated with temperature.

To look for and correct any autocorrelated errors, I used the SAS AUTOREG procedure to carry out the regression analyses. My data conformed to the requirements of this procedure which needed ordered and equally spaced time series data where embedded missing values are allowed (SAS Institute 1993). The binary variable ‘direction of kagu bodyweight change’ would have been best modelled by a binomial rather than a normal distribution, but it was probably more important to account for autocorrelated errors (G. Arnold pers. comm.) and I was only carrying out exploratory analyses. I used certain of the seven variables I treated as dependent as independent variables, along with independent-only variables. I only included as independent variables in each model those that might be biologically meaningful in explaining variation in the dependent variable (Table 6-3), and where this did not result in dependent variables being used as independent variables for each other. I only used mean altitude of roost sites as an independent variable for use of sheltered roosts and not with other kagu-related dependent variables. This was because I collected most of the data (kagu diet and bodyweight) from birds who were free-

Table 6-2. Spearman rank correlation coefficients between the 16 variables in section 6.2.1. '*' indicates significant correlations ($p < 0.05$). N ranges from 53 and 56 for tests not involving *C. dorsalata* egg numbers (PA), when $n = 48$ (samples sizes < 3 excluded). The variables are graphed together in Figure 6-1.

	AL	**AT**	**BC**	**HD**	**HT**	**HU**	**KB**	**MX**	**MI**	**PA**	**PF**	**PP**	**RA**	**SM**	**SR**	**TI**
AL	1.0	0.38*	0.37*	0.08	0.14	0.33*	0.38*	0.25	0.41*	-0.01	-0.21	0.09	0.31*	0.12	-0.27*	0.12
AT		1.0	0.71*	0.32*	0.08	0.36*	0.31*	0.79*	0.84*	0.52*	-0.71*	0.54*	0.58*	0.15	-0.75*	0.30*
BC			1.0	0.47*	0.00	0.25	0.10	0.70*	0.66*	0.49*	-0.41*	0.72*	0.38*	0.06	-0.74*	0.16
HD				1.0	0.13	-0.01	-0.07	0.68*	0.45*	-0.15	-0.34*	0.68*	-0.06	-0.15	-0.37*	0.03
HT					1.0	0.35*	0.75*	0.26	0.47*	0.13	-0.36*	-0.18	0.14	0.50*	-0.25	-0.70*
HU						1.0	0.49*	0.18	0.44*	0.29*	-0.36*	0.01	0.59*	0.54*	-0.22	-0.19
KB							1.0	0.18	0.47*	0.13	-0.41*	-0.31*	0.39*	0.57*	-0.30*	-0.46*
MX								1.0	0.87*	0.41*	-0.61*	0.77*	0.34*	0.04	-0.71*	0.09
MI									1.0	0.50*	-0.72*	0.58*	0.52*	0.27	-0.78*	-0.06
PA										1.0	-0.53*	0.36*	0.27	0.11	-0.38*	0.16
PF											1.0	-0.32*	-0.40*	-0.27	0.52*	-0.09
PP												1.0	0.11	-0.23	-0.56*	0.26
RA													1.0	0.56*	-0.53*	-0.06
SM														1.0	-0.21	-0.52*
SR															1.0	0.05
TI																1.0

AL = altitude of roost sites; AT = animal numbers in pitfall traps; BC = direction of kagu bodyweight change; HD = homogeneity of kagu diet; HT = homogeneity of pitfall trap fauna; HU = humidity; KB = kagu bodyweight; MX = maximum temperature; MI = minimum temperature; PA = *C. dorsalata* egg numbers in kagu faeces; PF = prey numbers in kagu faeces; PP = length of photoperiod; RA = rainfall; SM = soil moisture; SR = use of sheltered roosts; TI = time (intervals).

ranging and it was difficult to know exactly what altitude they had mostly been foraging at.

Table 6-3. The independent variables used for modelling each of the seven dependent variables in regression analyses. Pair-wise correlation tests between all variables are in Table 6-2.

Dependent variable	**Independent variables used**
(1) Animal numbers in pitfall traps	HU MI RA SM TI
(2) Direction bodyweight change	AT HT HU MX PA RA SM TI
(3) Homogeneity of kagu diet	AT HT HU MX PA RA SM TI
(4) Homogeneity of pitfall trap fauna	AT HU MI RA SM TI
(5) Kagu bodyweight	AT HT HU MI PA RA SM TI
(6) Prey numbers in kagu faeces	AT HT HU MI PA RA SM TI
(7) Sheltered roost use by kagus	AL AT BC HD HT HU KB MI PF RA SM TI

AL = altitude of roost sites; AT = animal numbers in pitfall traps; BC = direction of kagu bodyweight change; HD = homogeneity of kagu diet; HT = homogeneity of pitfall trap fauna; HU = humidity; KB = kagu bodyweight; MI = minimum temperature; PF = prey numbers in kagu faeces; PA = *C. dorsalata* egg numbers; RA = rainfall; SM = soil moisture; SR = use of sheltered roosts; TI = time (intervals).

My method for model simplification was biologically based. Because temperature represented seasonal effects in the data, I entered either maximum or minimum temperature (whichever had the strongest correlation with the dependent variable; Table 6-2) first as a permanent independent variable to explain any seasonal effects. As both maximum and minimum temperature were highly correlated (Table 6-2), I did not use the one that was least correlated with the dependent variable as an independent variable. I entered each of the other remaining independent variables selected to model a dependent variable (Table 6-3) one at a time with minimum temperature to see if they could explain additional variation. I used a manual forward-stepwise-selection model construction procedure, next entering the most significant independent variable, if any, and then re-entering the remaining independent variables one at a time and so on.

I checked for autocorrelation, and corrected for it when necessary, when each independent variable was entered into a model. I checked for autocorrelation in the first 27 (fortnightly) lags (this took into account annual seasonality), using probability values for generalized Durban-Watson statistics. When significant autocorrelation was present, I then used stepwise autoregression to identify for which of the 27 lags it was significant (SAS Institute 1993). I used Ordinary Least Squares estimates when no significant autocorrelation was present as the number of missing values was minimal, Yule-Walker estimates when autocorrelation without heteroscedasticity was present, and Maximum Likelihood estimates with autocorrelated errors and heteroscedastic data (kagu bodyweights only; see below).

I also checked each minimal model for significant heteroscedasticity with SAS AUTOREG procedure, and found it only in the model fitted to kagu bodyweight data. To correct for this, I fitted an autoregressive conditional heteroscedasticity (ARCH) model, which accounted for the heteroscedasticity as the Normality Test for normally distributed residuals was not significant.

Prior to the regression analyses, I fitted the data for each dependent variable against a normal distribution using the SAS UNIVARIATE procedure to see if they were normally distributed. I log-transformed three variables (animal numbers in pitfall traps, kagu bodyweights, and prey numbers in kagu faeces), and arcsin-square-root transformed the proportional data for use of sheltered roosts, to achieve approximate normality. For regression diagnostics, I inspected the residuals for any larger outliers that might indicate errors in data recording or classification. I also graphed the results of each minimal model in two ways to inspect its fit to the data. First, I plotted the raw data and predicted values against time. When autocorrelation was corrected for, I plotted the two sets of predicted values: those for the structural model with no correction for autocorrelation, and those for the full model after correction for autocorrelation. Second, I plotted the residuals against time (intervals).

I excluded intervals 50 and 56 from all the analyses because air temperatures were only n = 1 in those intervals (see Fig. 3-8), and only used data for *C. dorsalata* egg numbers when sample sizes in intervals were more than two.

When correcting for autocorrelation, the SAS AUTOREG procedure transforms independent variables, therefore the estimates cannot be used to directly calculate actual values for a dependent variable using untransformed data.

6.3 Results

6.3.1 Correspondence analyses

After examining the correlations between the row co-ordinates for dimensions one and two for pitfall trap data and 16 variables (Table 6-4), I selected seven (biologically meaningful) variables to include as supplementary information. These were animal numbers in pitfall traps, homogeneity of pitfall trap fauna, humidity, length of photoperiod, minimum temperature, soil moisture and time (Fig. 6-2a). Of these seven variables, the three strongest correlations with dimension one and the changing relative abundance of Amphipoda, Orthoptera and Scarabaeinae/Hybosoridae (section 5.3.9, Appendices X and XI) were homogeneity of pitfall trap fauna, minimum temperature and time. Amphipoda were relatively more abundant when minimum temperatures and homogeneity of trap fauna was low to moderate, especially in the mid to latter part of my study. Amphipoda were also more abundant when animal numbers in pitfall traps, soil moisture and humidity tended to be low. The three strongest correlations with dimension two were time, animal numbers in pitfall traps and photoperiod. Stronger correlations with dimension two suggested relatively more Araneae, Chilopoda and Orthoptera (section 5.3.9) were captured when animal numbers in traps were relatively low during the early part of my study.

Once I had examined the correlations between the row co-ordinates for dimensions one and two for kagu faecal data and 16 variables (Table 6-4), I selected animal numbers in pitfall traps, direction of kagu bodyweight change, diet homogeneity, length of photoperiod, minimum temperature, prey numbers in kagu faeces, and use of sheltered roosts to include as supplementary information (Fig. 6-2b). Although maximum temperature had a high correlation with dimension one, I only selected minimum temperature as the temperature variable because both were highly correlated. The three strongest correlations with dimension one and the relationship between the relative abundance of larvae and all other taxa (section

5.3.9, Appendices X and XI) were minimum temperature, diet homogeneity and photoperiod. Thus kagus were eating relatively high numbers of larvae when minimum temperatures and diet homogeneity were low during the shortest days. At these times also, abundance in pitfall traps was low, kagu bodyweights were decreasing and birds were roosting more at sheltered positions. The three strongest correlations with dimension two and the higher relative numbers of litter-dwelling animals in kagu faeces (section 5.3.9) were minimum temperature, animal numbers in pitfall traps and use of sheltered roosts. When kagus were eating relatively greater numbers of more mobile litter-dwelling animals (generally in the late dry season), minimum temperatures and abundance in pitfall traps were low, and birds were using mostly sheltered roosts. Also at these times, diet homogeneity was high, kagu bodyweights were decreasing and higher numbers of prey were in birds' faeces.

Table 6-4. Spearman rank correlation coefficients between 16 variables and dimensions one and two for correspondence analyses on the numbers of animals in 15 categories (Appendix X) in kagu faeces and pitfall traps at Pic Ningua. '*' = $p < 0.05$ (sample sizes varied from 53 to 56 intervals for all tests not including *C. dorsalata* egg numbers, when $n = 48$).

Analysis	**Kagu faeces**		**Pitfall traps**	
Dimensions	**one**	**two**	**one**	**two**
Animals in pitfall traps	0.64*	-0.67*	0.31*	-0.55*
Altitude of roosts	0.10	-0.35*	0.28*	-0.06
C. dorsalata egg numbers	0.46*	-0.48*	0.22	-0.31*
Direction of kagu weight change	0.60*	-0.59*	0.13	-0.49*
Diet homogeneity	0.67*	-0.05	0.12	-0.19
Homogeneity of pitfall trap fauna	0.29*	-0.31*	0.91*	0.45*
Humidity	0.21	-0.41*	0.39*	0.20
Kagu bodyweight	0.14	-0.42*	0.84*	0.23
Length of photoperiod	0.75*	-0.35*	-0.13	-0.46*
Maximum temperature in forest	0.87*	-0.52*	0.34*	-0.38*
Minimum temperature in forest	0.80*	-0.70*	0.60*	-0.30*
Prey numbers in faeces	-0.62*	0.50*	-0.50*	0.35*
Rainfall in forest	0.25	-0.53*	0.28*	-0.03
Soil moisture	-0.00	-0.37*	0.49*	0.29*
Use of sheltered roosts	-0.61*	0.68*	-0.36*	0.30*
Time (intervals)	0.05	0.05	-0.52*	-0.64*

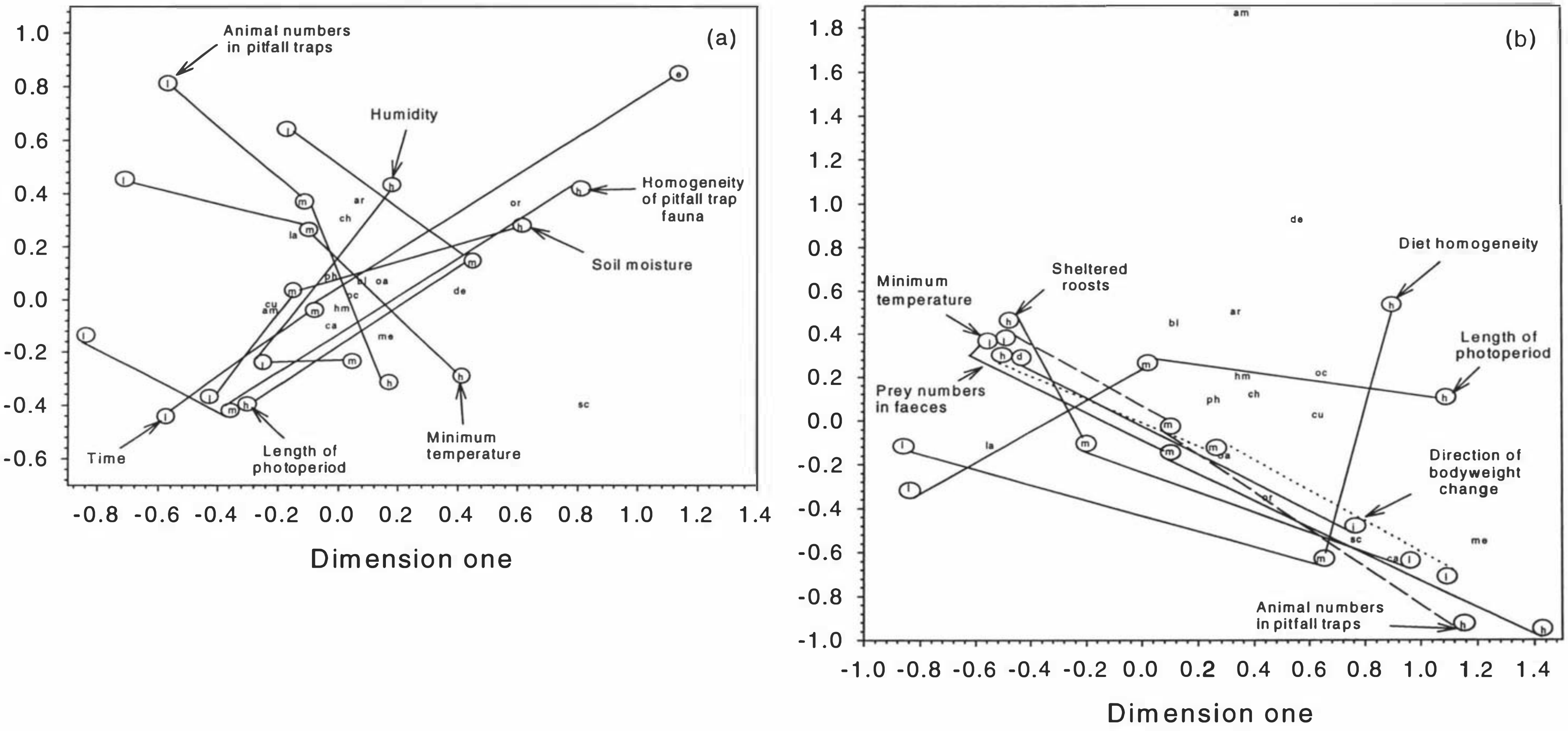


Figure 6-2. Seven supplementary variables plotted on correspondence analyses plots for pitfall trap (a) and kagu faecal (b) data. Uncircled two-letter symbols indicate the 15 categories (key to the symbols is in legend to Fig. 5-17). The circled letters connected by lines indicate the categories for each supplementary variable (indicated by labels and arrows). Key to circled letters for direction of bodyweight change: 'i' = increasing bodyweights, 'd' = decreasing bodyweights; for time: 'e' = early part of study, 'm' = middle of study, 'l' = last third of study; and for all other variables: 'l' = low, 'm' = moderate, 'h' = high. Different line types to connect circles are used in (b) for clarity.

6.3.2 Regression analyses

Of the seven variables I treated as dependent, only direction of kagu bodyweight change had no significant independent variables, and I do not give the results of this analysis here. As expected from its correlations with the other variables, temperature explained a significant amount of the variation in all remaining six dependent variables (Table 6-5). Maximum temperature replaced minimum temperature only in the minimal model fitted to homogeneity of kagu diet. All the six minimal models had additional independent variables, and temperature was the most significant variable in four of them (animal numbers in pitfall traps, homogeneity in kagu diet, prey numbers in kagu faeces and use of sheltered roosts).

Interestingly, the independent variable 'time' was significant in the minimal models fitted to animal numbers and homogeneity of pitfall trap fauna (Table 6-5). This was related to the obvious long-term trend for increased animal numbers in the traps (Fig. 6-1) and the associated decreased homogeneity.

Five of the six minimal models needed correction for autocorrelated errors (Table 6-5 and Figs. 6-3a-e). The structural parts for three of these five models fitted the data extremely well and their r^2 values were 0.79 or greater. The fit was not as close for prey numbers in kagu faeces (r^2 = 0.35) (Fig. 6-3e), and poor for kagu bodyweight data (the structural r^2 value was not given in the SAS output, but see Fig. 6-3d). Although the structural fit to kagu bodyweight data was poor the full model r^2 (0.97) was very high (Table 6-5). This was because the autocorrelation process was a good fit to the kagu bodyweight curve. The poor fit of the structural part of the model fitted to kagu bodyweights may have been an artefact of my drawing a smooth curve through the data. The model fitted to use of sheltered roosts did not require correction for autocorrelation, and was a good fit to the data (r^2 = 0.69, Table 6-5 and Fig. 6-3f).

There was one obvious larger residual, in interval 49 for use of sheltered roosts (Fig. 6-4f). Sheltered roost use was high in interval 49 when minimum temperatures dropped considerably, in-between intervals when use of these roost positions was low.

Table 6-5. Regression results for the minimal models fitted to data for six dependent variables. Columns 4 and 5 give the regression (structural model only) and total r-square (after correction for autocorrelation) figures, respectively. Column 6 indicates the method used to obtain estimates: M-L = Maximum likelihood; Y-W = Yule-Walker; OLS = Ordinary least squares. A full explanation of the statistical methods used is in section 6.2.3.

Source	df	MSE	Regression r-square	Total r-square	Type of estimate	Estimate	Standard error	*t* ratio	Approx. probability
Response variable: Log Animal numbers in pitfall traps									
Model	6	0.047	0.86	0.89	Y-W				
Intercept	1					2.9730	0.1703	17.453	0.0001
Minimum temperature	1					0.1782	0.0122	14.556	0.0001
Soil moisture	1					0.0054	0.0022	2.511	0.0001
Time (intervals)	1					0.0144	0.0021	6.835	0.0155
Response variable: Homogeneity of kagu diet									
Model	4	0.0346	0.79	0.74	Y-W				
Intercept	1					-1.6929	0.2460	-6.883	0.0001
Maximum temperature	1					0.1989	0.0164	12.134	0.0001
Animal numbers in pitfall traps	1					-0.0013	0.0002	-6.688	0.0001
Response variable: Homogeneity of pitfall trap fauna									
Model	6	0.0082	0.81	0.82	Y-W				
Intercept	1					1.0829	0.0898	12.059	0.0001
Minimum temperature	1					0.0377	0.0085	4.440	0.0001
Rainfall	1					-0.0013	0.0004	-3.062	0.0036
Time (intervals)	1					-0.0086	0.0006	-13.228	0.0001

Table 6-5 continued next page.

Table 6-5 continued.

Source	df	MSE	Regression r-square	Total r-square	Type of estimate	Estimate	Standard error	*t* ratio	Approx. probability
Response variable: Log Kagu bodyweight									
Model	7	0.0001	---	0.97	M-L				
Intercept	1					6.8360	0.0045	1524.919	0.0001
Minimum temperature	1					-0.0015	0.0005	-2.981	0.0029
Animal numbers in pitfall traps	1					0.0000	0.0000	3.082	0.0021
Response variable: Log Prey numbers in kagu faeces									
Model	4	0.1347	0.35	0.63	Y-W				
Intercept	1					3.7633	0.3295	11.422	0.0001
Minimum temperature	1					-0.1120	0.0294	-3.815	0.0004
C. dorsalata egg numbers	1					-0.0001	0.0000	-2.024	0.0491
Response variable: Arcsin-sqrt Use of sheltered roosts									
Model	3	0.0486	0.69	0.69	OLS				
Intercept	1					1.7193	0.1433	11.995	0.0001
Minimum temperature	1					-0.0786	0.0146	-5.380	0.0001
Direction of kagu bodyweight change	1					-0.2753	0.0788	-3.495	0.0010

Figure 6-3. Plots for each of the six minimal models (Table 6-5) comparing predicted and raw data (unbroken lines) values. Only structural predicted values (dashed lines) were available for use of sheltered roosts (f), as no significant autocorrelation was present. Full model predicted values (dotted lines) corrected for significant autocorrelation are also given for the other five models (a-e). The model fitted to kagu bodyweight data (d) was also corrected for heteroscedasticity.

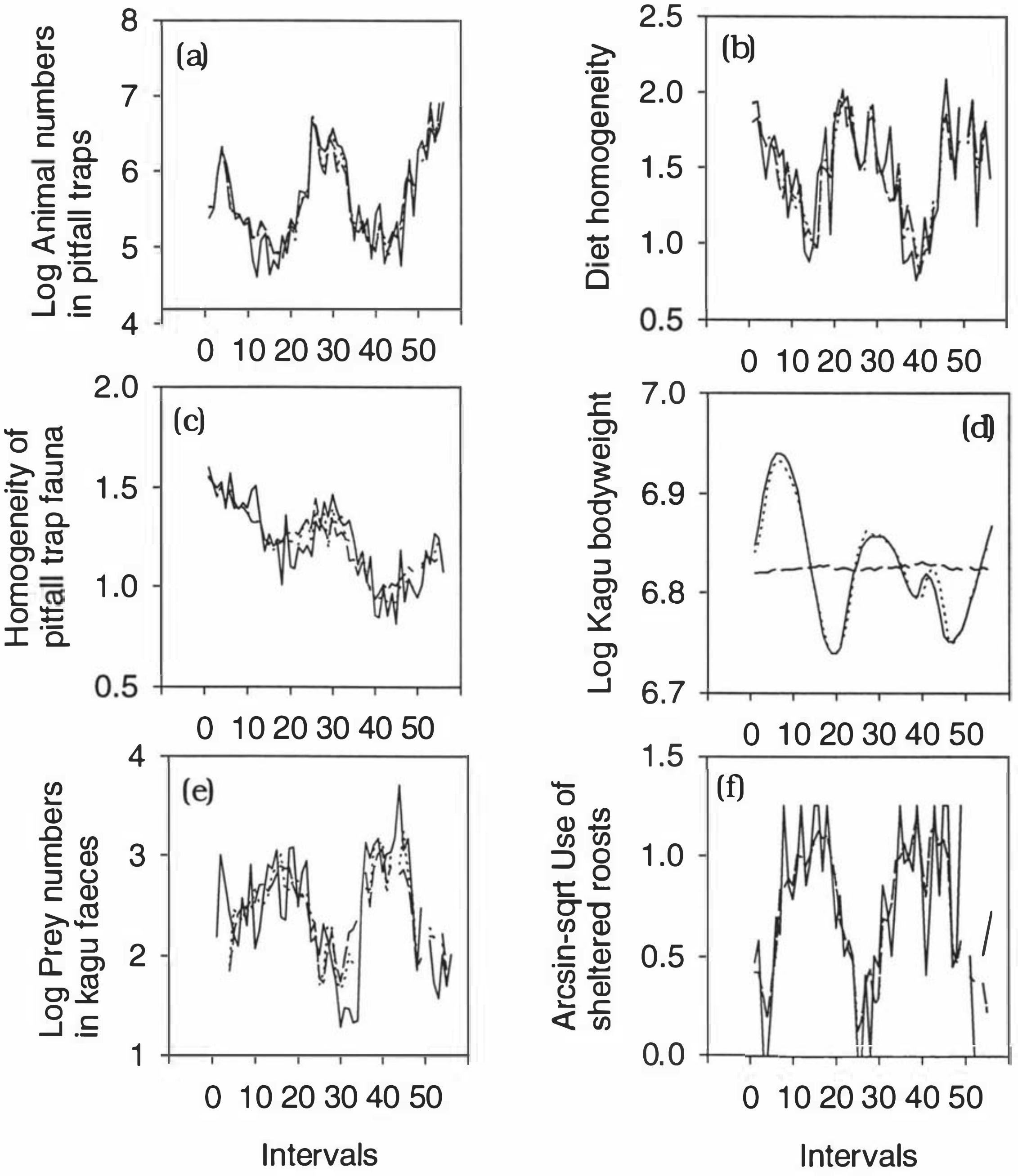
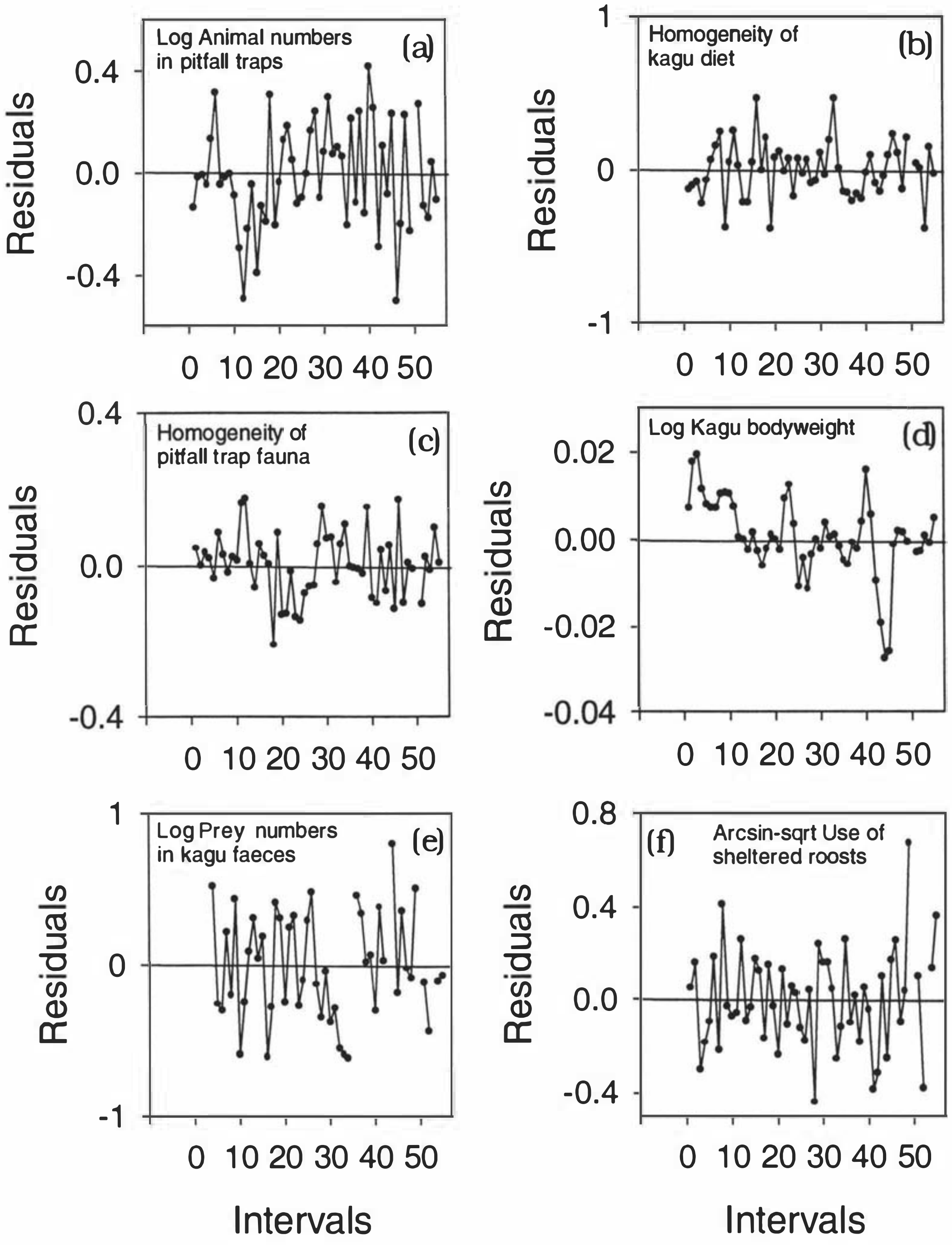


Figure 6-4. Plots of residuals (observed or transformed values - predicted values for the full models) against time (intervals) for each of the six minimal models in Table 6-5 (see also Fig. 6-3).



6.4 Discussion

6.4.1 Climate and its relationship with soil and litter fauna at Pic Ningua

Minimum temperature seemed strongly associated with the seasonal variation in animal numbers in pitfall traps. It co-varied closely with animal numbers in pitfall traps and had the strongest correlation with dimension one for the association between taxa in the traps over time. This was backed up by minimum temperature being highly significant in the minimal model fitted to abundance in pitfall traps, and that the r^2 for the fit of the structural model was very high (0.86). It had a relatively minor influence in the general trend for increased abundance in traps over time, as was probably indicated by its low correlation with dimension two in correspondence analysis. This would be expected since year-to-year variation in temperature patterns were small. Soil moisture and time probably helped explain the long-term trend for increased abundance in the minimal model for animal numbers in pitfall traps. My change in soil collection methods in 1994 may have resulted in lower soil moisture values then because I only collected samples on one day in an interval, instead of throughout the interval as I did in 1993 (section 5.2.10). Nevertheless, although slightly more rain probably fell at Pic Ningua in 1994 than 1993 (Fig. 3-3), conditions were generally drier in 1994 between periods when substantial rain fell.

Rainfall, commonly cited as the main climatic factor influencing insect abundance in tropical forests (section 5.1), co-varied less strongly with animal numbers in pitfall traps than minimum temperature and was relatively weakly correlated ($r = 0.28$) with dimension one for animal abundance. Rainfall did not explain any significant additional variation in the model fitted to animal numbers in pitfall traps, and may have been partly due to wet conditions being associated with both cool and warm weather. Rainfall was also discontinuous but its effects (e.g., wet soil conditions) were less so, however this should have been taken into account to a large extent by soil moisture. Many insect categories (e.g., Blattidae, Carabidae, Curculionoidea, Dermaptera, Hemiptera, Hymenoptera, Orthoptera and Scarabaeoidea) captured in pitfall traps at Pic Ningua had distributions more similar to temperature than to rainfall. An obvious difference between their distributions and that of rainfall occurred during wetter periods in July/August of both years when rainfall increased considerably but the abundance of these animals did so only slightly. There was little hint of what factors might have lead to the trend for increased abundance in traps over time.

Rainfall, along with minimum temperature and time, was included in the minimal model fitted to data for homogeneity of pitfall trap fauna. As it did in the model fitted to animal numbers in traps, minimum temperature explained the seasonal variation in homogeneity, whereas time probably explained the long-term variation of homogeneity over the period of my study. Homogeneity was higher in the wet season compared to the dry season because taxa such as Blattidae, Carabidae, Hymenoptera and Orthoptera increased in abundance relatively more than Amphipoda did. High homogeneity was also associated with increased rainfall in the wet season, but the relationship was not close at other times. This might explain why the estimate for rainfall was negative. Homogeneity was low during wet periods in colder dry season months (July/August) and increased considerably in the driest interval in both years (19 and 46, respectively) when Amphipoda numbers declined and rainfall was low. Minimum temperature therefore, was the principal climate-related factor closely associated with seasonality in abundance and community patterns of the soil and litter fauna.

6.4.2 Kagu diet

Minimum temperature was also the variable most closely associated with the distinct seasonal differences (particularly in use of larvae) in kagu diets across 15 prey categories identified by correspondence analyses in *Chapter 5*. Maximum temperature was most highly correlated with dimension one, possibly because it tended to increase considerably after the coldest months in close association with a large decrease in the relative numbers of larvae eaten by kagus. Minimum temperature had the strongest correlation with dimension two.

The close relationship between minimum temperature and diet homogeneity was however not evidence that kagus were selecting larvae more than other potential prey in colder conditions. However, it was consistent with the idea that birds might use these prey relatively more in colder conditions (section 5.4.2).

A close relationship between air temperature and kagu diet was also supported by the (negative) inclusion of maximum temperature in the model fitted to homogeneity of kagu diet. The variation in the numbers and types of animals in pitfall traps and kagu diet were strongly influenced by seasonality at Pic Ningua, however the relationship between the variation in the numbers and types of animals in pitfall traps and kagu diet was not close. This was graphically demonstrated by different patterns in the correspondence plots in *Chapter 5*, and that diet homogeneity was not closely correlated with either dimension for pitfall trap data. As I discussed in *Chapter 5*, one factor causing this would be that animals like larvae were rare in pitfall traps, another could be that kagus were selecting from a seasonally varying subset of potential prey types.

The contribution of time in explaining variation in diet homogeneity was small, indicating that the seasonality in diet composition was more similar between years than for homogeneity of pitfall trap fauna. The variation in the traps though, was strongly influenced by Amphipoda which kagus rarely used. There was obvious variation in prey numbers in kagu faeces between years with a greater contrast between the wet and dry season in 1994 than 1993, but this was not explained well by time.

6.4.3 Kagu roosting behaviour

Evidence for a thermal benefit at winter roosts might be masked by other factors (section 3.4.7), and thermal variation would probably be more difficult to detect if roosts in both winter and summer were perches. The lack of confounding effects influencing kagu roosting behaviour and the close negative association between kagu use of sheltered roosts and minimum temperature strongly indicated that birds chose these roost positions for their thermal benefits. I am not aware of any other bird study (see section 3.1) where the evidence for the role of temperature in causing seasonal variation in roosting behaviour and the use of sheltered roosts seems so clear. The inclusion of direction of kagu bodyweight change provides an additional clue as to why kagus seek shelter when minimum temperatures decline; birds might be attempting to reduce their overnight energy expenditure.

The link between minimum temperature, direction of kagu bodyweight change and roosting behaviour is important for five reasons. First, it indicates that birds appear to be responding behaviourally to physiological and environmental changes, and that aspects of their life styles are closely linked to the environment. Second, it is consistent with the positive seasonal relationships between minimum temperature and kagu food supplies and bodyweight variation. That is, birds attempt to behaviourally reduce their overnight energy costs at the same time that food is in short supply and they are loosing condition. Third, it suggests that kagus exhibit phenotypic plasticity (in their roosting behaviour) in response to their environment because birds at Parc Rivière Bleue where temperatures are warmer rarely used sheltered roost positions. Fourth, it is consistent with the idea that food is generally not abundant for kagus for much of the dry season placing them under physiological stress. This comes from the fact that birds started making more use of sheltered roosts as soon as their bodyweights began to decline in association with colder conditions, even though their bodyweights were relatively high. This would seem beneficial behaviour, especially at the start of an extended and predictable period of weight loss, to ensure bodyweights bottomed out as high as possible in the driest period of the dry season around late October. Also, kagus tended to use sheltered roosts less when their bodyweights began increasing after reaching their lowest values around late October, even when minimum temperatures were still quite low. When birds were gaining weight there might have been less need for them to try and reduce overnight energy expenditure. Acclimation effects might also be involved in causing these differences (section 3.4.7). For example, birds may better cope with cold weather when temperatures are rising because they would have probably acclimatised to some degree to even colder temperatures in the immediate past. Last, the relationships between the three variables were evidence that temperature had an important direct effect on kagu bodyweight variation. In the wet season in intervals 26-28, kagu bodyweights mostly stabilised or declined at Pic Ningua and Mt Cindoa when conditions became drier between periods of heavy rainfall. During this period when minimum temperatures were high kagus did not increase their use of sheltered roosts. In contrast, kagus increased their use of sheltered roosts when their bodyweights declined in the dry season and when minimum temperatures were low. Thus at high altitude, cold temperatures and food shortage are both likely to be directly causing bodyweight loss in kagus.

Future work should attempt to compare thermal attributes, such as wind velocity and air temperature, between sheltered and unsheltered sites in similar weather conditions. Nevertheless, there was strong circumstantial evidence that sheltered positions provided more favourable micro-climates for kagus in colder conditions when food was in short supply. That some sheltered roosts had apparently been used for many years was additional evidence that the patterns of seasonality in temperature, at least, that I observed varied little year-to-year at Pic Ningua and Mt Cindoa.

6.4.4 Kagu bodyweights

Although the structural part of the minimal model fitted to kagu bodyweight data explained only a small amount of the variation in the data, minimum temperature and animal numbers in pitfall traps were included in the model. The lack of model fit was probably strongly influenced by the smooth nature of the curve leading to strong autocorrelation and heteroscedasticity. The data in Figure 6-1 suggest a close relationship between animal numbers in pitfall traps and kagu bodyweights, and is supported by the high correlation between kagu bodyweight and dimension one (Table 6-3). The seasonal patterns in minimum temperature and kagu bodyweights were also quite close, and I discussed earlier (section 6.2.3) possible reasons for the fact that bodyweights appeared to lag behind temperature. It is likely that both minimum temperature and food shortage had important direct affects on kagu bodyweight variation (section 6.4.3).

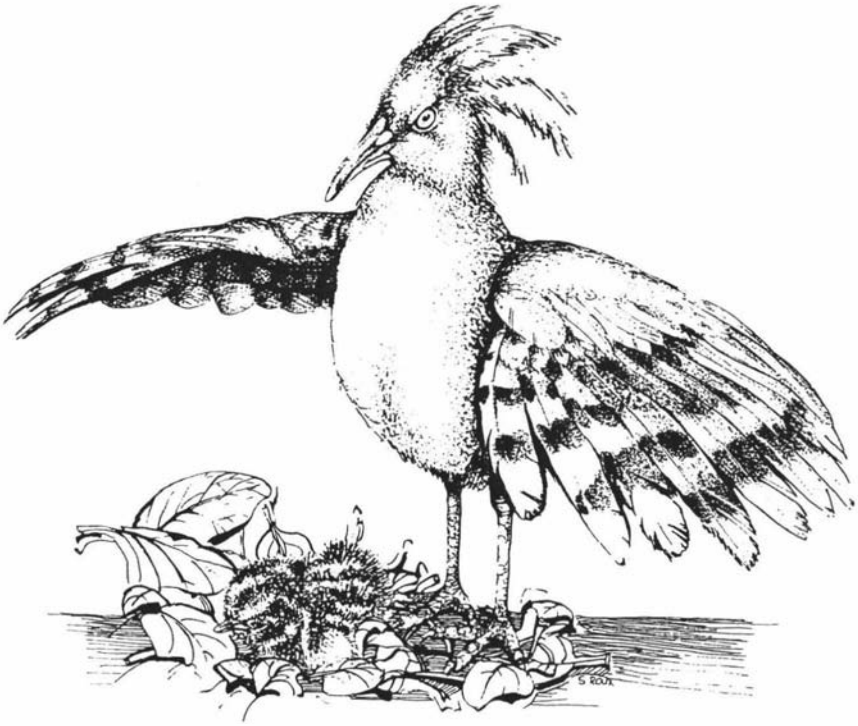
Fat deposition in kagus at my high altitude study areas was closely positively associated with temperature and food supplies, and may have resulted from changing environmental conditions and not have been an energy storage strategy. Deposition of fat reserves over the wet season though, enabled kagus to cope with food scarcity over much of the dry season until the following wet season. The strong link between food supplies and minimum temperature, and that the latter was highly predictable year-to-year, suggested that the seasonal trend seen in bodyweights was also highly predictable each year. This was supported by the fact that use of sheltered roosts, which was closely associated with loss of bodyweight, was very similar between years and that some of these roosts had been used for many years. That birds appeared to try and conserve energy when their bodyweights were in decline by using sheltered roosts indicated that fat deposition before the dry season was an energy storage strategy. The close positive relationship between food supplies and bodyweight variation suggested that kagus deposited fat whenever possible, which might be expected if food was generally scarce for kagus. Thus birds probably used periods of abundant food supplies in the wet season for moult, and fat deposition to prepare for food shortage in the dry season.

Kagus at Pic Ningua apparently suffered seasonal density-independent energy deficits from the combined effects of cold temperatures and food shortage that resulted in kagu bodyweight decline over much of the dry season. There were a lack of other factors that could have influenced bodyweight decline in the dry season. First, any effects of breeding activity on my study birds' bodyweights were minimal. Second, moult was still in progress after the wet season at both study areas up until June, and this may have caused loss of bodyweight in association with declining food supplies. However, bodyweights generally continued to decline until October so moult would not have been a major influence on loss of bodyweight. Third, foraging kagus did not face a constant predation threat as they foraged (*Chapter 4*) nor a constant threat of direct inter-specific competition for food. Their foraging may have been interrupted by pigs and myself, but this would have occurred only infrequently. The dog attacks in 1993 (*Chapter 4*) may have adversely affected the bodyweights of birds on the peak who descended to lower altitudes (section 3.3.3). However, the general seasonal pattern of kagu bodyweight variation at Pic Ningua was similar to that for birds at Mt Cindoa who were not preyed on by dogs and who moved in relatively small home ranges. Fourth, intra-specific disputes between kagu were not known to greatly reduce their foraging time (Létocart 1991), and intra-specific competition for food should have been minimal when numbers of birds were greatly reduced soon after I began collecting data there (*Chapter 4*). Last, there were few data to suggest that parasite loads were causing kagu bodyweights to decline. *C. dorsalata* egg numbers were more numerous when kagu bodyweights were high or increasing. The effect of reproductively inactive adult *C. dorsalata* on kagus in the dry season was unknown, but inactive nematodes can cause morbidity in birds (e.g., red grouse *Lagopus lagopus scoticus*; Dobson and Hudson 1994).

Thus for substantial periods of both dry seasons at Pic Ningua, kagus were unable to maintain their bodyweights probably mostly because of density-independent factors, but their fat deposition and roosting behaviour appeared to be strategies to lessen the effect of food shortage and cold temperatures on their bodyweight loss in the dry season. However, kagus on the peak might not face density-independent food limitation for reproduction if they generally bred just before the wet season when their bodyweights were on the upswing (discussed in *Chapter 7*).

7

Implications of my study for understanding kagu life history and for future kagu conservation management and research



7.1 Introduction

I carried out field research for a two-phase kagu recovery project between June 1991 and March 1995. I first established kagu abundance and distribution on Grande Terre, and used this knowledge to help in planning my following 32-month field-research programme. For this programme, I described environmental conditions (climate, food supply) and radio-tracked kagus at two high altitude study areas, which provided me with data on (1) kagu ecology at high altitude; and (2) predation risk to the birds there. I also collected data on climate and food supply for kagus at Parc Rivière Bleue to enable a better comparison between my study areas and Yves Létocart's kagu study area at the Parc. In this chapter, I discuss my survey and field-research results and Létocart's work to see (1) whether environmental conditions might be influencing the kagu's annual cycle and fecundity; (2) what the implications of kagu demography and threats are for future kagu conservation management; and (3) what the priorities are for kagu research in the future.

7.2 Environmental conditions and the kagu's annual cycle

In north temperate regions the generalised annual cycle for birds sees them breed after winter when sufficient food supplies become available to allow them to do so (Perrins 1970), followed by moult (Murton and Westwood 1977). Thus food resources are commonly accepted to be the main proximate factor associated with the organisation of annual cycles. Photoperiodism and temperature are thought to be ultimate factors (Murton and Westwood 1977). This type of annual cycle strongly suggests birds approach local optima in allocation of time and energy resources (Murton and Westwood 1977). For example, energy expensive phases like moult and reproduction are commonly partitioned, and this was also largely the case with kagus.

'Annual' cycles of birds in tropical regions show greater variation than those in temperate regions. Breeding is generally seasonal (e.g., Moreau 1950, Voous 1950, Fogden 1972, Diamond 1974, Dittami and Gwinner 1985, Dittami 1987), but breeding seasons tend to be longer than those of temperate birds (Murton and Westwood 1977). Some species have less than annual (Hartley and Hustler 1993) or double (Moreau 1950) breeding seasons, and others seem to breed year-round (Dittami 1987, Chapman 1995). Breeding commonly coincides with increased food supplies in association with rain for species in tropical non-rainforest habitats (Lack

1950, Sinclair 1978, Fogden and Fogden 1979, Zann *et al.* 1995), but rainforest birds often breed outside the period of heaviest rains (Voous 1950, Fogden 1972, Diamond 1974) followed by moult. This might be because of unsuitable weather conditions like heavy rain or lower temperatures which may reduce food availability and/or foraging time and possibly make nesting difficult at that time (section 3.1).

Based on my pitfall trapping data at Parc Rivière Bleue and data on kagus there (Létocart 1989 1991, section 1.4), birds at the Parc breed outside the period of peak food supplies as breeding begins in June after primary moult has probably finished. Pairs who lay only in the June-August period probably begin primary moult after their offspring become fully independent at around four months of age (section 1.4), in association with wet conditions in the early wet season. Mated pairs at the Parc are therefore usually either breeding or undergoing moult, with the possibility of brief periods between these two activities when neither occurs, depending on weather conditions. Pairs raising two offspring in the same breeding season can overlap juvenile provisioning and moult in the wet season, but do not appear to overlap moult and incubation (Y. Létocart in litt.). Why do kagus at the Parc mostly breed outside the wet season at a time when their food supplies appear to be below their peaks and on the downswing?, as may also be the case with their bodyweights then. One reason might be that conditions associated with heavy rain are unsuitable for breeding in the wet season (see above) so birds breed at the first most appropriate time (June-August) after moult is complete to maximise their fitness. Birds can breed successfully between September and the start of the wet season (Létocart 1991), but food supply in this period is probably reduced because of drier conditions which might be a problem for incubating birds (section 1.4) and for chick provisioning (section 1.5). Pairs at Parc Rivière Bleue and at Pic Ningua can successfully raise chicks in the wet season from eggs incubated in the early part (December) of that season (sections 1.4 and 3.3.12). Most might not do so at the Parc because pairs who moult in the wet season and early part of the dry season and nest soon afterwards (June-August) have on average higher reproductive success. Although food supplies peak in the wet season, this is mostly dependent on cyclonic weather which is unpredictable, as the rainfall pattern in the wet season at Pic Ningua showed (Fig. 3-3). In contrast, food supplies would probably be more predictable in the early dry season when cooler and damp conditions usually prevail. Birds may still have high bodyweights then following the wet season as mean minimum temperatures in forest at the Parc were usually above about 10°C, and any loss of condition for birds there due to colder weather would be reduced compared to that for birds at high altitude. Moult, on the other hand, may best be carried out in the wet season when food supplies peak and the exact time of the peak(s) is unpredictable (most of the energy for moult comes directly from food, and the speed of moult can be regulated to cope with changing food availability; section 3.4.6). That most non-breeding kagus at Pic Ningua lost bodyweight in the 1994 wet season when conditions became dry showed that birds can have difficulty finding and capturing potential prey even when temperatures are high, and this could have implications for chick provisioning then. Another scenario is that moult outside the wet season and the first two months (April/May) of the early dry season might be difficult for birds whereas they can successfully breed then. Snow (1976) noted in Cotingidae (bird species mostly inhabiting primary tropical forest) that moult was also more timed to coincide with the period of peak food supplies rather than breeding. This also appears the case for kagus at Parc Rivière Bleue who start breeding three months into the dry season and after the period of peak food supplies, and just after they appear to have completed primary moult.

If kagus at Pic Ningua mostly breed just before the wet season as the two breeding records I observed at that time might indicate (section 3.3.12), then probably in contrast to pairs at Parc Rivière Bleue they do so when their bodyweights are on the upswing. Given that birds lost bodyweight from about April to late October at high altitude and also moulted from around January to May, it would seem sensible for them to nest as soon as conditions were suitable after their bodyweights began increasing in the late dry season, but before hot, humid weather in the wet season triggered moult. More data is needed to establish if this is the case (section 7.5), but it would mean a much shorter breeding season at high altitude. One important implication of this would be the lack of time for replacement or second clutches. Also, if colder and drier (El Niño) conditions continued up until the start of the wet season then there may be little opportunity at all to breed before moult commenced. This might have been the situation at Pic Ningua in 1993 and at Mt Cindoa in 1993 and 1994. If so, birds faced problems obtaining sufficient nutrient reserves to make breeding attempts before the first heavy rains of the wet season even when their bodyweights were on the upswing. Jones and Ward (1976) proposed that red-billed queleas *Queleas quelea* commenced breeding only when they had sufficient body condition to do so, and supplementary-fed female kestrels *Falco tinnunculus* were heavier and bred earlier than non-fed ones (Drent and Daan 1980). The likely longer breeding season for kagus at low altitude would mean that pairs there could attempt at least one clutch each year, which seems to be generally the case at Parc Rivière Bleue (Létocart 1991). Thus pairs at the Parc may have on average higher reproductive success than those at high altitude, and this might be achieved with lower food availability given the possibility of a mid-altitude peak in kagu food supplies. The weaker seasonality and higher temperatures at low altitude would probably help compensate for any reduced food availability. The limited kagu bodyweight data at the Parc (Létocart 1991) suggested that birds there were generally lighter (< 1 kg) than those at Pic Ningua where weights of over 1 kg were common in the wet season. Thus kagu bodyweights at the Parc may be lower on average and fluctuate in magnitude to a lesser degree, but this is yet to be established.

Kagus appeared to mostly breed at appropriate times in the dry season, however reasons why birds do not incubate or generally raise chicks in the wet season (at least at Parc Rivière Bleue) when food supplies peak are unclear. The scenario above does not provide clear support for prediction four that kagus time their breeding to maximise reproductive success (section 1.6).

7.3 Food supply and the kagu's fecundity

My main research objective was to see if food supply was limiting the kagu's annual fecundity (section 1.1). Annual fecundity in birds is a combination of clutch size and the number of clutches per year, and the kagu's small clutch and low rate of iteroparity is contrary to predictions from the nest predation hypothesis (section 1.5). Kagu clutch size is invariable and may have been fixed before any kagu evolution in New Caledonia took place (section 1.5). If it is linked to local environmental conditions, then evidence for this might be seen in the relationships between food supplies and aspects of kagu reproduction like egg formation, length between renesting attempts and chick provisioning. There is little information on whether or not kagus in the wild have difficulty in procuring food to provision chicks, but Létocart's data (section 1.5) suggest that this might be the case. Small clutches in altricial birds are significantly associated with lower provisioning rates but reasons for this other than food limitation might exist, for example parents might not provision at the maximum rate (Sæther 1994). Sæther suggested though that the positive relationship between clutch size and provisioning rate he found was support for the importance of food limitation for life history evolution in birds. Longer intervals between nesting attempts might be associated with greater food limitation (Martin 1987 1996). Two females at Parc Rivière Bleue laid replacement eggs many weeks after losing their first egg or chick (Létocart 1991), but environmental conditions for breeding must be taken into account. Females appear to require many days or weeks to produce an egg, and this could also be related to low resource availability. A captive female laid a replacement egg 19 days after her last egg was removed (Campbell 1905, section 1.4). There is little direct evidence that the kagu's annual fecundity is constrained by food limitation.

There were three aspects to prediction three (section 1.6) about the relationship between the kagu's food supplies and their reproduction: (1) annual 'invariability' in food supplies; (2) food limitation; and (3) food limitation independent of kagu densities. I next discuss in turn the support that my results and those of Létocart's (see also section 1.5) provide for each of these three aspects. First, if clutch size is linked to food supplies in New Caledonia, it could arguably only have come about due to highly similar year-to-year patterns in them (section 1.5). My data suggest that the kagu's food supply does vary seasonally in highly similar ways each year in close association with variation in temperature. The food supplies were also relatively spatially homogenous at Pic Ningua and between the three study areas. Support for the latter was that the kagu's social system seemed to vary little between Pic Ningua and Parc Rivière Bleue, where birds at high densities were able to live and reproduce on relatively small, fixed territories. This was probably an indication of the relative stability of the kagu's food supply in the forest understorey due to the generally uniform nature of the soil and litter environment and that it was buffered from extreme physical conditions. Thus my results support predictions one and two about the spatial and temporal nature of the kagu's food supplies, and that their abundance is closely linked to climate (section 1.6). The year-to-year environmental 'invariability' that I found is also consistent with the kagu's relatively invariable number of broods per year at Parc Rivière Bleue. As the number of broods pairs raised per year at the Parc varied from zero to two but was generally one (Létocart 1991), it seemed that annual fecundity there was constrained by some factor(s).

Second, several reasons point to food supply limiting the kagu's annual fecundity: (1) Potential food supplies at any time for a predator are often considerably more than those which they are able to use (Andrewartha and Birch 1954), and this also probably applies to kagus. The abundance of potential kagu prey in the soil and litter, and within reach of birds above the forest floor, is almost certainly substantially greater than might be suggested by the decline in kagu bodyweights that I recorded in the dry season at high altitude. Densities of soil and litter taxa in other tropical rainforests indicated potential kagu prey should be considerable even per square metre (Table 5-6; these forests were at lower latitudes than New Caledonia). Not all prey present at any time are able to be used by kagus because prey are hidden and unavailable (e.g., earthworms in dry conditions), and difficult to find and/or to capture. An important foraging constraint for kagus then is finding and/or capturing potential prey present in the environment. Support for this is the amount of time that birds spend foraging, they spend considerable time standing waiting to detect prey, some birds attempt to flush prey and after detecting a prey item their search for it (by moving litter and/or soil with their bills) is not always successful (pers. obs.). At lower prey densities in drier and/or cold conditions many prey probably become even more difficult to obtain as kagu bodyweight decline at high altitude in these conditions showed. Small tropical insectivores foraging above the forest floor probably also face the same foraging constraint that kagus do, as well as having to cope with a probably greater array of inedible and/or toxic prey (Owen 1977, Thiollay 1988). The nature of the kagu's food supply was similar between all three study areas therefore birds at the Parc probably also had difficulty finding and/or capturing prey that were present in the dry season when they breed; (2) That non-breeding birds at Pic Ningua had negative energy budgets over most of the period that birds at Parc Rivière Bleue were breeding, and animal abundance in pitfall traps was similar at both areas then, suggests that food supplies at the Parc were not abundant at that time; (3) Kagu bodyweights tended to be lower at Parc Rivière Bleue (section 7.2) than at Pic Ningua and this might also indicate that food is not abundant for birds at the Parc when they breed. Kagus weighed at the Parc mostly breed each year (Létocart 1991) and this may have affected their condition, however birds' bodyweights at Pic Ningua in early 1993 reached high levels when at least some pairs there bred in late 1992. Birds' beak and tarsus measurements at the Parc (Létocart 1991) were similar to those of birds at my study areas; (4) Pair 119 and 120 bred in 1994 at Pic Ningua but not 1993 when their bodyweights tended to be lower in November and December (section 3.4.3). Also, birds' bodyweights were lower at Mt Cindoa than at Pic Ningua, and I detected no breeding at Mt Cindoa where food supplies also appeared to be lower; (5) As incubating birds can do at Parc Rivière Bleue (Létocart 1991, section 1.5), female 119 lost bodyweight (around 100 g) when she was incubating in December 1994 (Fig. 3-30) and had access to a large foraging area, but I did not know if male 120 lost bodyweight over incubation. Therefore incubating birds restricted to foraging for around half a day do not appear to be able to find sufficient food to maintain their bodyweights. Daily incubation shift changes at around mid day would be the optimal solution to food shortage as it means each partner can forage for a similar length of time each day; (6) Both parents forage long hours to feed themselves and only one chick at Parc Rivière Bleue (section 1.4), and this may also be the case at high altitude; and (7) From the relationship between their diets and food supplies, birds at Pic Ningua and Mt Cindoa appeared to forage in ways that suggested they were attempting to efficiently use the food resources available to them. Therefore, due to a lack of other factors influencing them (section 6.4.4), birds' bodyweight decline in the dry season on the peaks was probably associated with food limitation and this may prevent them breeding when birds do at Parc Rivière Bleue. If the kagu's annual fecundity was lower in high compared to low altitude areas because of a likely shorter breeding season (section 7.2), then greater food limitation would be strongly implicated in causing this.

Third, three reasons point to kagu food supplies being independent of pair densities: (1) Because food supplies for kagus are relatively evenly dispersed in forest and territory size varied considerably at both Pic Ningua and Parc Rivière Bleue (Létocart 1991, section 1.4), there seemed to be a poor relationship between territory sizes and food supplies within areas. Fecundity at the Parc was also poorly related to territory size given that pairs there generally raised only one offspring per year, although the pair that raised two offspring at the Parc in 1988 had a relatively large territory at that time (30 ha; Létocart 1991). The sizes of pairs' territories in an area might be larger than needed for successful reproduction and survival and vary considerably in area because of one or a combination of reasons, for example (a) pair densities are below carrying capacity; (b) because pairs live on relatively fixed territories they should be able to cope with times when food supplies are at their seasonal lows, and as most birds do not appear to breed at those times this could mean a poor relationship between territory size and annual fecundity; and (c) territory sizes are regulated by factor(s) other than food like space requirements (Stamps 1994). Taborsky and Taborsky (1992) thought that there was a poor relationship between the sizes of New Zealand brown kiwis' *Apteryx australis mantelli* territories and food supplies at their study area. They suggested that brown kiwi territoriality was more related to obtaining space and a mate to breed with, as may also be the case for kagus. There is little data on whether or not annual fecundity of kiwi pairs is related to territory size or food supplies. Factor(s) other than supplies of food and time may also limit fecundity of kiwis, for example the number of the large eggs that a male can incubate (McLennan 1988); (2) Kagu pairs appear to have relatively few aggressive interactions with neighbouring pairs and are tolerant of independent offspring on their territories. This suggests that intraspecific competition for food is not strong. Along with food limitation, a requirement for competition is that birds can deplete food levels so as to affect abundance for other individuals (Schluter and Repasky 1991). It may be difficult for at least one kagu offspring to significantly deplete prey availability for its parents given the likelihood of the numbers of potential prey probably present in the soil and litter on a territory; and (3) Similar patterns in bodyweight variation for free-ranging kagus (Pic Ningua) and those living on small home ranges (Mt Cindoa), and the close relationships I found between kagus' bodyweights, diets, food supplies and roosting behaviour and climate, suggest that variation in kagus' bodyweights and therefore possibly fecundity is directly linked to food supplies and not indirectly through density-related effects. Differences in bodyweight variation between years at Pic Ningua appeared to be related to changing environmental conditions and not a consequence of larger home ranges after the dog attacks (sections 3.4.5 and 5.4.1).

Thus I suggest that there was some support for prediction three that kagus face annual, highly predictable density-independent food limitation for reproduction (section 1.6). In the absence of human-associated disturbance, the kagu breeding population though is probably regulated by density-dependence largely through the spacing behaviour of pairs.

Most studies linking density-independent food limitation to fecundity in birds have focused on seabirds (e.g., Ashmole 1963) where the evidence for this is strong at least for the success or failure of breeding attempts. There is little data to suggest that density-independent food limitation has influenced the evolution of life histories and fecundity in birds, but this is cited as the reason for one-egg clutches in seabirds like albatrosses *Diomedea* spp. (Ashmole 1963, Lack 1968). The influence of food supply on the evolution of seabirds' fecundity is far from clear, however. Recently, Gebczynski *et al.* (1996) found that dovekie *Alle alle* parents (females lay one-egg clutches) failed to respond to increased food demand when additional chicks were placed in nests, and suggested that this might have been because they were physically or genetically unable to do so. Bolton (1995) suggested that food regulation rather than food limitation may set food provisioning rates of storm petrel *Hydrobates pelagicus* chicks. Studies of flycatchers *Ficedula* spp. have suggested that variation in their clutch sizes was due to density-independent changes in abundance of caterpillars (Török and Tóth 1988 and references therein). Factors that cause within-species variation in clutch-size though may not have been responsible for shaping the modal clutch size (Martin 1995). The nature of a species food supply is obviously important in whether density-independent factors can operate. It is more likely that food limitation for a fruit- or seed-eating bird will be dependent on densities of other fruit- or seed-eating animals unless there is complete crop failure because food abundance is closely related to food availability. An important role of density-independent food limitation in shaping annual fecundity of birds at lower latitudes appears consistent with the positive association between clutch size and latitude given the lack of evidence of a corresponding increase in bird densities at least within species (Karr 1990) or iteroparity in the tropics (Martin 1996).

One consequence of density-independent food limitation of fecundity should be that life history characteristics are mainly shaped by selection to maximise energy resources (e.g., food) through interaction with the environment rather than by competition with other individuals. This might result in relatively stable social and breeding systems like the kagu's where aggression is reduced leading to greater foraging time. Monogamous relationships on fixed territories where aggression is reduced and there is greater tolerance of subordinates are more common in tropical land birds (Kunkel 1974, Farabaugh 1982) whose food supplies may be more limiting than for northern birds (section 1.5). This seems contrary to the idea that extended parental care in the tropics might function to raise young that can better compete for limited resources (section 3.4.2). Reduced aggression and greater tolerance of subordinates are also common characteristics of territorial species on islands (Stamps and Buechner 1985), where food supplies may be more limiting than on continents (section 1.5). I propose that density-independent food limitation has been important in shaping forest birds' annual fecundity and other life history characteristics like social organisation in the tropics and possibly south temperate regions, especially those species where pairs hold relatively fixed territories year-round and live in long-term pairs. This appears to be a novel theoretical contribution for understanding the evolution and diversity of land birds' life histories.

New Zealand kiwis *Apteryx* spp., south temperate birds, have social systems remarkably similar to the kagu's, which could be related to the similarity between the two species' food supplies (section 5.4.3). Kiwi pairs hold territories, form long-term pairbonds, duet, share territorial defence, engage in few disputes with neighbouring pairs, and tolerate subordinates on their home ranges (Colbourne and Kleinpaste 1983, Colbourne and Kleinpaste 1984, McLennan *et al.* 1987, McLennan 1988, Taborsky and Taborsky 1991, Taborsky and Taborsky 1992). Kiwis' life styles might suggest that density-independent food limitation has also been important in shaping aspects of their social organisations and other life history characteristics.

7.4 Implications for future kagu conservation management

My results include five important implications for kagu conservation management: (1) only a relatively small number of kagus now exist, and that these are in the remoter parts of the kagu's potential range is almost certainly due to human-associated factors; (2) the dog attacks at Pic Ningua confirmed that dogs *Canis familiaris* are dangerous predators of adult kagus, and this may have been an important factor shaping kagu distribution; (3) kagu reproductive success may be greater in low altitude rainforest than in high altitude rainforest if the breeding season at low altitude is considerably longer; (4) because kagu clutch size is low and invariable, and the number of successful broods per year is also low and seems to be more influenced by density-independent factor(s), birds are especially vulnerable to predation because they cannot respond to lower densities by lifting their reproductive output; and (5) feral pigs *Sus scrofa* at sufficiently high densities have the potential to reduce prey availability for kagus.

The number of kagus known in the wild at the beginning of 1992 (654; Hunt 1996a) was considerably more than that for many endangered species (Collar *et al.* 1994). However, it was very low given that the decline in kagu numbers outside Parc Rivière Bleue (where 491 of the 654 kagus recorded in 1991 lived) is probably continuing (e.g., at Pic Ningua) and the importance to avian diversity of the kagu. The kagu is the last surviving species of probably a much larger group of taxonomically similar birds (e.g., extinct Messelornithidae; Hesse 1988). It is the only extant species in the sub-order Rhynocheti, and remnant lineages like the kagu represent a large fraction of avian life history diversity (Bennett and Owens 1997).

Capture of kagus by humans is now rare, so emphasis for kagu conservation can be directed at other agents of decline (introduced predators, habitat loss) and kagu recovery in the wild. The kagu distribution pattern and the events at Pic Ningua suggest that kagus outside areas managed for kagu conservation may only survive the medium term because of dog predation (stray dogs or dogs with hunters). Control of dogs to protect kagus needs to reduce the occurrence of dogs straying and stop them entering kagu areas. Reducing the occurrence of straying dogs will not be easy. Because tribal villages are generally closer to forest and remaining kagus than municipal towns, it will be especially important to involve these communities in kagu conservation. The stray dog problem can only be solved over the longer term, with continuing education campaigns about the dog threat to kagus to encourage greater responsibility about dog ownership and enforcement of dog control laws. Preventing dogs entering kagu areas must involve the establishment of intensively managed reserves where dogs and other kagu predators (e.g., cats *Felis catus* and pigs) are controlled. Demarcation of kagu reserves is necessary, but special regulations could apply in them to take account of, for example, traditional hunting for animals like notous *Ducula giganta* (native pigeon).

At present, only a small percentage of the kagu population live in protected habitat where management for kagu conservation is undertaken: 63 pairs censused at Parc Rivière Bleue in 1991 (Létocart 1992), and possibly up to 60 individuals (A. Duncan pers. comm.) in the recently established much smaller reserve in the upper Nodela River catchment on Mé Maoya Massif, northwest of Bourail (Figs. 2-1 and 2-2). This number of birds is not adequate to provide a reasonable chance of long-term kagu persistence in the wild. The dog attacks at Pic Ningua demonstrated this clearly (Hunt *et al.* 1996c). Kagus may not survive the long-term at all except in large populations in managed reserves like Parc Rivière Bleue. Therefore, additional large managed reserves similar to the Parc are needed in the short term, preferably encompassing a variety of vegetation types and altitudes where forest fragmentation is minimal (Wilcox and Murphy 1985), to protect significant numbers of breeding pairs and better insure against catastrophes (Mangel and Tier 1994). This would also preserve the range of kagu behaviour and life history diversity that exists, like the variation in roosting behaviour between low and high altitudes. Trade-offs will be needed between manageability of reserves and their location. Reserves in remoter areas (e.g., at higher altitude) will be logistically more difficult to manage, but probably require less effort to maintain kagu numbers at reasonable levels. The opposite will apply for reserves close to human settlements.

The kagu's future is brighter than that of many endangered birds because its decline in an area can be successfully reversed. Kagus can be raised in captivity and released back into the wild to pair with wild birds (section 1.4), and the successful recovery programme at Parc Rivière Bleue has demonstrated that kagu recovery in the wild is possible and has developed the methods to achieve this (Létocart 1992). Although the actual factor(s) leading to the large increase in kagu numbers at the Parc is unclear, the management there has shown that the prohibition of hunting (e.g., for pigs and deer *Cervus timorensis*) and the control of stray dogs in kagu habitat, combined with kagu introductions, are techniques that will probably result in kagu recovery. These management methods can probably be easily applied elsewhere on Grande Terre given the resources (suitable reserves, staff and funds) to do so.

That kagus now mostly live at higher altitudes is also an important point relevant to their conservation. Although birds in this habitat may generally be better protected from human-associated disturbance, they might be less able to recover from a large reduction in their densities because (1) their breeding season may be too short to allow replacement or second clutches; (2) kagus numbers in areas at higher altitudes tend to be small; and (3) there is less chance of immigration of birds because they have largely disappeared at low altitude and kagus at high altitude tend to be isolated from each other by mountainous terrain (Hunt 1996a). Thus it is important to prevent any serious predation of kagus in an area at high altitude if birds are to remain there.

In summary, steps needed to ensure long-term kagu persistence in the wild are: (1) the establishment of at least two additional intensively-managed reserves like Parc Rivière Bleue where dog control would be a priority; (2) the identification of reasons for the disappearance of young kagu chicks (section 7.5); (3) continuing awareness programmes to educate the public and administrators about the need for kagu protection and associated dog control; (4) the involvement of tribal communities in kagu conservation, in association with promoting the kagu as an important part of Kanak culture that should be protected; and (5) the enforcement of dog control laws. Addressing these points will mean the establishment of new reserves and a more secure future for the kagu, and also help protect the high endemism and biodiversity in New Caledonia (e.g., Chazeau 1993, Jaffré *et al.* 1994) and educate the public about the pressing need for conservation in the Territory (Mittermeier *et al.* 1996).

7.5 Priorities for kagu research in the future

Although the techniques for successful kagu recovery in the wild are generally established (section 7.4), there are important areas of kagu ecology that need further research to better aid the species' conservation and to increase our limited understanding of life history evolution in tropical forest birds:

(1) To better understand the timing of kagu breeding, data on seasonal bodyweight variation of adult kagus at Parc Rivière Bleue are needed, and clarification of the breeding period at high altitude.

(2) Data are needed on whether rats *Rattus* spp., cats and pigs are significant predators of kagu eggs and/or chicks because this is unclear. It would be important to establish the reason(s) for the quite high rate of disappearance of chicks aged up to around ten days old that Létocart (1992) reported.

(3) Ways of hunting pigs and deer without endangering kagus should be investigated, for example, use of humane snaring methods or well-trained muzzled dogs (Pavlov *et al.* 1992).

(4) Quantitative work is needed to investigate whether pig foraging affects fecundity of kagus and pair densities through competition for food.

(5) Investigation of chick provisioning by parents could provide insights into whether this aspect of kagu reproduction might be a ‘bottleneck’ limiting their clutch size. Food delivery rates, numbers of broods per year and length of inter-brood intervals may be better reproductive parameters with which to study food limitation (Martin 1996), especially in a bird species with an invariable clutch. Following on from Létocart’s (1991) preliminary observations, research could concentrate on how different environmental conditions affect food provisioning and chick growth rates. Food supplementation in the wild when parents are provisioning might result in increased chick growth rates compared to chicks whose parents do not receive additional food. The research above could indicate if parents have difficulty in feeding only one chick.

(6) Food supplementation of kagu pairs in the wild could help to determine if food supply is limiting the numbers of successful broods per year that they can raise. At high altitude, it would be especially important to supply food for most of the dry season when kagus’ bodyweights there are low and/or declining. At Parc Rivière Bleue, food addition may only be required when offspring raised from eggs laid in June-August approach independence.

(7) The kagu can be used as a study species to investigate my density-independent food limitation hypothesis. As well as investigating whether or not food supply is limiting the kagu’s reproductive output (points 5 and 6 above), it is necessary to test predictions from the hypothesis like a poor relationship between territory size and annual fecundity and food supply, and that variation in chick growth and provisioning rates are independent of pair densities.

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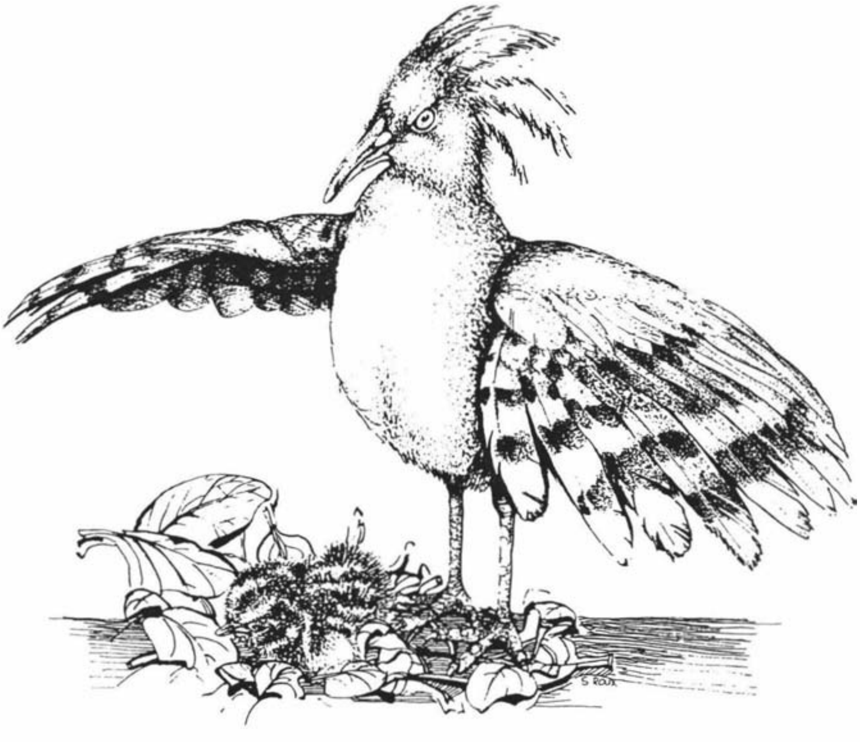

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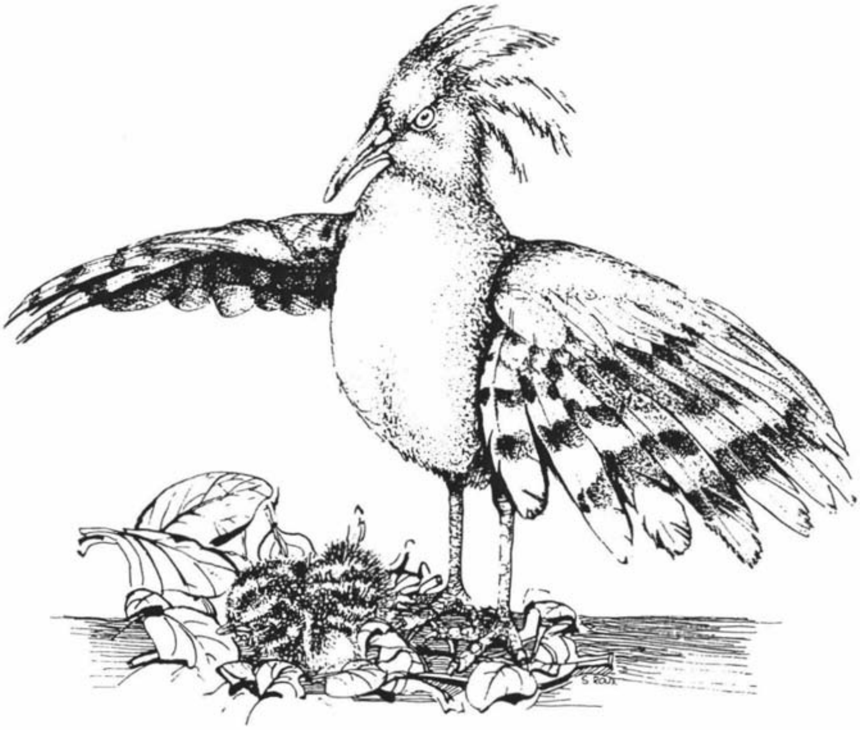
Appendices



Appendix I.

Reprint of results in Chapter Two.

‘Environmental variables associated with population patterns of the Kagu *Rhynochetos jubatus* of New Caledonia’

Appendix II.

Survey data used for the generalised linear modelling analyses in *Chapter 2*. Rows represent the 83 different listening areas. Column 1 gives the listening site ID number from the original report (Hunt 1992). Column 2 gives the number of kagus recorded in each area. Columns 3 to 10 give the data for the eight variables measured in each area. Variable abbreviations are: AC = Access; AL = Altitude; GE = Geology; FO = Forestry history; LS = Listening area size; RO = Nearest in-use road; SE = Nearest settlement; VE = Vegetation type. Raw data are given for variables AL (m), LS (ha), RO (km) and SE (km), but these were categorised for the analyses (section 2.2.2). Categorised values are given for AC, GE, FO and VE. Complete survey results are in Hunt (1992).

Site	Kagu Nos.	AC	AL	GE	FO	LS	RO	SE	VE
31	3	3	700	1	1	661	4.3	2.2	3
32	1	3	650	1	1	330	5	5.3	3
33	5	3	750	1	1	552	6.5	6.5	3
34	12	3	850	1	1	491	6.5	6.5	3
36	1	2	400	1	1	731	4	4.5	3
37	2	3	700	1	1	241	5	6.8	3
44	3	2	600	1	3	491	1.8	7.7	3
45	2	1	450	1	3	855	2.3	8.6	2
47	1	2	550	1	1	380	2.4	5.3	2
48	1	1	350	1	2	422	0.7	1.9	2
56	1	2	200	1	3	416	2	9.5	1
57	2	2	500	1	3	330	2.8	2.7	1
59	1	1	200	1	3	491	1.5	1.5	1
60	5	2	700	1	2	347	2	7.5	3
61	7	1	750	1	2	453	3.3	6.5	3
62	5	2	450	1	1	398	3.1	3.5	3
63	24	3	550	1	3	363	0.2	8.5	3
66	19	3	650	1	3	398	1.3	6.2	3
67	1	3	1150	1	3	143	2	3	3
68	1	3	1400	1	3	44	3.7	4.4	3
69	6	1	550	2	1	363	3	4	3
70	3	2	600	2	1	255	5.5	6	3
71	3	2	600	2	1	269	3.3	4	3
72	3	1	550	2	1	355	3.3	5	3
73	2	1	400	1	1	269	0.2	4	3
75	5	1	200	1	2	299	2.5	2.5	2
76	9	2	500	1	1	638	1.4	5	3
77	3	1	700	1	3	207	0.4	6	1
78	2	1	600	1	3	207	2.1	4.5	3
80	4	1	500	1	3	154	3.1	5.5	1
82	8	2	550	1	3	201	0.9	8	3
83	5	1	300	1	2	330	1.3	6	2
84	4	1	500	3	1	380	0.8	3.5	3
85	2	1	450	3	1	138	0.2	3.5	3
87	5	2	500	1	1	195	2.4	4	3

Appendix II continued next page.

Appendix II continued.

Site	Kagu Nos.	AC	AL	GE	FO	LS	RO	SE	VE
88	4	1	500	1	2	416	3	4	3
89	3	2	450	2	2	220	3.3	3.3	3
94	1	1	400	3	2	363	1	6	3
97	5	2	650	1	2	552	4.2	5.8	3
98	2	1	400	3	1	241	0.2	4.7	3
100	2	1	450	3	1	330	0.2	7	3
101	2	1	400	3	1	314	0.2	5.5	3
106	2	1	450	2	1	638	0.3	5.4	3
107	4	2	550	1	1	269	3.3	3.3	3
109	2	2	330	1	1	434	1.6	4.7	3
111	2	2	500	1	1	416	3.3	2.2	3
114	1	1	650	2	1	398	1.4	2	3
116	11	1	600	1	2	731	2.5	3	2
118	10	2	800	1	1	143	0.8	4.5	3
119	15	2	900	1	1	214	2.3	5.1	3
120	2	2	850	1	2	347	4	5	3
121	1	2	800	1	1	363	2.7	5.6	2
122	8	2	700	1	1	363	1.9	3.4	3
123	7	2	350	1	2	990	0.2	6.6	2
124	10	3	350	1	2	299	1.4	8.2	2
125	22	2	700	1	2	661	3.9	4.5	2
126	13	2	500	1	2	416	4	5.3	2
127	18	3	350	1	2	347	2.9	7.1	2
128	16	3	550	1	2	780	1.1	5.2	2
129	1	2	750	1	1	472	2.2	6.3	2
130	3	2	300	1	3	241	5.3	6.6	3
131	1	3	700	1	3	104	5.8	6	3
132	1	2	350	1	3	472	1.5	8.6	1
133	12	2	1100	1	3	64	0.8	8.6	3
134	20	2	1150	1	3	123	0.2	4.6	3
135	10	3	950	1	3	241	9	15	3
136	5	3	100	1	2	113	1.1	9	2
137	9	3	250	1	1	398	1.5	5.3	2
138	2	3	500	1	1	398	0.2	3	3
141	12	3	850	1	3	143	7.5	8.8	3
142	11	3	1200	1	3	87	8.5	8.7	3
143	18	3	900	1	3	57	9	9.5	3
147	17	3	400	1	2	453	4.5	8	3
155	1	3	1250	1	3	269	10	13	3
158	4	3	1100	1	3	104	6.7	9.2	3
166	1	3	150	1	3	416	8	10.5	1
173	4	1	800	2	3	434	0.2	10.5	3
174	6	2	800	3	2	189	0.4	13	3
177	4	3	250	1	3	347	5.8	7	1
179	5	3	200	1	3	284	5	7	1
181	12	3	650	1	3	780	4.9	8.5	3
182	6	1	350	2	2	511	1.5	6	3
183	2	2	250	2	3	638	5	5	3

Appendix III.

Dates for the 56 fortnightly sampling intervals from 25/1/93 to 19/3/95 into which most of the data I collected at the three study areas (Pic Ningua, Mt Cindoa and Parc Rivière Bleue) were organised.

Fortnightly sampling interval	**Date**	**Fortnightly sampling interval**	**Date**
1	25/1/93 - 7/2/93	29	21/2/94 - 6/3/94
2	8/2/93 - 21/2/93	30	7/3/94 - 20/3/94
3	22/2/93 - 7/3/93	31	21/3/94 - 3/4/94
4	8/3/93 - 21/3/93	32	4/4/94 - 17/4/94
5	22/3/93 - 4/4/93	33	18/4/94 - 1/5/94
6	5/4/93 - 18/4/93	34	2/5/94 - 15/5/94
7	19/4/93 - 2/5/93	35	16/5/94 - 29/5/94
8	3/5/93 - 16/5/93	36	30/5/94 - 12/6/94
9	17/5/93 - 30/5/93	37	13/6/94 - 26/6/94
10	31/5/93 - 13/6/93	38	27/6/94 - 10/7/94
11	14/6/93 - 27/6/93	39	11/7/94 - 24/7/94
12	28/6/93 - 11/7/93	40	25/7/94 - 7/8/94
13	12/7/93 - 25/7/93	41	8/8/94 - 21/8/94
14	26/7/93 - 8/8/93	42	22/8/94 - 4/9/94
15	9/8/93 - 22/8/93	43	5/9/94 - 18/9/94
16	23/8/93 - 5/9/93	44	19/9/94 - 2/10/94
17	6/9/93 - 19/9/93	45	3/10/94 - 16/10/94
18	20/9/93 - 3/10/93	46	17/10/94 - 30/10/94
19	4/10/93 - 17/10/93	47	31/10/94 - 13/1194
20	18/10/93 - 31/10/93	48	14/11/94 - 27/11/94
21	1/11/93 - 14/11/93	49	28/11/94 - 11/12/94
22	15/11/93 - 28/11/93	50	12/12/94 - 25/12/94
23	29/11/93 - 12/12/93	51	26/12/94 - 8/1/94
24	13/12/93 - 26/12/93	52	9/1/95 - 22/1/94
25	27/12/94 - 9/1/94	53	23/1/99 - 5/2/95
26	10/1/94 - 23/1/94	54	6/2/95 - 19/2/95
27	24/1/94 - 6/2/94	55	20/2/95 - 5/3/95
28	7/2/94 - 20/2/94	56	6/3/95 - 19/3/95

Appendix IV.

Summary data on individual kagus captured, sighted, or found dead at Pic Ningua and Mt Cindoa. Column 2: 'A' = Adult; 'SA' = subadult/adult; 'J' = Juvenile less than one year old; '?' age unknown. Column 3: 'F' = Female; 'M' = Male; '?' = sex unknown. Column 8 gives method of first capture. Mean bodyweights were rounded. One of the unknown dead birds 130-133 might have been bird 136 who was not banded. As well, remains of dead kagus 132 and 134 were incomplete and these birds may have been banded. At Mt Cindoa, bird 206 and the two unknown birds (indicated by '?'s in column 1) I saw in late December 1994 could have been the same individual. A '----' = no data or not applicable.

Bird ID No	Age	Sex	Status	Date fitted with transmitter	No. of times weighed	Mean weight (s.e.)	Capture method
Pic Ningua							
101	A	?	paired with Bird 102 (dog-related death in April 1993)	28/1/93	1	1103	model / net
102	A	?	paired with Bird 101 (dog-related death in April 1993)	3/2/93	1	865	roost with 101
103	A	F	paired with Bird 104 (dog-related death in April 1993)	19/1/93	1	855	playbacks / location after dark
104	A	M	paired with Bird 103 (dog-related death in April 1993)	11/2/93	1	890	roost with 103
105	A	M	paired with Bird 106 (dog-related death in April 1993)	19/1/93	1	1033	model / foot snare
106	A	F	paired with Bird 105 (transmitter removed on 1/3/95)	3/2/93	21	951(12.81)	playbacks / net
107	A	M	paired with Bird 108 (dog-related death in April 1993)	20/1/93	1	963	model / net
108	A	F	paired with Bird 107 (dog-related death in April 1993)	8/2/93	1	895	roost with 107

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Appendix IV continued.

Bird ID No	Age	Sex	Status	Date fitted with transmitter	No. of times weighed	Mean weight (s.e.)	Capture method
109	A	F	paired with Bird 110 (transmitter removed 14/2/95)	21/1/93	19	910(15.72)	model / foot snare
110	A	M	paired with Bird 109 (dog-related death in August 1993)	18/3/93	2	980(19.50)	on roost of 109
111	A	F	partner disappeared early in 1993 (transmitter removed on 9/4/95)	24/1/93	21	819(12.06)	roost with 112
112	A	?	family of Bird 111 (banded on 24/1/93)	-----	-----	-----	roost with 111, 128
113	A	?	paired with Bird 114 (dog-related death in May 1993)	23/1/93	1	1000	model / net
114	A	?	paired with Bird 113 (dog-related death in May 1993)	1/2/93	1	845	roost with 113
115	A	F	paired with Bird 116 (dog-related death in August 1993)	20/1/93	3	981(37.07)	model / foot snare
116	A	M	paired with Bird 115 (dog-related death in May 1993)	19/2/93	2	1048(22.50)	roost with 115
117	A	?	same family as Bird 118 (dog-related death in August 1993)	8/6/93	1	925	model / net
118	A	?	same family as Bird 117 (dog-related death in August 1993)	9/6/93	1	1135	roost with 117
119	A	F	paired with Bird 120 (transmitter removed on 21/3/95)	14/6/93	20	906(10.75)	model / foot snare

Appendix IV continued next page.

Appendix IV continued.

Bird ID No	Age	Sex	Status	Date fitted with transmitter	No. of times weighed	Mean weight (s.e.)	Capture method
120	A	M	paired with Bird 119 (transmitter removed on 21/3/95)	14/6/93	19	964(11.81)	model / net
121	A	M	new partner of Bird 115 (dog-related death in August 1993)	29/7/93	1	877	roost with 115
122	J	?	unknown (< 1 year old) (banded on 7/4/93, and dog-related death in May 1993)	27/4/93	1	815	on perch by chance
123	J	F	unknown (< 1 year old) (dog-related death in August 1993)	7/6/93	1	785	model / net
124	SA	M	unknown (transmitter failed in February 1994)	27/11/93	1	730	roost with 111
125	SA	?	unknown (transmitter removed on 14/2/95)	12/4/94	10	837(11.71)	roost with 106
126	A	?	unknown (transmitter removed on 5/3/93)	21/1/93	1	893	model / foot snare
127	A	?	unknown (transmitter removed in March 1993)	23/1/93	1	860	model / foot snare
128	A	?	family of Bird 111 (transmitter removed on 24/1/93)	23/1/93	1	813	model / foot snare
129	SA	?	Offspring of Birds 103 & 104 (banded on 12/2/93)	-----	1	830	roost with 103, 104

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Appendix IV continued.

Bird ID No	Age	Sex	Status	Date fitted with transmitter	No. of times weighed	Mean weight (s.e.)	Capture method
130	J	?	Juvenile of Birds 109 & 110 (banded on 22/4/93)	-----	1	723	roost with 109, 110
131	A	?	unknown (found dead on 9/5/93, dog-related death)	-----	0	-----	-----
132	?	?	unknown (feathers found on 21/5/93, possible dog-related death)	-----	0	-----	-----
133	A	?	unknown (found dead on 23/5/93, dog-related death)	-----	0	-----	-----
134	?	?	unknown (found dead on 12/10/93, possible dog-related death)	-----	0	-----	-----
135	J	?	offspring of Birds 119 and 120 (banded on 28/2/95)	-----	0	-----	at roost site with 120
136	SA	M	possible offspring of 113 and 114 (sighted only with 113 and 114)	-----	0	-----	----
137	SA	?	possible new partner of 111 (roosting with 111 on 9/4/95)	-----	0	----	----
Mt Cindoa							
201	A	?	paired with Bird 202 (transmitter removed on 21/2/95)	1/10/93	11	859(19.77)	model / foot snare
202	A	?	paired with Bird 201 (transmitter removed on 21/2/95)	1/10/93	22	872(9.08)	model / foot snare

Appendix IV continued next page.

Appendix IV continued.

Bird ID No	Age	Sex	Status	Date fitted with transmitter	No. of times weighed	Mean weight (s.e.)	Capture method
203	A	?	possibly paired with Bird 204 (transmitter removed on 7/2/95)	6/10/93	17	820(16.78)	model / foot snare
204	A	?	unknown (transmitter removed on 29/12/93)	15/11/93	2	801(37.50)	model / foot snare
205	A	?	possibly paired with Bird 203 (transmitter removed 29/11/94)	12/7/94	2	627(11.00)	roost with 203
206	SA	?	on territory of Bird 202 (banded 24/1/95)	-----	1	773.5	on perch by chance
?	?	?	unknown (found roosting with 202 on 9/12/94)	-----	0	-----	-----
?	?	?	unknown (roosting on 202's territory on 29/12/94)	-----	0	-----	-----

Appendix V.

Monthly summary of the numbers of kagus fitted with radio-transmitters at Pic Ningua and Mt Cindoa from January 1993 to April 1995. Birds are indicated by their ID numbers. I removed radio-transmitters from kagus either during (dead birds 101, 102, 103, 104, 105, 107, 108, 110, 113, 114, 115, 116, 117, 118, 121, 122, and 123; live birds 126, 127, 128, 204 and 205) or at the finish of my study (birds 106, 109, 111, 119, 120, 125, 201, 202, and 203). Columns 4 and 5 give the total number of birds wearing transmitters at the end of each month ('PN' = Pic Ningua; 'MC' = Mt Cindoa).

Month	**Birds whose radio-transmitters were:**		**Total numbers of birds wearing transmitters**	
	Fitted	**Removed**	**PN**	**MC**
Jan 93	101, 103, 105, 107, 109, 111, 113, 115, 126, 127, 128	128	10	0
Feb	102, 104, 106, 108, 114, 116		16	0
Mar	110	126, 127	15	0
Apr	122	101, 102, 103, 104, 105, 107, 108	9	0
May		113, 114, 116, 122	5	0
Jun	117, 118, 120, 121, 123		10	0
Jul	121		11	0
Aug		110, 115, 117, 118, 121, 123	5	0
Sep			5	0
Oct	201, 202, 203		5	3
Nov	124, 204		6	4
Dec		204	6	3
Jan 94			6	3
Feb		124 (failed?)	5	3
Mar			5	3
Apr	125		6	3
May-Jun			6	3
Jul	205		6	4
Aug-Oct			6	4
Nov		205	6	3
Dec-Jan 95			6	3
Feb		109, 125, 203, 201, 202	4	0
Mar		106, 119, 120	1	0
Apr		111	0	0

Appendix VI.

Eight body measures (cm) taken from 37 kagus caught or found dead (bird 131) at Pic Ningua (n = 31) and Mt Cindoa (n = 6). Full descriptions of the measures are in 3.2.5. Column 2 gives the colour-codes for leg-bands (from left to right leg) fitted to birds ('DG' = dark green; 'BL' = blue; 'Y' = yellow; 'R' = red; 'W' = white; 'G' = light green). Column 3: 'F' = female; 'M' = male; '?' = sex unknown. Column 4: 'A' = adult; 'SA' = adult/subadult; 'J' = juvenile less than one year old. A '----' = no data or not applicable.

Bird No.	Colour band	Sex	Age	Beak length	Beak width	Beak depth	Tarsus length	Foot length	Mid toe length	Mid claw length	Wing length
Pic Ningua											
101	DGR-BLW	?	A	4.56	1.10	1.92	11.40	9.07	7.14	1.25	31
102	GW-DGY	?	A	4.34	1.07	1.91	10.75	8.57	6.83	1.23	26
103	RY-DGY	F	A	4.50	1.14	1.88	11.97	8.51	6.50	1.03	30
104	BLR-GW	M	A	4.52	1.08	1.95	11.03	8.50	6.64	1.13	32
105	RY-DGW	M	A	4.39	1.14	1.88	11.87	9.63	7.17	1.30	31
106	WY-GW	F	A	4.41	1.17	1.88	10.61	9.44	7.92	1.21	32
107	RY-DGR	M	A	4.07	1.15	1.92	11.35	9.32	7.30	1.17	30
108	BLG-GY	F	A	4.29	1.08	1.94	11.53	9.56	6.95	1.23	29
109	BLY-RY	F	A	4.23	1.07	1.80	11.75	8.93	6.92	1.17	31
110	YW-BLW	M	A	4.71	1.10	1.78	11.54	9.60	7.33	1.38	29
111	DGY-DGW	F	A	3.78	1.01	1.67	9.80	8.41	6.60	1.02	27
112	BLW-DGY	?	A	4.07	1.05	1.73	10.29	8.43	6.63	1.03	29
113	RY-YG	?	A	4.20	1.09	1.77	11.57	9.69	7.29	1.16	31
114	GW-BLW	?	A	3.87	1.13	1.89	10.78	8.93	6.91	1.14	28
115	RY-BLG	F	A	4.47	1.01	1.94	11.10	9.49	7.65	1.17	30
116	WY-DGY	M	A	4.46	1.13	1.99	11.50	9.05	7.08	1.22	30

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Appendix VI continued.

Bird No.	Colour band	Sex	Age	Beak length	Beak width	Beak depth	Tarsus length	Foot length	Mid toe length	Mid claw length	Wing length
117	GW-DGW	?	A	4.30	1.08	1.82	10.94	8.88	6.97	1.26	32
118	RY-RW	?	A	4.24	1.02	1.85	11.32	9.45	7.50	1.23	32
119	BLW-RBL	F	A	4.31	1.02	1.92	11.19	8.82	6.96	1.03	30
120	BLDG-RDG	M	A	4.49	1.18	1.95	10.63	9.02	6.99	1.12	29
121	BLR-BLG	M	A	4.53	1.20	1.88	10.55	8.55	6.42	1.20	26
122	BLR-GY	?	J	4.01	1.11	1.60	10.20	9.13	7.12	1.15	28
123	WY-DGW	F	J	4.43	1.05	1.72	10.46	8.55	6.64	1.16	30
124	DG-	M	SA	4.12	1.04	1.88	10.52	8.56	6.75	1.08	31
125	-----	?	SA	4.04	1.06	1.79	11.40	9.22	7.10	1.20	---
126	GW-RY	?	A	4.24	1.14	1.94	11.63	9.70	7.80	1.19	30
127	GR-RY	?	A	4.30	1.09	1.92	11.28	9.55	7.31	1.21	26
128	BLW-RY	?	A	4.39	1.16	1.93	11.58	8.83	6.85	1.08	31
129	BLG-BLY	?	SA	4.03	1.04	1.77	11.29	8.61	6.67	1.03	31
130	DGR-GW	?	J	3.74	0.94	1.58	11.10	8.98	7.02	1.11	29
131	-----	?	A	4.07	0.98	1.70	10.30	8.83	6.92	1.14	27
135	G-	?	J	---	---	---	---	---	---	---	---
Mt Cindoa											
201	DG-BL	?	A	4.24	1.02	1.80	10.99	9.14	7.18	1.11	30
202	Y-G	?	A	4.29	1.20	1.84	11.04	9.64	7.49	1.20	27
203	-----	?	A	4.11	1.20	1.85	10.77	8.69	6.80	1.09	30
204	-----	?	A	3.82	1.02	1.77	10.20	8.99	7.02	1.00	25
205	-----	?	A	4.15	1.00	1.70	10.49	8.66	6.78	1.04	---
206	BL-	?	SA	4.22	1.09	1.83	10.74	8.80	6.67	1.23	---

Appendix VII.

Summary of roost data collected from 37 known and two unknown ('?' in column 1) kagus at Pic Ningua and Mt Cindoa. Roost types: 'S' = Sheltered roosts, 'US' = Unsheltered roosts. The number of roosts in column 3 that were previously used roosts (column 7) is only a minimum figure as re-use of roosts, especially on perches, can be difficult to detect (section 3.3.13). The roost data do not include parents incubating chicks on the ground. A '?' in column 7 = unknown.

Bird ID No	**Period roosts were found**	**No. of roosts**	**Mean altitude of roosts (m)**	**Roost types 'S'**	**'US'**	**No. of roosts used before**
Pic Ningua						
101	3/2/93 - 19/4/95	7	1155	0	7	6
102	3/2/93 - 19/4/93	7	1160	0	7	4
103	1/2/93 - 12/4/93	7	1020	1	6	3
104	12/2/93 - 26/4/93	8	1025	2	6	3
105	31/1/93 - 14/4/93	7	1105	0	7	5
106	5/2/93 - 1/3/95	54	1104	36	18	17
107	31/1/93 - 20/4/93	7	1205	2	5	5
108	9/2/93 - 20/4/93	6	1220	2	4	4
109	10/2/93 - 14/2/95	51	1098	25	26	14
110	10/2/93 - 26/7/93	11	1100	6	5	8
111	2/2/93 - 31/1/95	91	1079	62	29	53
112	24/1/93 - 24/1/93	1	1120	0	1	?
113	1/2/93 - 29/4/93	8	1175	2	6	6
114	1/2/93 - 29/4/93	8	1135	2	6	4
115	10/2/93 - 29/7/93	15	1190	3	12	9
116	19/2/93 - 18/5/93	8	1170	2	6	7

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Appendix VII continued.

Bird ID No	Period roosts were found	No. of roosts	Mean altitude of roosts (m)	Roost types		No. of roosts used before
				‘S’	‘US’	
117	9/6/93 - 4/8/93	8	1135	2	6	2
118	9/6/93 - 4/8/93	8	1140	6	2	4
119	17/6/93 - 21/3/95	46	1085	20	26	21
120	17/6/93 - 21/3/95	64	1015	37	27	35
121	29/7/93 - 29/7/93	1	1175	0	1	0
122	7/4/93 - 27/4/93	2	1105	1	1	2
123	15/6/93 - 27/7/93	4	1230	4	0	2
124	27/11/93 - 1/2/94	6	970	1	5	2
125	12/4/94 - 14/2/93	17	1126	9	8	3
126	11/2/93 - 5/3/93	2	1195	1	1	2
127	23/1/93 - March 1993	1	1180	0	1	?
128	24/1/93 - 24/1/93	1	1120	0	1	?
129	12/2/93 - 12/2/93	1	980	0	1	1
130	25/3/93 - 19/5/93	3	1088	0	3	3
137	9/4/95 - 9/4/95	1	330	0	1	1
Mt Cindoa						
201	2/10/93 - 21/2/95	20	1136	12	8	10
202	2/10/93 - 21/2/95	36	1165	22	14	28
203	16/11/93 - 7/2/95	21	1192	17	4	15
204	16/11/93 - 28/12/93	2	1295	1	1	2
205	12/7/94 - 29/11/94	3	1157	3	0	2
206	24/1/95 - 24/1/95	1	1145	0	1	1
?	9/12/94 - 9/12/94	1	1125	1	0	1
?	29/12/95 - 29/12/95	1	1150	0	1	1

Appendix VIII.

Path diagrams detailing the movements of individual birds (106, 109, 111, 119, 120 and 125) at Pic Ningua, and bird 201 at Mt Cindoa. Movement data were collected from telemetry fixes only (section 3.2.7). The diagram runs chronologically from top to bottom as the dates under circles indicate. Numbers within the circles give the region (Fig. 3-1) a bird was in before I detected it in another region (next circle). The date under each circle indicates when I first detected a bird in the respective region, and the approximate (see below) number of days spent there is above the circle (date one minus date two). For birds 106, 109 and 111, a box separates the first circle (the period that each bird and its partner held a territory before the partner was killed) from the rest of the diagram (when birds became widowed). For bird 109, the first circle after the box is dated 8/8/93 as I took her to Nouméa for treatment after she was wounded by dogs on 5/8/93. Although I often took many telemetry fixes in the period between two adjacent dates, I did not locate birds every day. Therefore, the range of regions visited, and the number of visits to a region, are only minimum estimates of a bird's movements. Likewise, the numbers of days spent in each region is only an average estimate. The arrows indicate the approximate dates when I captured and weighed each bird.

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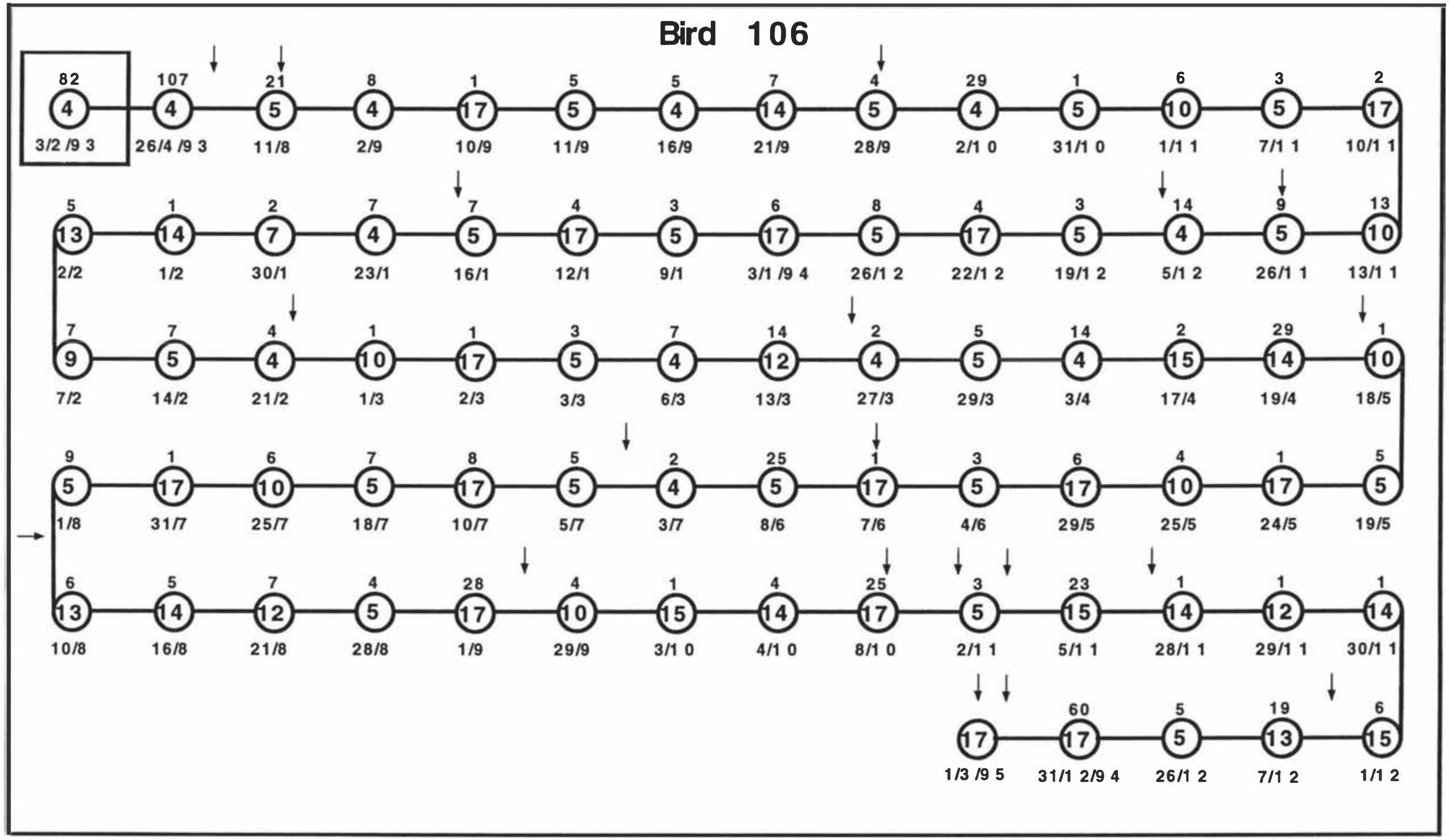

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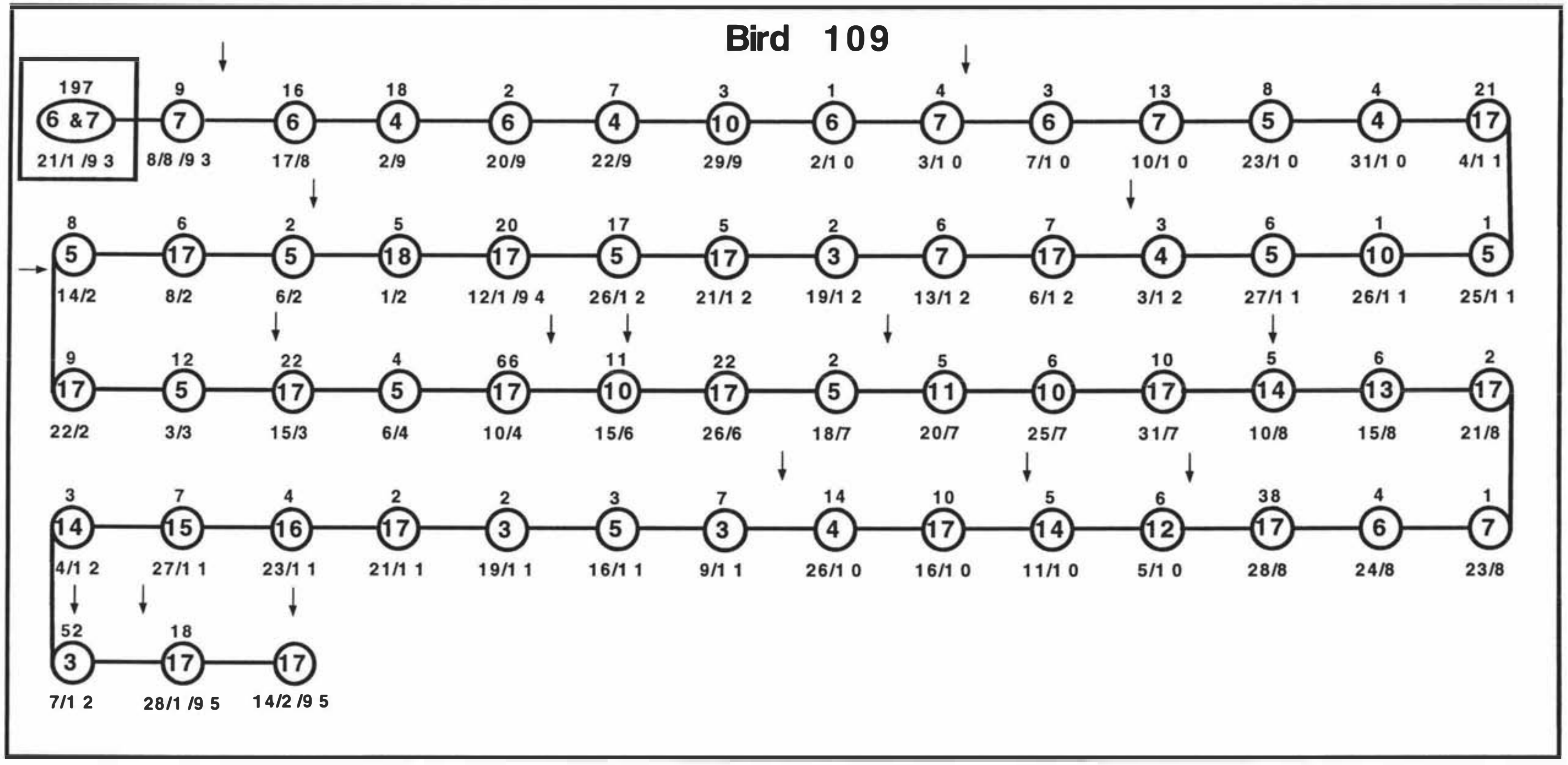

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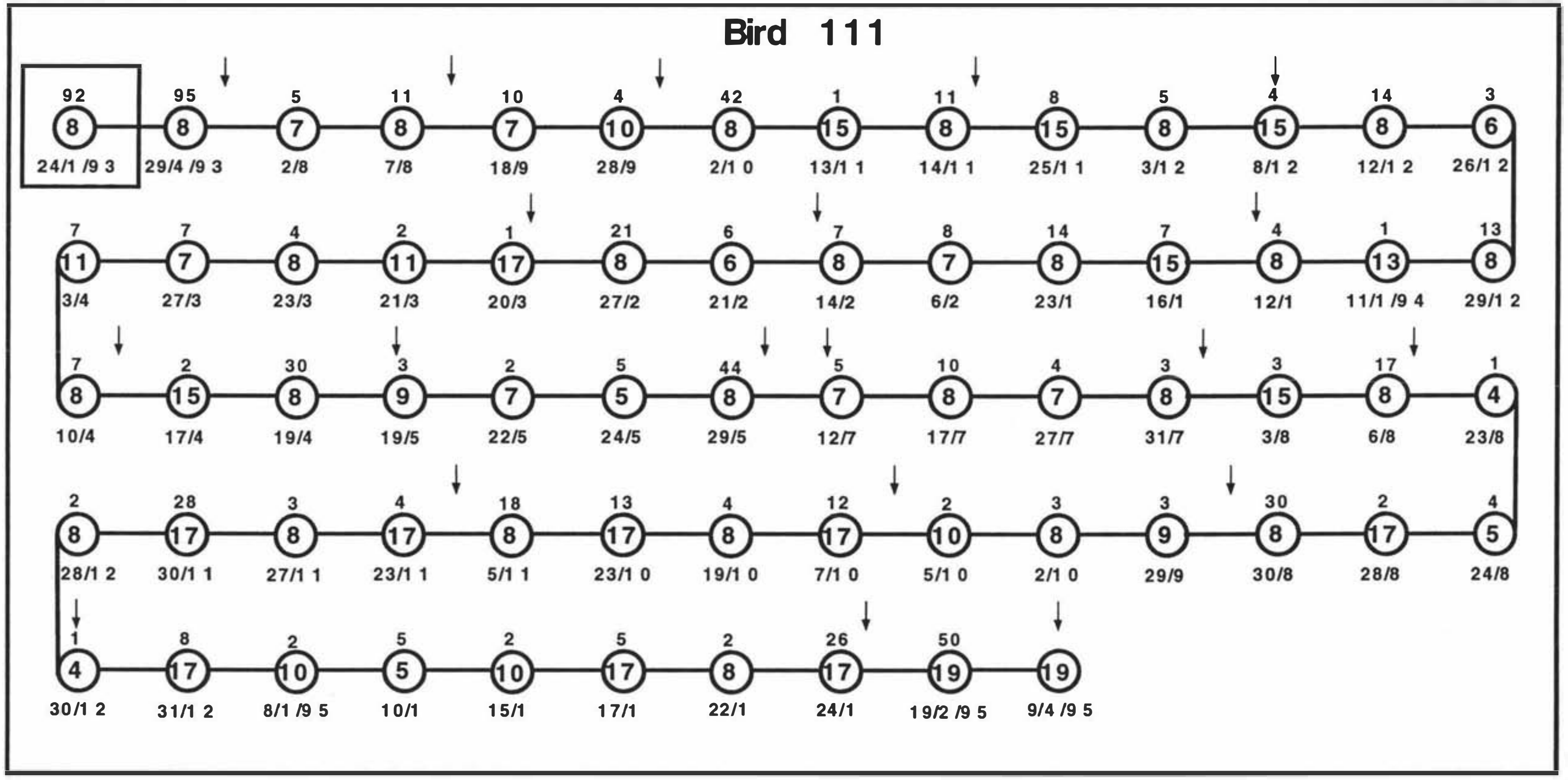

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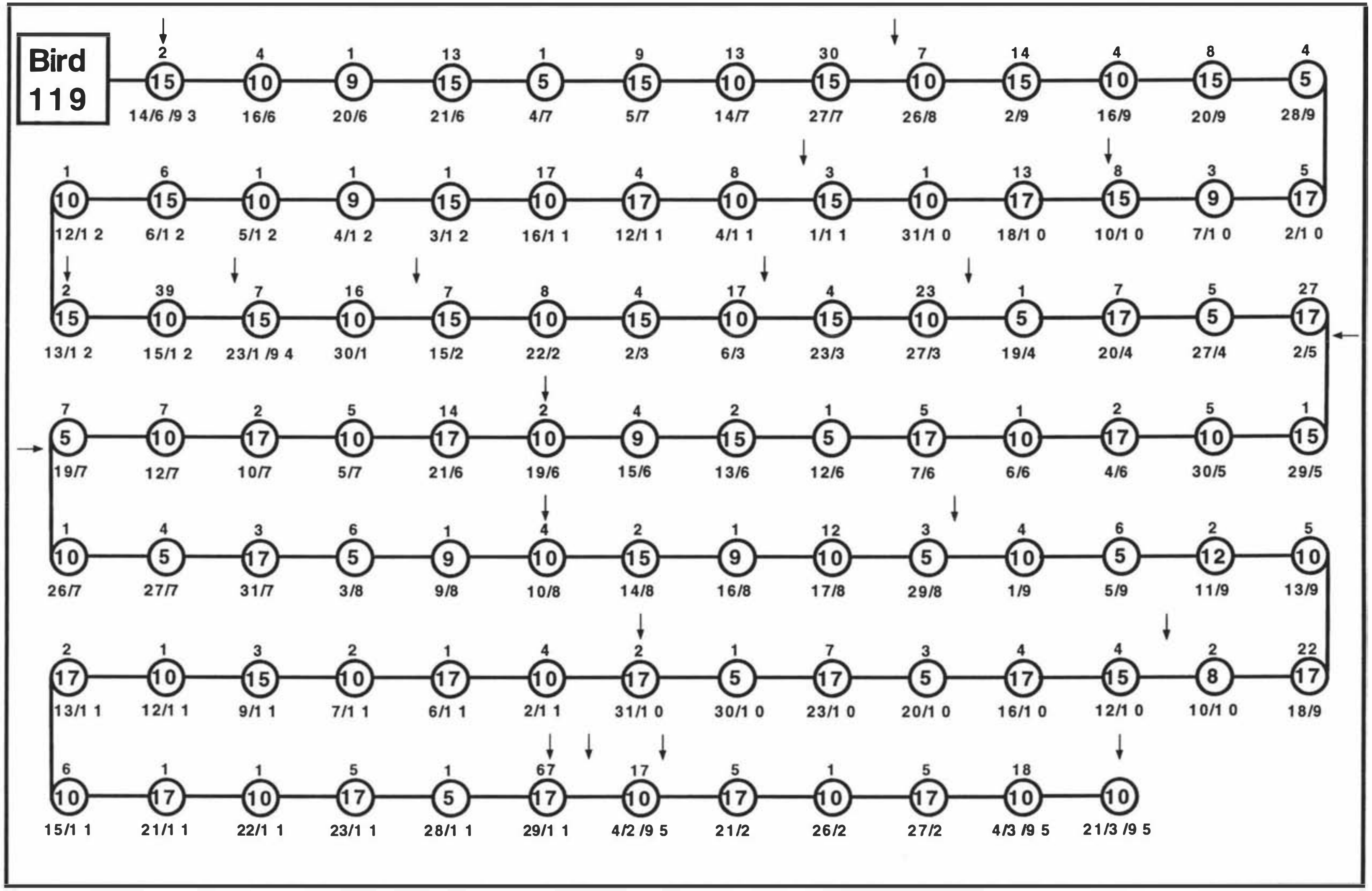

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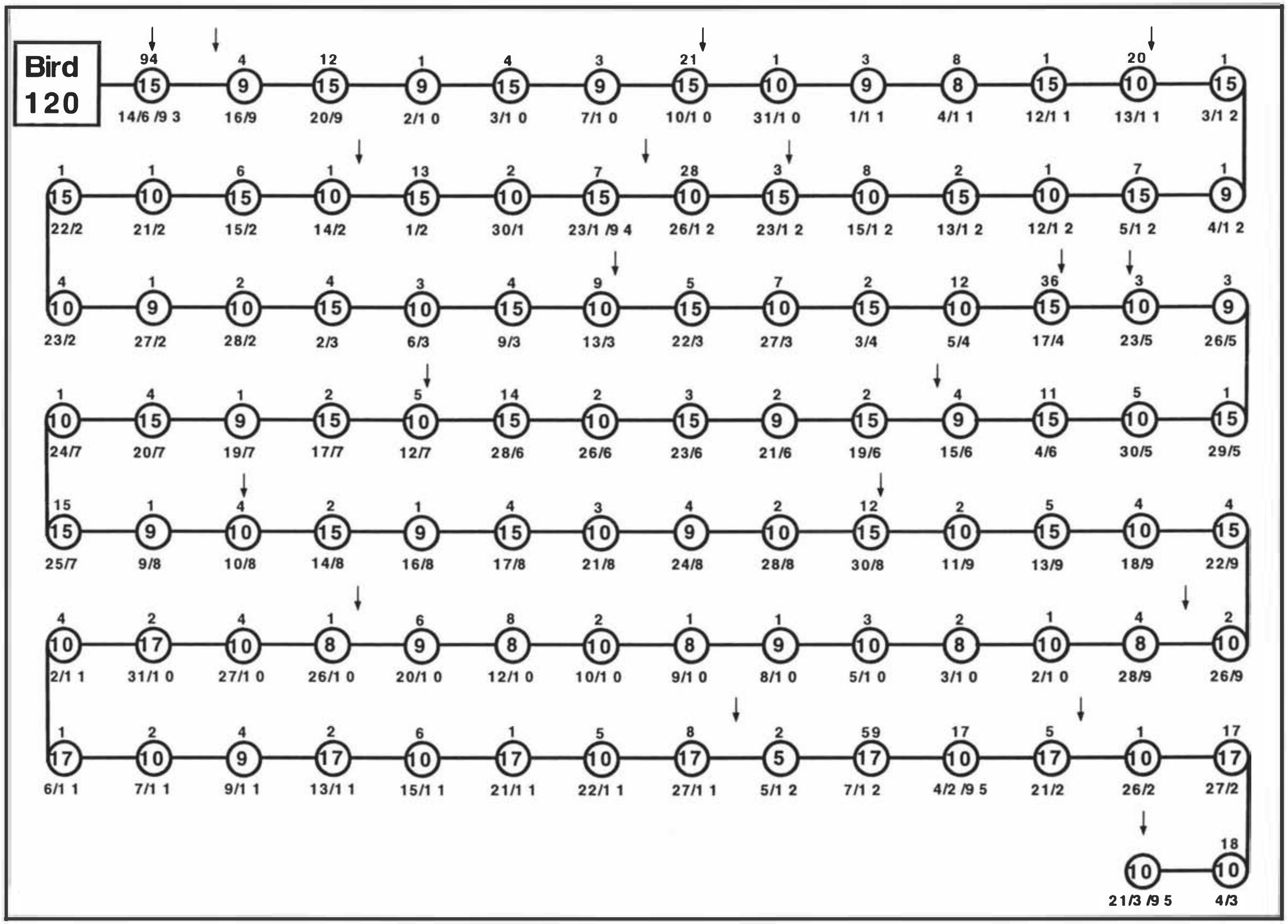

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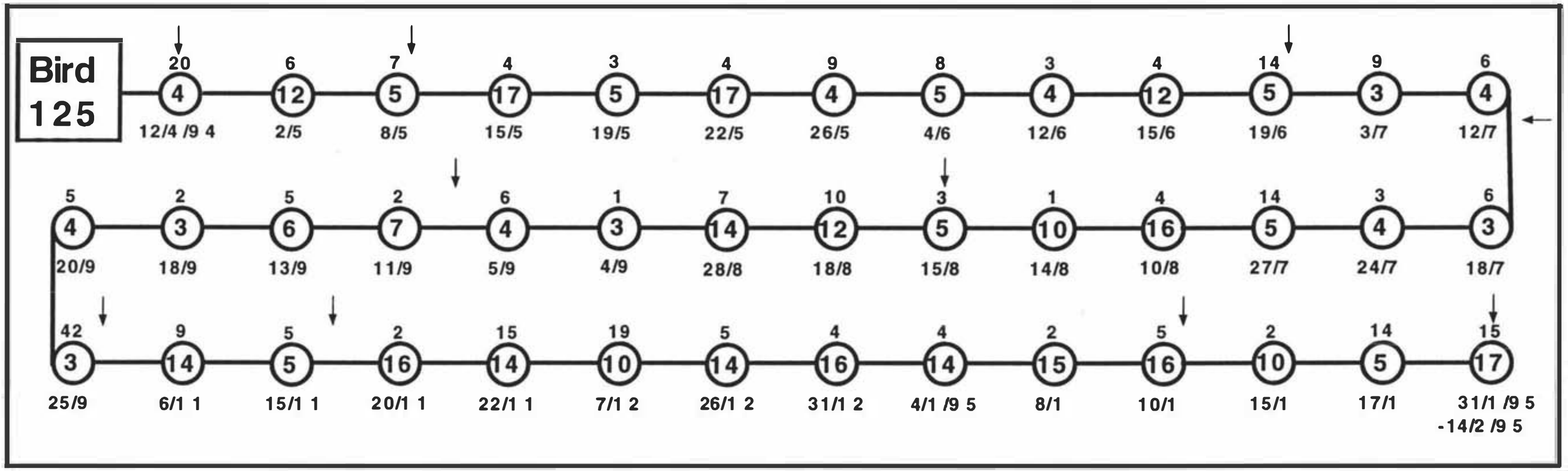

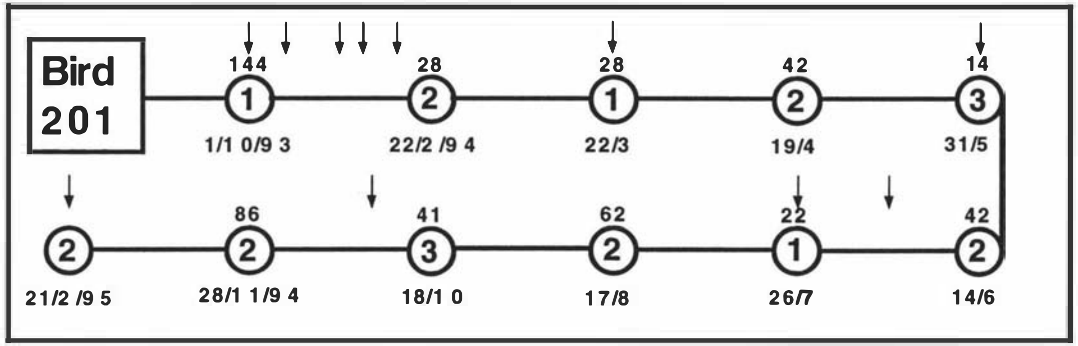

Appendix IX.

Reprint of results in Chapter Four.

'Multiple Kagu *Rhynochetos jubatus* deaths caused by dog attacks at a high-altitude study site on Pic Ningua, New Caledonia'

Appendix X.

Graphs showing mean percent occurrence of animal dryweight biomass (unfilled bars) and numbers (hatched bars) captured in pitfall traps at Pic Ningua for 15 categories (section 5.2.14) in each interval (1-56) ($n = 9$ for all bars, error bars = 1 s.e.). Black bars give percent occurrence data for the numbers of animals recorded in kagu faeces at Pic Ningua (sample sizes and total animal numbers per 10 g in each interval are in Fig. 5-14a). I collected no faecal data in interval 50. I excluded unidentified animals from the faecal data. Names of categories only appear on the bottom graph on each page, and are abbreviated by respective letters on most of the other graphs. The Other adults category included Hymenoptera, Isopoda, and Neuroptera. Scarabaeoidea are Hybosoridae/Scarabaeinae. The categories are ranked left to right along the *x* axis from the highest dryweight value per individual animal to the lowest, based on values calculated from pitfall trap data at Pic Ningua (Table 5-5). Seven of the correlation tests between percent occurrence of animal numbers in faeces and pitfall traps for each of the 15 categories were significant (Spearman correlation coefficients, $p < 0.05$, $n = 55$) (Amphipoda: $r = 0.38$; Carabidae: $r = 0.53$; Larvae: $r = 0.67$; Melolonthinae: $r = 0.66$; Orthoptera: $r = 0.41$; Other Coleoptera: $r = 0.27$; Hybosoridae/Scarabaeinae: $r = 0.39$).

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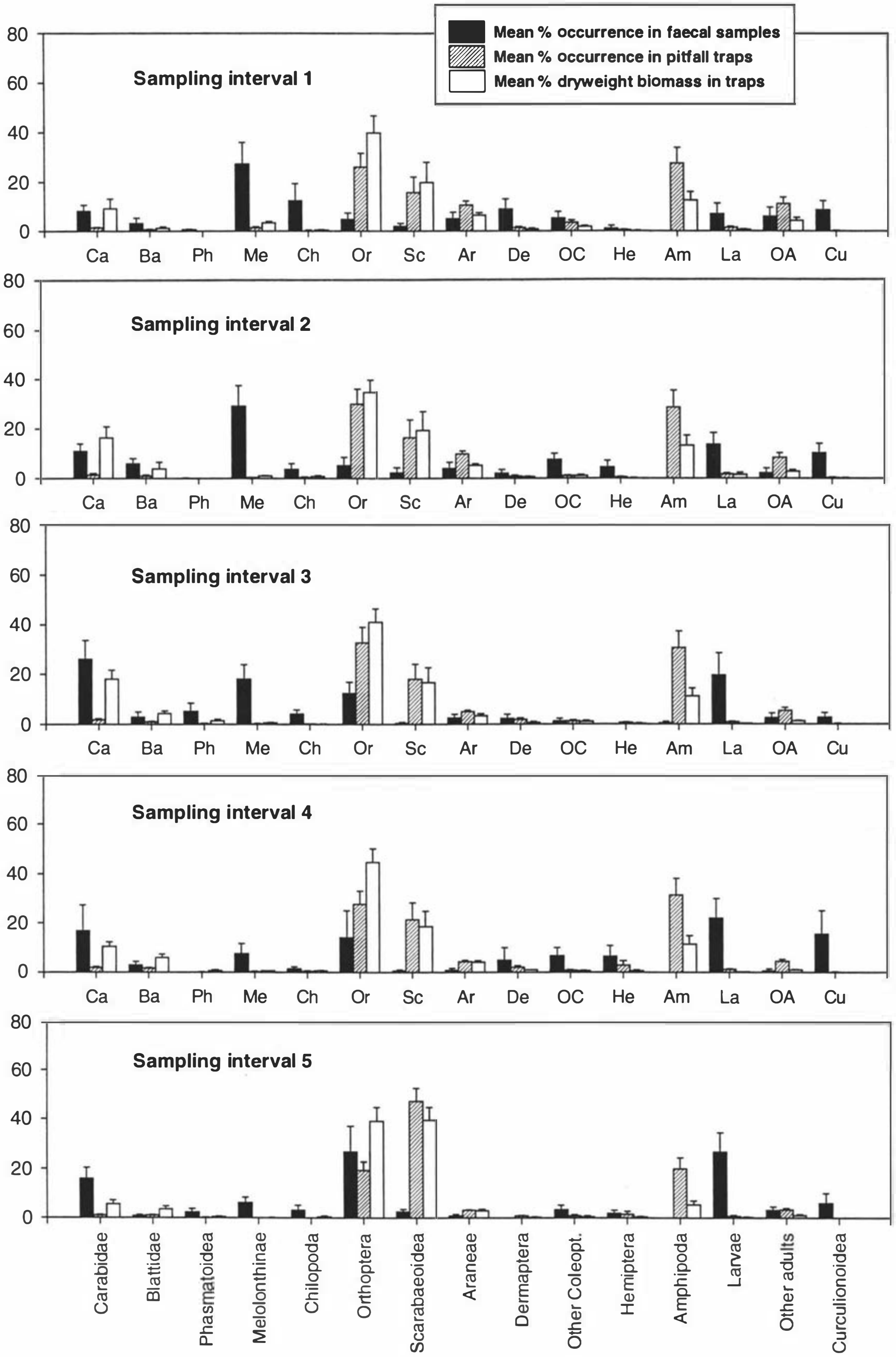

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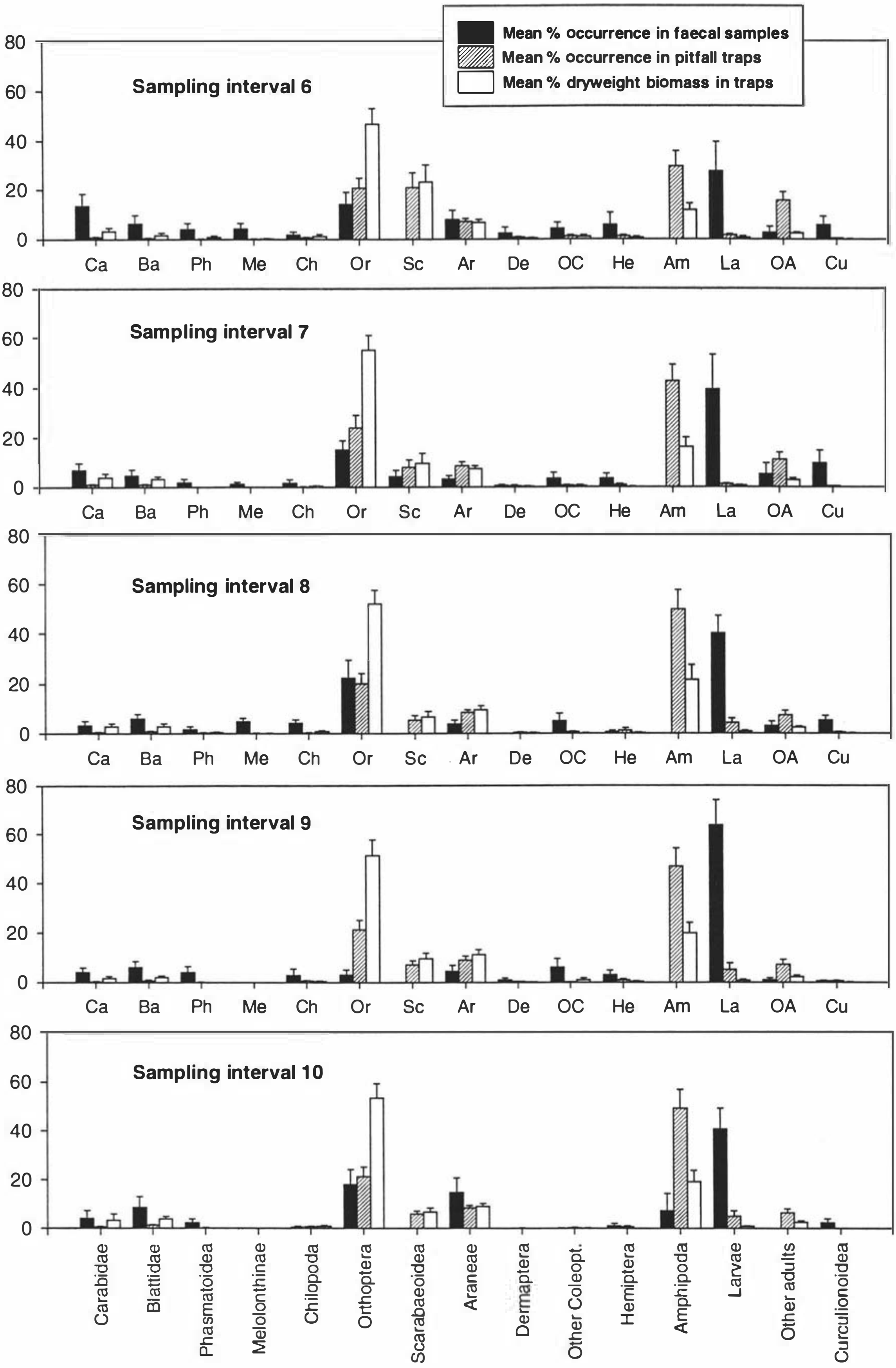

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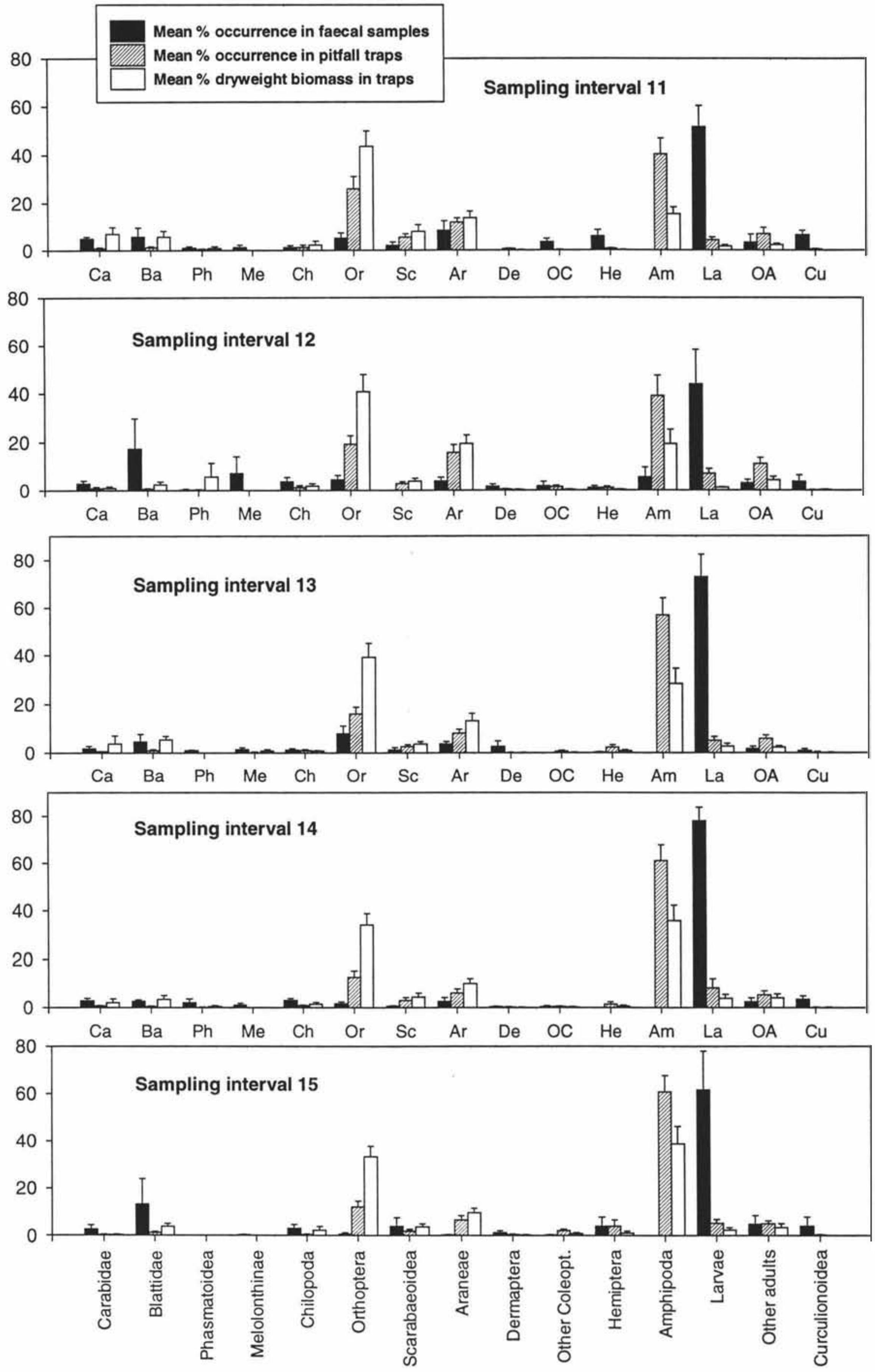

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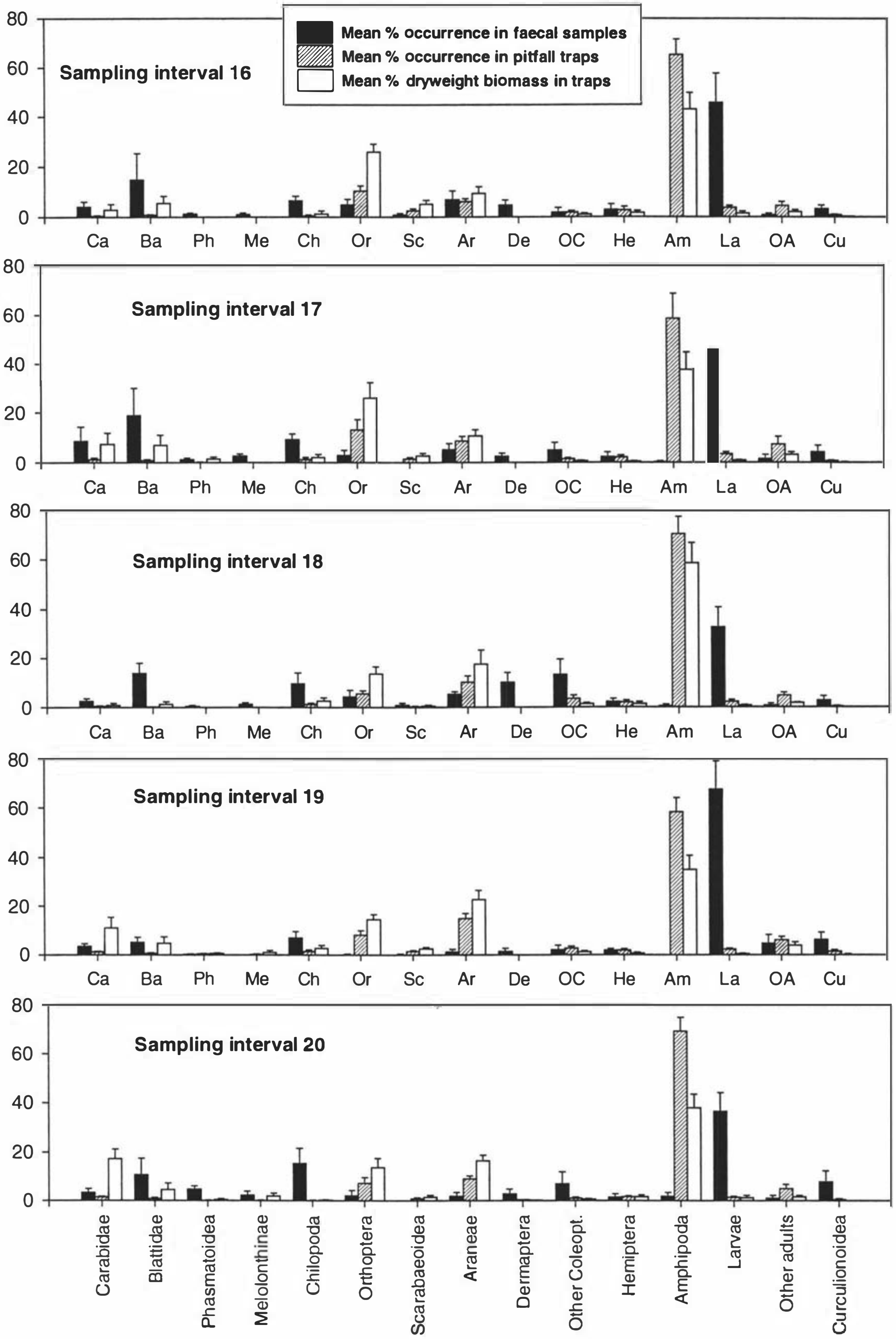

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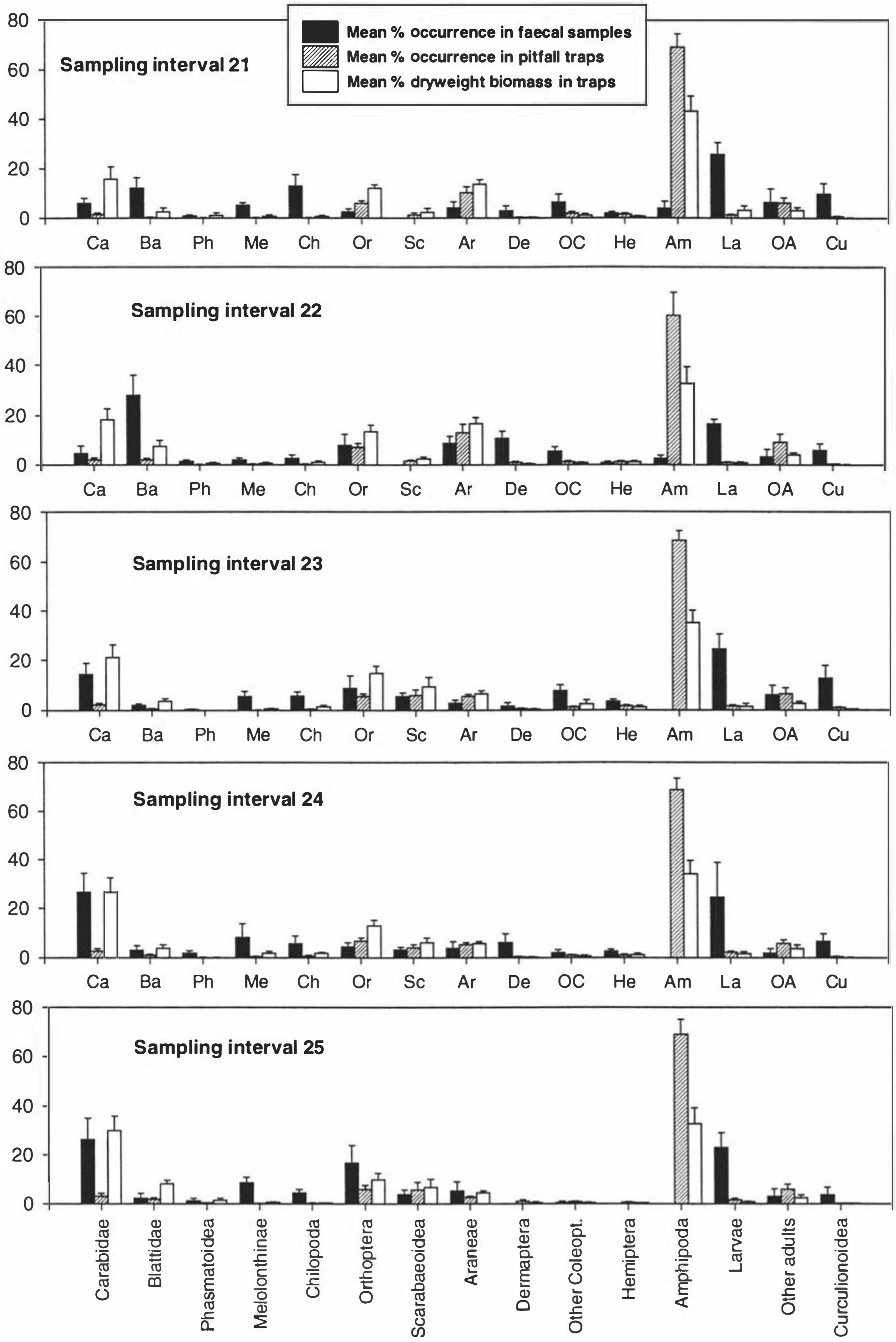

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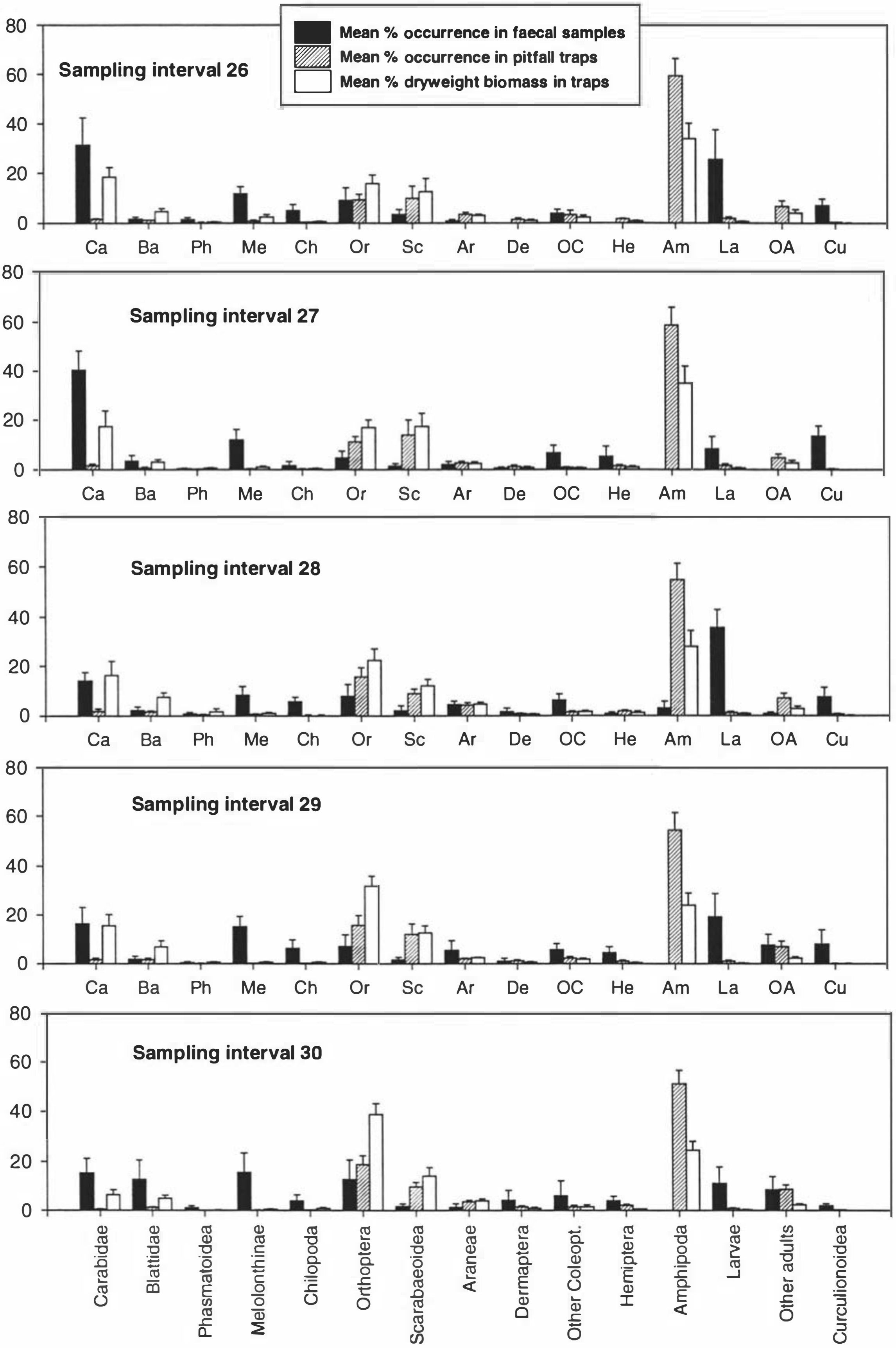

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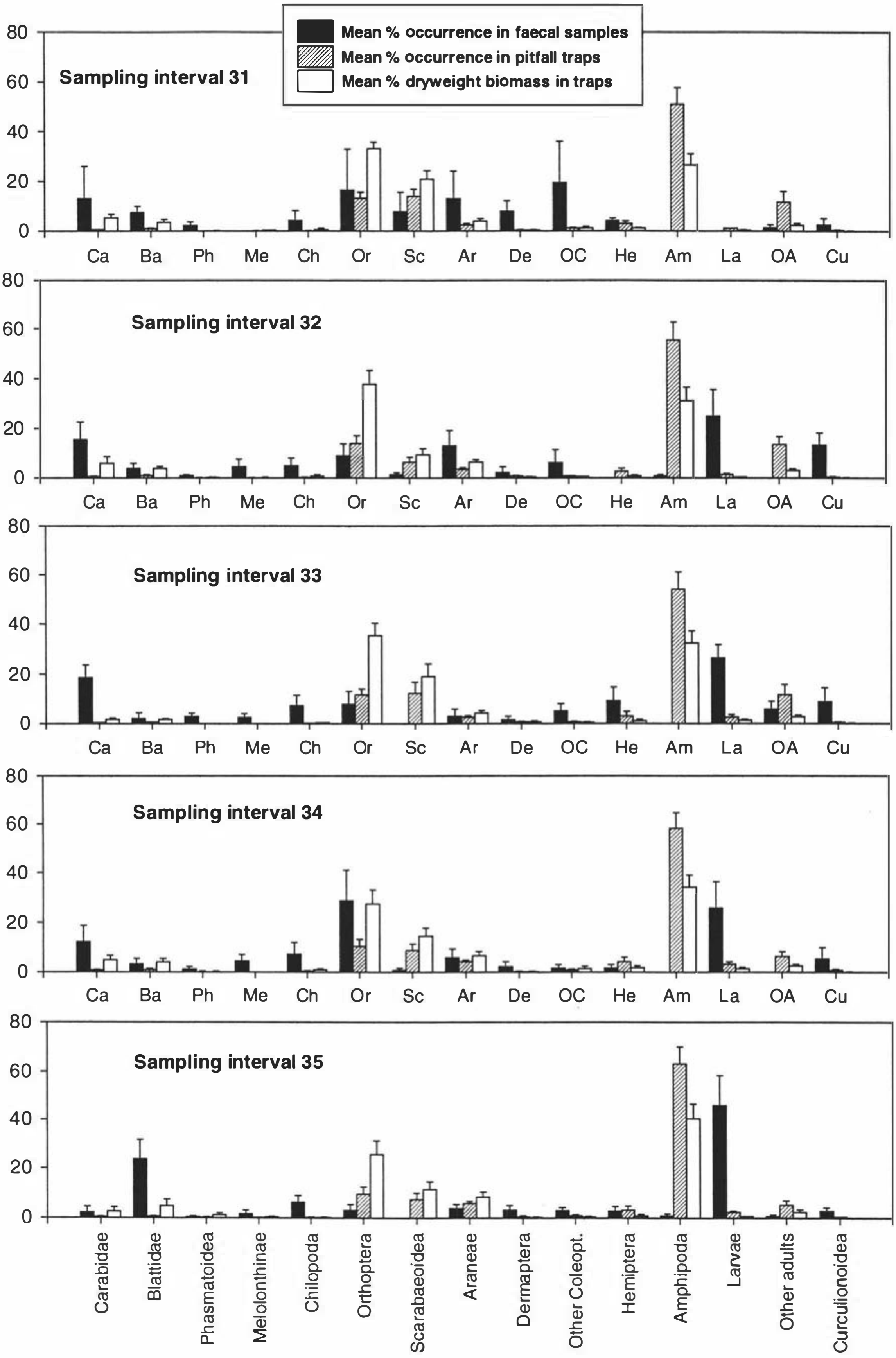

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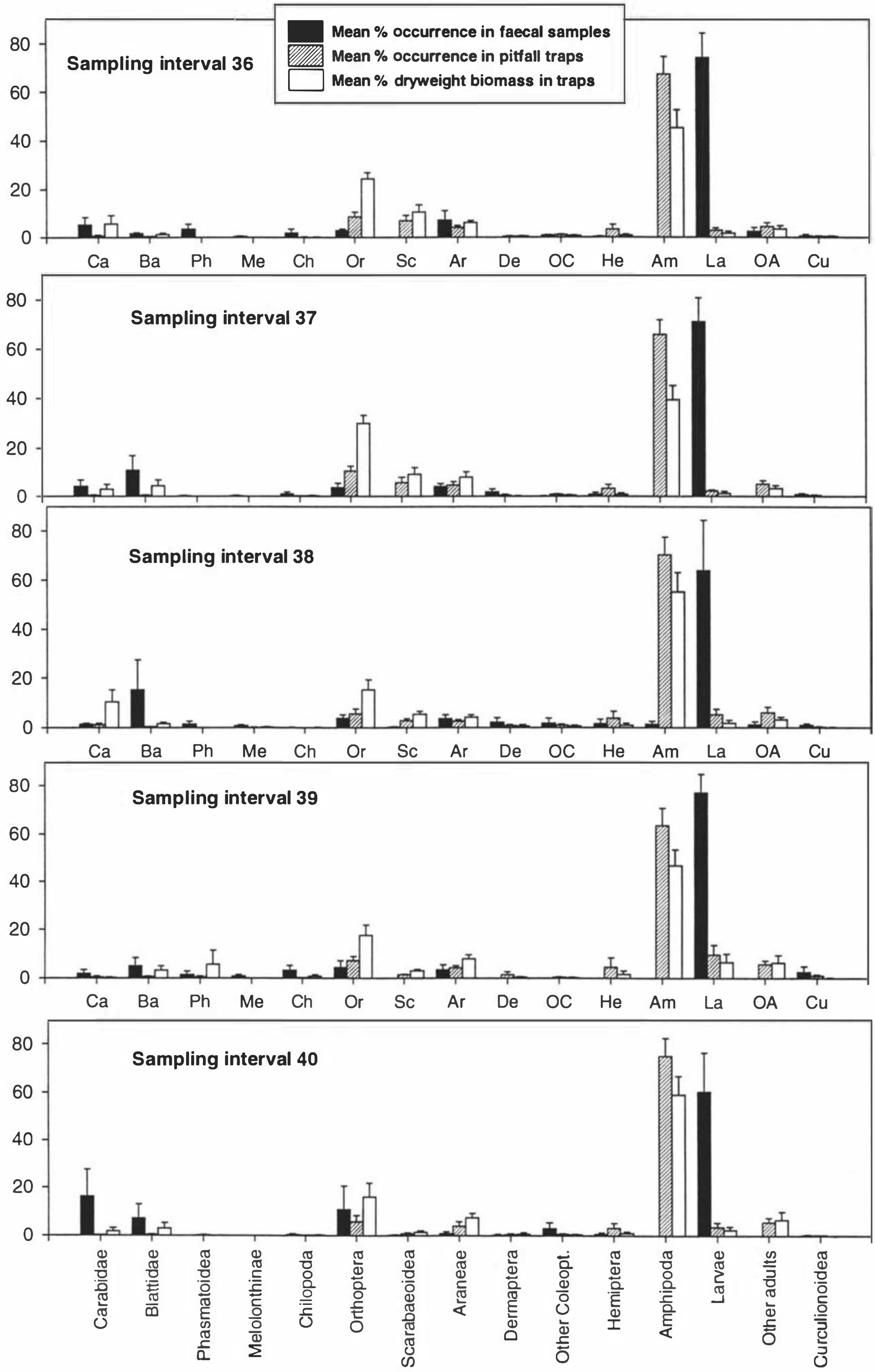

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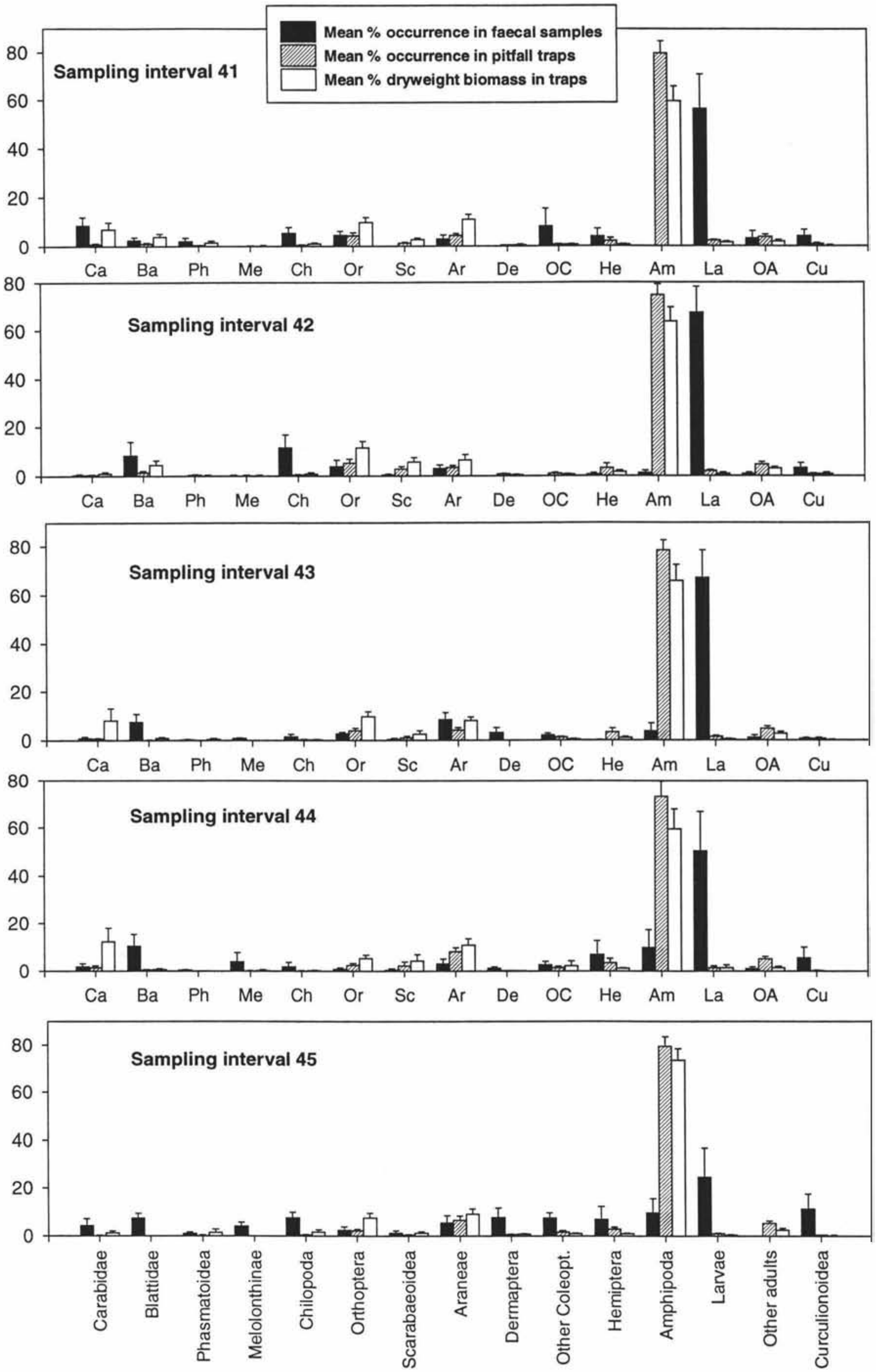

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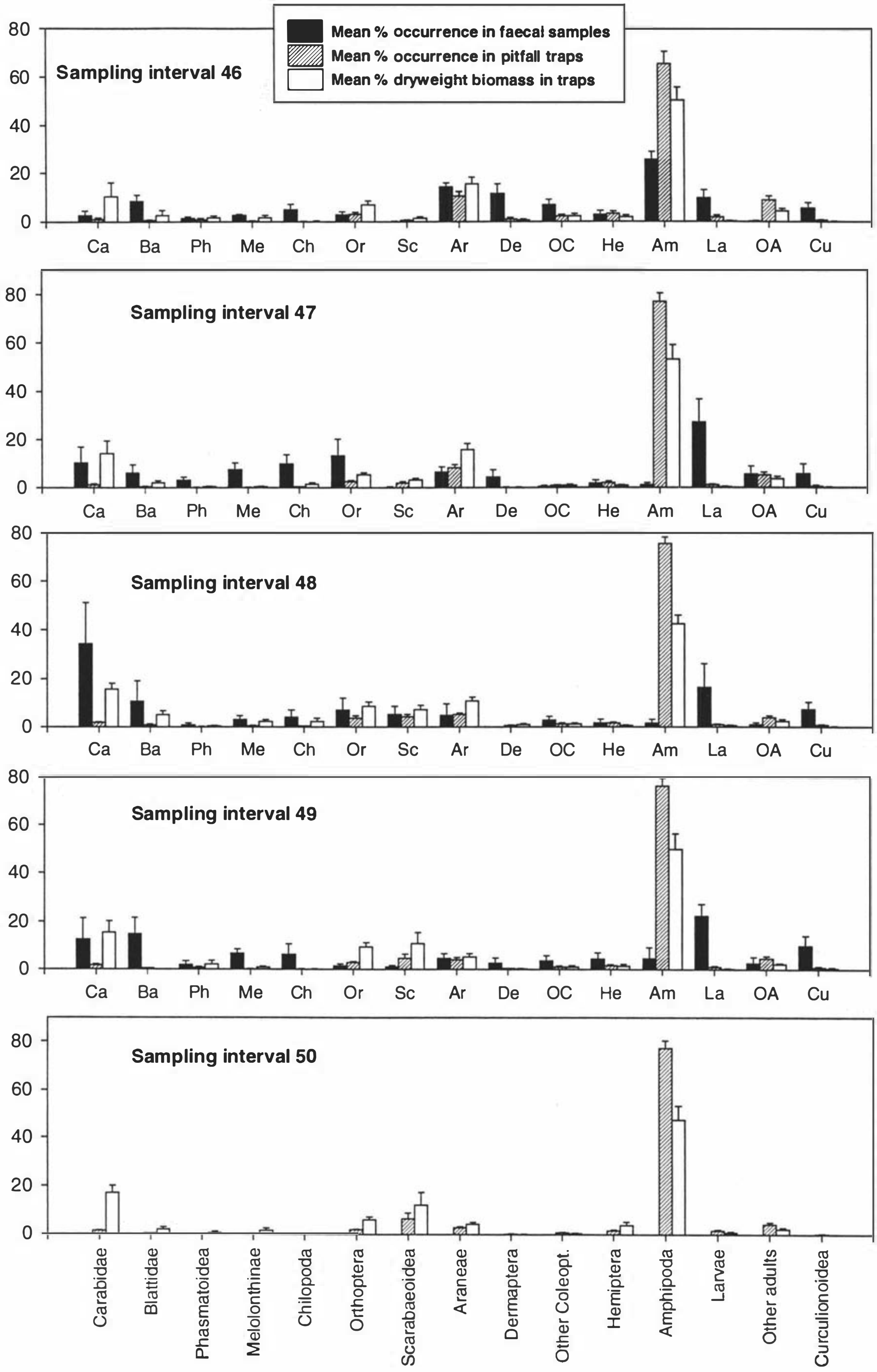

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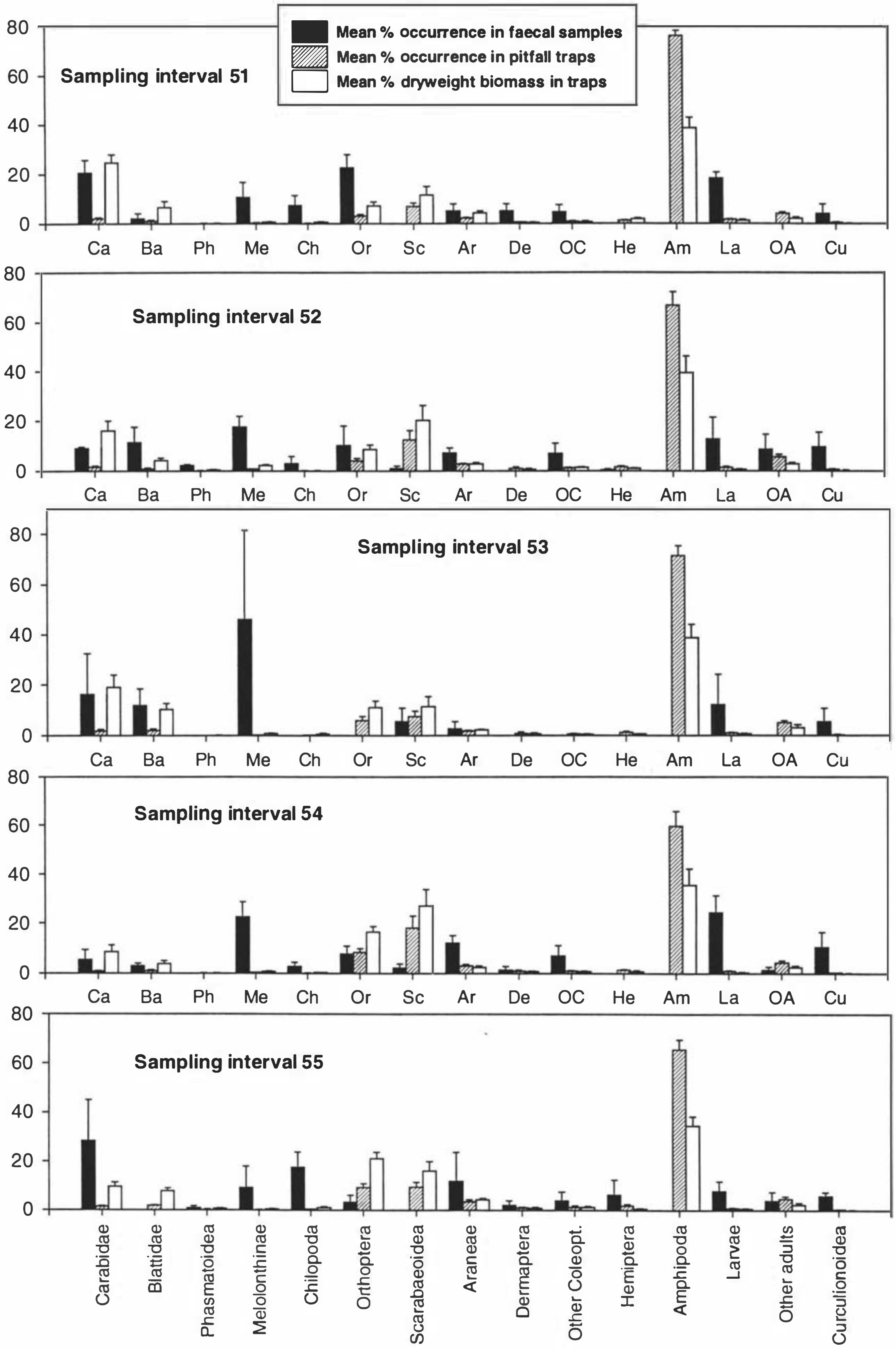

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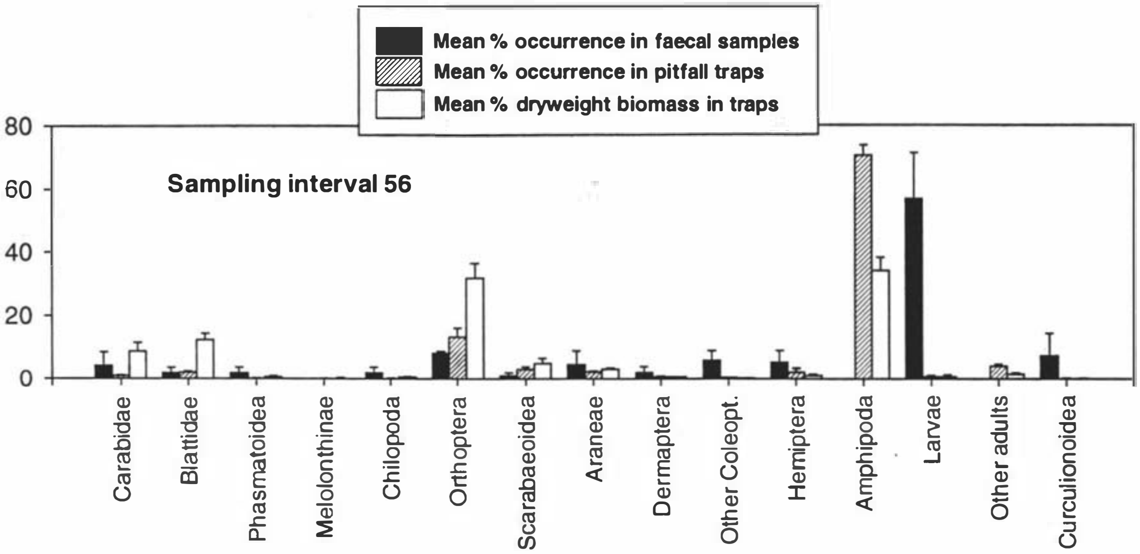

Appendix XI.

Row (56 intervals) and column (15 categories) squared cosines (indicating the contribution to the inertia) for correspondence analyses on 15 categories in intervals in kagu faeces and pitfall trap samples at Pic Ningua. A '----' = no data.

Analysis	**Pitfall trap samples**		**Faecal samples**	
Dimension	**one**	**two**	**one**	**two**
Rows				
s1	0.60	0.13	0.58	0.03
s2	0.77	0.17	0.55	0.06
s3	0.73	0.18	0.52	0.20
s4	0.84	0.06	0.37	0.11
s5	0.80	0.17	0.17	0.25
s6	0.78	0.00	0.06	0.11
s7	0.36	0.48	0.06	0.19
s8	0.04	0.75	0.00	0.09
s9	0.21	0.49	0.87	0.05
s10	0.05	0.67	0.00	0.02
s11	0.18	0.63	0.07	0.04
s12	0.01	0.55	0.00	0.25
s13	0.10	0.59	0.85	0.09
s14	0.25	0.21	0.83	0.08
s15	0.28	0.27	0.73	0.04
s16	0.63	0.09	0.07	0.08
s17	0.56	0.20	0.06	0.08
s18	0.75	0.10	0.02	0.23
s19	0.13	0.20	0.77	0.06
s20	0.61	0.10	0.07	0.05
s21	0.73	0.03	0.28	0.36
s22	0.62	0.07	0.13	0.35
s23	0.69	0.10	0.30	0.08
s24	0.84	0.00	0.50	0.18
s25	0.70	0.03	0.35	0.30
s26	0.03	0.25	0.38	0.27
s27	0.15	0.68	0.57	0.18
s28	0.14	0.19	0.51	0.24
s29	0.03	0.00	0.60	0.15
s30	0.44	0.23	0.58	0.07
s31	0.48	0.04	0.29	0.00
s32	0.00	0.08	0.17	0.00
s33	0.39	0.12	0.24	0.07
s34	0.00	0.02	0.22	0.11
s35	0.31	0.00	0.59	0.02

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Analysis	Pitfall trap samples		Faecal samples	
Dimension	one	two	one	two
s36	0.62	0.00	0.84	0.08
s37	0.53	0.08	0.91	0.04
s38	0.50	0.00	0.89	0.01
s39	0.17	0.05	0.88	0.06
s40	0.84	0.00	0.82	0.09
s41	0.93	0.00	0.87	0.08
s42	0.85	0.00	0.68	0.00
s43	0.91	0.00	0.65	0.10
s44	0.85	0.00	0.28	0.39
s45	0.85	0.00	0.14	0.75
s46	0.35	0.05	0.12	0.75
s47	0.80	0.00	0.22	0.00
s48	0.82	0.04	0.30	0.15
s49	0.77	0.10	0.15	0.08
s50	0.68	0.28	-----	-----
s51	0.61	0.30	0.36	0.19
s52	0.07	0.74	0.57	0.05
s53	0.50	0.25	0.40	0.19
s54	0.28	0.68	0.43	0.05
s55	0.18	0.47	0.40	0.05
s56	0.26	0.11	0.40	0.04
Columns				
Amphipoda	0.96	0.03	0.03	0.75
Araneae	0.01	0.38	0.16	0.37
Blattidae	0.02	0.02	0.02	0.29
Carabidae	0.00	0.04	0.46	0.22
Chilopoda	0.00	0.24	0.24	0.02
Curculionoidea	0.14	0.00	0.57	0.00
Dermaptera	0.43	0.00	0.18	0.51
Hemiptera	0.00	0.01	0.16	0.05
Larvae	0.04	0.09	0.95	0.04
Melolonthinae	0.02	0.02	0.55	0.11
Orthoptera	0.69	0.26	0.19	0.11
Other Coleoptera	0.01	0.00	0.45	0.05
Other adults	0.12	0.03	0.08	0.02
Phasmatoidea	0.00	0.01	0.07	0.01
Scarabaeinae/ Hybosoridae	0.80	0.19	0.23	0.12