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ASPECTS OF THE BIOLOGY OF THE AUSTRALASIAN HARRIER

(*CIRCUS AERUGINOSUS APPROXIMANS* PEALE 1848)

A thesis presented for the degree of
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in Zoology at
Massey University

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NOTE

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ABSTRACT

The study is based on 18 months intensive field-work during which 212 Australasian harriers were trapped, retrapped, measured, sexed, aged, individually marked and observed. Fortnightly observations of the individually marked population were made over a further seven months. The Australasian harrier and European marsh harrier are considered to be conspecific. Evidence is presented showing that there is no valid reason for considering *Circus aeruginosus* of the Pacific Islands to be a different subspecies from *C. aeruginosus* of Australia and New Zealand. During the breeding season ten territories in the 12 km² study area averaged 31 ha, nest sites averaged 910 m apart, pairs' overlapping home ranges averaged 9 km² and favourite hunting areas 3 km². A high population density of one bird per 50 ha was calculated. A low fledging success rate of 1.8 young per successful pair and 1.1 young per nest site, and two cases of polygyny were recorded during two breeding seasons. Territorial and courtship behaviour, nest parameters and the parental division of labour is described. Seasonal movements and the dispersion of all age and sex classes from the study area at the end of the breeding season are described. Most (66.7%) individually marked adults returned after the autumn dispersal phase and established winter home ranges averaging 9 km². The home range of an adult female in open farmland was calculated to be 14 km² using radio-telemetry techniques. A non-breeding season population density of one bird per 80 ha was calculated. Communal roosting, which occurred throughout the year, is discussed. Four hundred and seventy food items were identified in the diet from pellets, prey remains, stomach contents and field observations. In descending order of numerical importance in the diet were mammals (46.4%), introduced passerines (29.0%), insects (7.6%), game birds (6.7%), birds' eggs (4.8%) and aquatic prey (4.6%). Australasian harriers ate significantly greater numbers of live prey than carrion annually. Adults took significantly greater numbers of agile food items than juveniles. Females ate significantly more large (>200 g) and fewer agile food items than did males. Seven search techniques and five attack techniques, including some buteonine techniques, are identified and described in the Australasian harriers' wide range of hunting techniques. Ninety five attacks on prey are recorded and 15.8% of these were successful. Adults were significantly more successful hunters than juveniles. Co-operative

hunting, hunting in the daily cycle, feeding behaviour at carrion, interspecific competition for carrion, interspecific disruption of hunting and prey escape tactics are described. From a computer analysis of hunting behaviour data it is concluded that adult males are more manoeuvrable and less conspicuous than adult females and juveniles because they flew significantly lower and faster. Adult males also hunted, to a significantly greater degree, those habitats where there were greater numbers of agile prey. The hunting inexperience of juveniles was quantified. The Australasian harrier is moderately sexually dimorphic. Current hypotheses proposed to explain the degree of sexual dimorphism in raptors and why the females of most raptor species are larger than males are critically reviewed.

ACKNOWLEDGEMENTS

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Andy Garrick and Tom Caithness of the Wildlife Service always provided a warm welcome when I arrived at Pukepuke Lagoon. Andy Garrick and Bill Pengelli also kept a record of sightings of individually marked Australasian harriers.

I was billeted in the Wildlife Service's newly erected house at Pukepuke Lagoon for four months. Prior to this I used a shooter's hut owned by the Department of Lands and Survey for accommodation. The manager of the Department of Lands and Survey's Tangimoana farm, Mr H. Ellison, kindly allowed me to set traps on the farm and to travel to and from the traps at will. Neil Bowick of the Manawatu Pest Destruction Council provided a steady supply of rabbits which were used as bait in the traps.

Besides allowing me to use equipment at Pukepuke Lagoon, the Wildlife Service of the Department of Internal Affairs provided \$300 towards travelling expenses. The Botany and Zoology Department, Massey University, paid for the materials for the 11 traps I built. I travelled between Palmerston North and Pukepuke Lagoon and around the study area on a Honda C.T.90 motorbike my parents generously lent to me.

I have benefited from correspondence with ornithologists Dr R. Fitzner, Dr Nick Fox, Dr F. Hamerstrom, Lex Hedley and Mervyn Jukes. Dr Nick Fox and Lex Hedley also provided designs for the traps I used and they both read and commented on a draft of a chapter of the thesis. Dr I. Andrew and Dr J. Skipworth read and commented on a chapter. Andy Garrick, Dr Phil Moors and Hugh Robertson all reviewed four chapters. I would like to thank all these people and particularly Dr Phil Moors who constructively criticised my first chapters. Several members of the Ornithological Society of New Zealand sent records of sightings of individually marked Australasian harriers to me. These were gratefully received.

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INTRODUCTION

This thesis was initially proposed as part of a more general study of the influence of predators on the fauna at Pukepuke Lagoon Wildlife Management Reserve. The broad aim of the thesis is to describe the Australasian harriers' hunting behaviour and to discuss the factors influencing that behaviour. A further aim is to elucidate differences in morphology, diet, hunting techniques and habitat use between the Australasian harrier age and sex classes, and to relate these differences to current theories on sexual dimorphism in raptors.

Hunting behaviour is an integral part of the birds' breeding and non-breeding biology. In the course of the study numerous original observations and data were collected pertinent to the Australasian harriers' biology, and although breeding and non-breeding biology are discussed individually, frequent reference is made to their effect on diet and hunting behaviour.

Within the text of the thesis I have endeavoured to describe at all times the data collected and what I observed, rather than what I felt. However I believe that some of the understanding gained during the study is expressed in a short verse written in my field-notes as I observed an adult female hunting at the end of the 1976-77 breeding season.

Already she feels the winter, and it is sad.
 Still she flies to feed her young, but the excitement,
 expectation and wonder of the sexual spring is gone.
 The race is almost run, and she can see the finish line.
 She's a little tired, but it was a great race,
 full of tactics and new doors opened.
 And there's all those wonderful memories of finding out
 what few have seen and fewer still noted.
 There's still time, and more,
 a need for that new feather dress to greet next spring.
 Will she choose again the same C-1,
 or will she mate a-new?
 Yes winter's coming, but then so is spring.
 She wonders what it will bring?
 Life, I hope, for you A-2.
 The free life to hunt the long grasses,
 and soar on the wind, and on ... and on ... and on ...

CHAPTER ONE

NOMENCLATURE

There is considerable error and confusion among New Zealand ornithologists about which species, subspecies and common names to use for the Australasian harrier (*Circus aeruginosus*). For example the Australasian harrier was referred to as *Circus approximans gouldi* in the "Annotated checklist of the birds of New Zealand" published in 1970, and in all other scientific works published in New Zealand up to and including 1977. However, since Vaurie's (1965) work on the genus *Circus* was published most authors outside New Zealand have referred to the Australasian harrier as *C. aeruginosus*. Hereinafter *C. aeruginosus* is referred to as *C. ae* when abbreviated, and *C. approximans* as *C. a*.

A. Species

The Australasian harrier may be classed as either a species or a subspecies. This depends on whether one accepts that *C. ae aeruginosus* of central and western Eurasia and *C. ae spilonotus* of eastern Asia are conspecific. If this is accepted then all other subspecies, including the Australasian harrier, are related to one of these two (Brown and Amadon 1968: 382). Vaurie (1965) stated that *spilonotus* and nominate *aeruginosus* interbreed where they come into contact. This lack of reproductive isolation, coupled with morphological similarity, at the periphery of the ranges of the two populations strongly suggest that they are conspecific.

Brown and Amadon (1968: 382) agreed with Vaurie (1965) and recognised ten species in this worldwide genus. Nieboer (1973) came to the same conclusion in his study of geographical and ecological differentiation in the genus *Circus*. In more recent Australian publications (Frith, editor 1976, Morris 1976) the Australasian harrier is referred to as *C. aeruginosus*. Thus the weight of evidence and scientific opinion favours Vaurie's (1965) classification.

B. Subspecies

In the past various attempts to define subspecies of the Australasian harrier have been made, mainly based on size. To date Amadon's (1941) investigations from which two subspecies were distinguished from five previously described forms, is the most widely accepted work. The subspecies he defined were: *C. a. approximans* Peale (Fiji harrier) and *C. a. gouldi* Bonaparte (Australasian harrier). Amadon (1941) was definite about his criteria when he said that smaller size of *C. a. approximans* seemed to be the only valid character for erecting subspecies. He also stated that, "This series of 124 skins of *C. approximans*, made it possible, perhaps for the first time, to investigate carefully the alleged racial variations in colour in this species. None seems to exist. Statements to the contrary have presumably been based on differences due to age, sex, or individual variation. The forms *approximans*, *wolfi* and *gouldi* were, as a matter of fact, all described independently and without comparison *inter se*." However this stance was slightly modified by Brown and Amadon (1968: 383) who stated that *C. ae. gouldi* was much larger than *C. ae. approximans* and rather darker above and more heavily streaked below.

Following the general acceptance of Amadon's (1941) distinction of two subspecies, there was speculation among New Zealand and Australian ornithologists as to why the measurements of wing and tail length of harriers from Norfolk Island and the Kermadec and Chatham Islands should have fallen into the *C. a. approximans* range, when the islands lie much closer to Australia and New Zealand where *C. a. gouldi* was resident.

As the major criterion for retaining subspecies is still size differences, a comparison of the measurements taken by Amadon (1941) with those available today is needed to test his classification, and to elucidate the origins of the harriers found on Norfolk Island and the Kermadec and Chatham Islands. In reference to this point Oliver (1955) stated that, "there is no good evidence for subdividing the species on size or coloration. Some of the ranges in size overlap." Although he refuted Amadon's (1941) classification, Oliver (1955) did not provide the necessary data to support his statement.

In Tables 1.1 and 1.2 I have summarised the available data on wing and tail length of *C. a. gouldi* in New Zealand for comparison with the same two measurements taken by Amadon (1941). Because his data on *C. a. gouldi* were rather scanty Amadon (1941) did not determine averages. However this stance was again modified by Brown and Amadon (1968: 383) where the mean values and ranges were presented, so I too have included them.

The range of measurements of wing and tail length that Amadon (1941) took of *C. a. approximans* and *C. a. gouldi* overlapped very little. But as may be seen in Tables 1.1 and 1.2, the ranges of the measurements for both subspecies lie within the range of *C. a. gouldi* recorded by other workers in New Zealand. Thus the measured ranges of wing and tail length of the subspecies overlap completely. Furthermore the mean measurements of most samples are similar except Amadon's (1941) of *C. a. gouldi* and Carroll's (1970) inexplicably low mean wing length of female *C. a. gouldi*.

Amadon (1941) stated that his measurements of *C. a. gouldi* were taken from very poorly sexed and otherwise unsatisfactory material. Yet he thought that the average wing and tail lengths of adult *C. a. gouldi* would prove to be close to the maxima he recorded for the two sexes. The data in Tables 1.1 and 1.2 show this inference to be incorrect.

It will be obvious from my arguments that I believe there is no valid reason for distinguishing subspecies based on differences in colour or mean wing and tail length. It is appropriate to record here Mayr's (1963) advice, "The better the geographic variation of a species is known, the more difficult it becomes to delimit subspecies and the more obvious it becomes that many such delimitations are quite arbitrary."

I therefore propose that both previously defined subspecies be combined under the nominate form: *Circus aeruginosus approximans* Peale 1848.

Under this classification arguments about the origin of the harriers on Norfolk Island, the Kermadec and Chatham Islands become redundant. A combination of the data of Amadon (1941), Oliver (1955), Brown and Amadon (1968) and Kinsky (1970) gives the known range of *C. ae. approximans* as: south-eastern New Guinea, northern, eastern and southern Australia, Tasmania, New Caledonia, New Zealand, Chatham, Society, Tonga, Fiji, New Hebrides and Loyalty Islands, Wallis (Uea) Island, a regular visitor to the Kermadec Islands, Norfolk and Lord Howe Islands and straggling to Samoa.

Table 1.1: Male harrier measurements

Collector	Collector's classification	Wing length (mm)			Tail length (mm)		
		Mean	Range	No	Mean	Range	No
Amadon (1941)	Fiji harrier <i>C. a. approximans</i>	403	392-412	20	231	222-239	27
Amadon (1941)	Australasian harrier <i>C. a. gouldi</i>	419	410-425	7	240	234-252	8
Carroll (1970)	Australasian harrier <i>C. a. gouldi</i>	402	381-429	58	231	211-251	61
Fox (1977b)	Australasian harrier <i>C. a. gouldi</i>	408	390-430	22	229	220-240	22
Chapter 8	Australasian harrier <i>C. ae. approximans</i>	404	385-425	95	225	195-240	95

Table 1.2: Female harrier measurements

Collector	Collector's classification	Wing length (mm)			Tail length (mm)		
		Mean	Range	No	Mean	Range	No
Amadon (1941)	Fiji harrier <i>C. a. approximans</i>	423	418-430	4	247	240-252	10
Amadon (1941)	Australasian harrier <i>C. a. gouldi</i>	436	430-444	6	254	249-259	6
Carroll (1970)	Australasian harrier <i>C. a. gouldi</i>	408	390-455	66	239	224-258	70
Fox (1977b)	Australasian harrier <i>C. a. gouldi</i>	428	412-450	29	244	230-255	27
Chapter 8	Australasian harrier <i>C. ae. approximans</i>	423	400-440	107	236	214-257	107

C. Common name

I believe the name Australasian harrier more aptly describes the birds' distribution than Fiji harrier and that the Australasian harrier should therefore be retained as the common name of *C. ae. approximans*. I also think this is more appropriate than swamp harrier, the name by which it is generally referred to in Australia (Morris 1976); for the Australasian harrier is not restricted to swamp habitat throughout most of its range (Oliver 1955, Sharland 1958). The harrier hawk is the common name of the African and Madagascan species *Polyboroides typus* and *P. radiatus* and I do not think it should be used for *C. ae. approximans* as Redhead (1968a, 1968b, 1969) has done.

In summary, the evidence presented shows that the marsh harrier (*C. ae. aeruginosus*) and the Australasian harrier are conspecific, there is no valid reason for considering *C. aeruginosus* of the Pacific Islands to be a different subspecies from *C. aeruginosus* of Australia and New Zealand, and the Australasian harrier is the most appropriate common name for the subspecies.

CHAPTER TWO

THE STUDY AREA AND METHODOLOGY

INTRODUCTION

This chapter is composed of two parts. In the first, the study area is described and the history of the area is considered in relation to the effect it may have had on the Australasian harrier population. In the second part, methodology, the means by which the data from trapped birds was made available and the collection processes are described. The results thus obtained are presented and discussed.

PART ONE : THE STUDY AREA

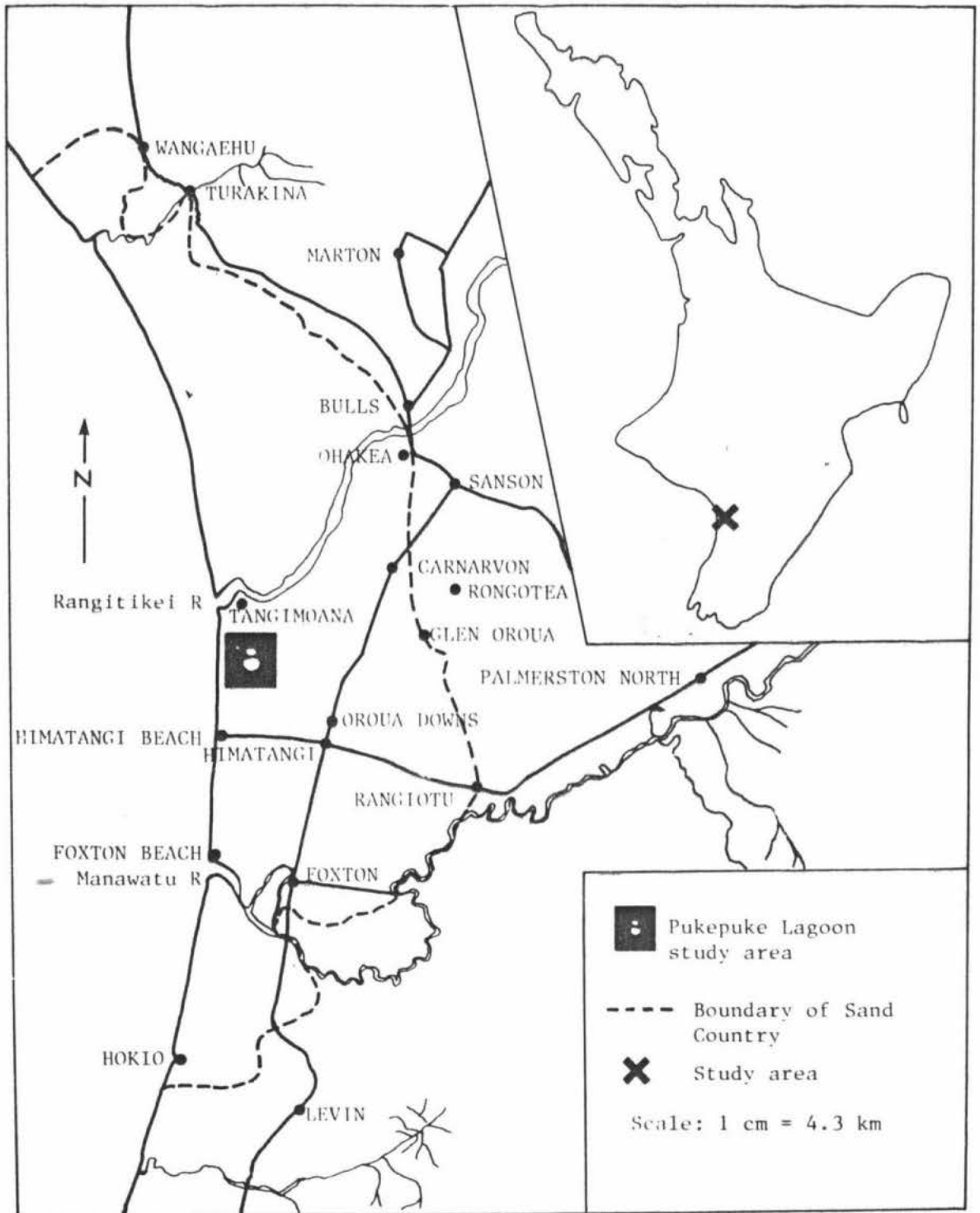
A. General description

The Manawatu-Rangitikei sand country covers an area of approximately 4,200 km² on the west coast of the southern part of the North Island (Figure 2.1). The complex of dunes, sand plains and peaty swamps bordering the coast in these districts extend from Hokio Beach in the south to Wangaehu River in the north (Cowie *et al.* 1967). Pukepuke lagoon is one of eight larger lakes in the sand country and lies in the centre of this area. The study area I used was centred on the New Zealand Wildlife Service's game management reserve at Pukepuke Lagoon and covered an area of 12 km² (Figure 2.2).

Pukepuke Lagoon lies on the boundary between the younger and older dune complexes (Cowie and Smith 1958). The younger dune complex borders the coast, extends inland for 0.4 - 6.4 km, and is composed of unconsolidated dunes and flats, large areas of which have insufficient plant cover to prevent wind erosion of the sand. The consolidated dunes and flats of the older dune complex lie further inland and are well vegetated and there is little serious wind erosion.

The farming practices on the younger dune complex are to a large extent dictated by the wind erosion potential. On the Department of Lands and Survey's Tangimoana block, which comprised much of my study area, most unconsolidated dunes had been fenced to keep domestic stock off them and had then been planted in pines (*Pinus radiata*). Only the

FIGURE 2.1



dune hollows had been sown in introduced grasses. Temporary ponds cover substantial areas of the dune hollows during winter and the water table is too high for satisfactory growth of pines (Hocking 1957). The New Zealand Forest Service has planted large areas of unstabilised and eroding sand country in marram grass (*Ammophila arenaria*), tree lupin (*Lupinus arboreus*) and pines. Several sawmills operate in the sand country to mill the pine plantations that have been established. Dairying is the principal type of farming on the older dune complex. Locally grown flax (*Phormium tenax*) is processed for woolpacks at Foxton, the only town in the sand country.

The Foxton port and railway lines are no longer used as the Wellington-Wanganui, Palmerston North-Himitangi and Foxton-Shannon highways, plus a network of roads now provide access to most of the sand country.

B. Soils

Cowie *et al.* (1967) described the parent material of most of the soils in the sand country as wind-blown sand, derived chiefly from greywacke of the central ranges. As a result of sorting during transport down rivers, along beaches, and inland by wind, these sands are of a fairly uniform size grade with negligible amounts of silt and clay. Quartz and feldspar are the dominant minerals.

C. Seasons and climate

In this study I have defined the seasons as: summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). Cowie *et al.* (1967) recorded that most of the rain in the sand country is brought by the dominant west and north-west winds which frequently reach gale force in spring and early summer. There is a well defined increase in rainfall from March, the driest month, to June, the wettest month, followed by a decrease in September, a marked increase in October, and a decrease over the summer months. Air temperatures are highest in February and lowest in July when the mean monthly temperatures are 17.2°C and 8.0°C respectively. Seasonal trends in climate are moist and mild winters with some frosts especially on the low-lying dune hollows; in spring, westerly winds increase in frequency and during September, when rainfall is low, may cause loss of soil moisture and erosion on exposed sites.

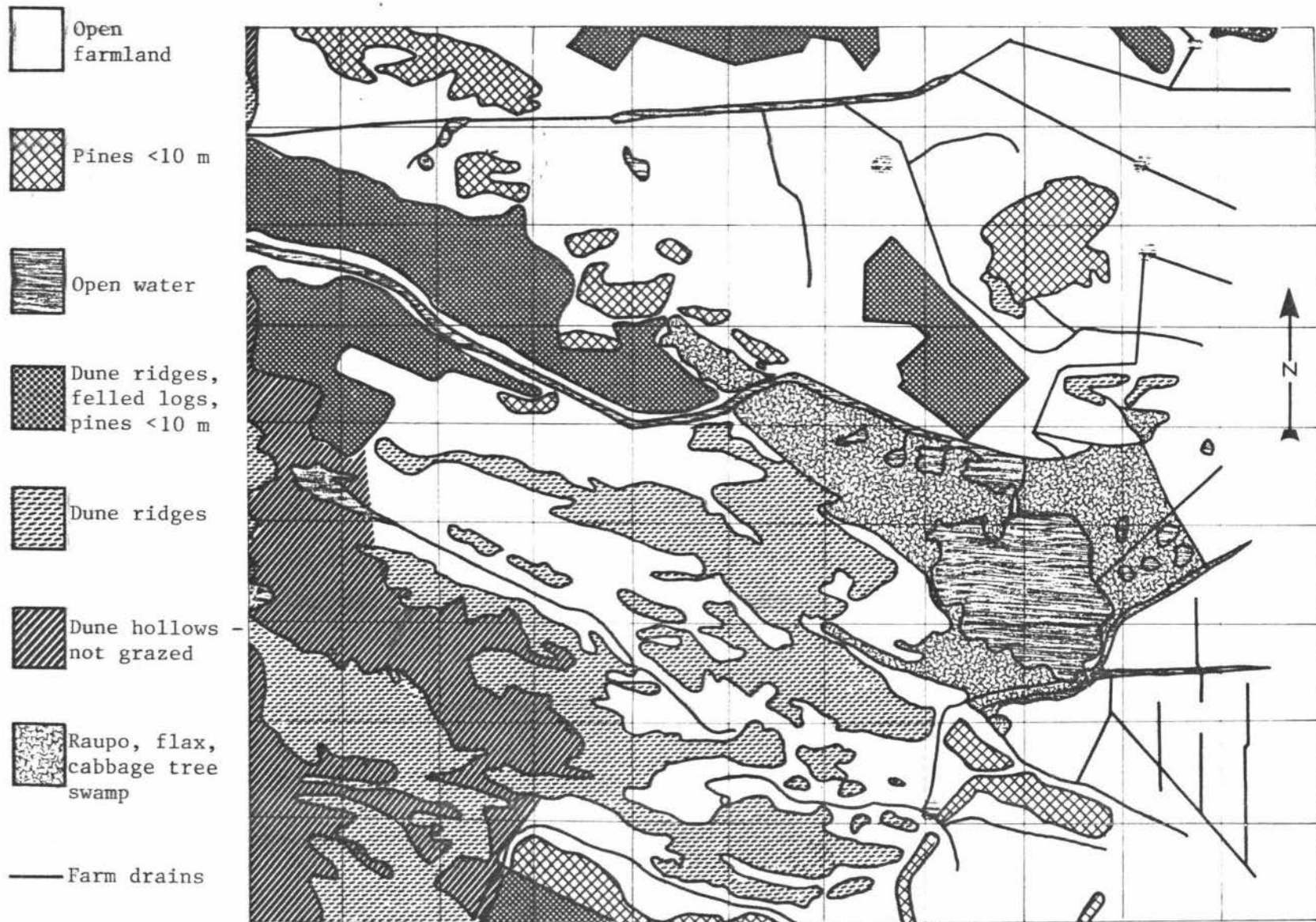


FIGURE 2.2: STUDY AREA

Scale: 1 cm = 200 m

During summer, which is warm, rainfall is comparatively low and variable, so that drought conditions can occur. Autumn is warm, having higher temperatures and humidities than spring.

D. Physiography

The sand country slopes gently inland from sea level to a maximum height of 50 m approximately 10 km east of Pukepuke Lagoon (Cowie *et al.* 1967). The low overall relief of the sand country is obscured by the alternation of dunes and sand plains which affect drainage. Where the flow of the surface water away from the dune hollows is restricted by encircling dunes, peaty swamps, ponds or lakes are formed. Pukepuke Lagoon is one such formation (Plate 2.1).

E. Vegetation

Carnahan (1957) described the successional stages of the vegetation on dune ridges and hollows separately. On the foredune are sand-binding plants that are able to tolerate strong, salt-laden winds and a certain amount of burial by sand. These include marram, spinifex (*Spinifex hirsutus*) and pingao (*Desmoschoenus spiralis*). These plants are also found on moderately well stabilised sand immediately inland together with shrubs such as tauhinu (*Cassinia leptophylla*), sand coprosma (*Coprosma acerosa*), sand pimelea (*Pimelea arenaria*) and tree lupin. Sand gunnera (*Gunnera arenaria*) is the pioneer plant of the dune hollows and is succeeded by the red rush (*Leptocarpus simplex*) which is later displaced by toetoe (*Cortaderia toetoe*) and flax. Introduced grasses and lupins are also found in the sand hollows. All stages of this succession can be seen in the study area (Plate 2.2). Pines are usually planted at least 80 m from the beach.

Carnahan (1957) stated that the native vegetation on the older dune complex consisted mainly of manuka (*Leptospermum scoparium*), bracken fern (*Pteridium aquilinum*), tutu (*Coriaria arborea*) and grasses. Most of these areas have now been drained, cleared and sown to pastures. On the wetter flats of this complex, shrubs such as *Olearia* sp. and *Coprosma* sp. were present with flax, mariscus (*Mariscus ustulatus*), toetoe, rushes, and cabbage trees (*Cordyline australis*). In the peaty swamps flax and raupo (*Typha orientalis*) were the dominant plants. These can still be seen in the few swamps that remain undrained. On the wetter flats the climax community was a semi-swamp forest composed mainly of

PLATE 2.1: STUDY AREA



PLATE 2.2: STUDY AREA



pukatea (*Laurelia novae-zelandiae*), kahikatea (*Podocarpus dacrydioides*) and tawa (*Beilschmiedia tawa*). On the drier sand plains and dunes the forest consisted chiefly of totara (*Podocarpus totara*), tawa and titoki (*Alectryon excelsum*).

F. Fauna

The common birds, mammals, amphibians, fish and large insects of the sand country are described in Chapter 5 concerning the diet of the Australasian harrier.

G. History and discussion

Because the climax community of the younger dune complex was shrubland (Carnahan 1957), this coastal strip probably contained better hunting for the Australasian harrier than most of the rest of New Zealand which was heavily forested prior to settlement by Maoris. Repeated burning by Maoris who settled in the sand country several hundreds of years before European settlers arrived (Cowie *et al.* 1967) would have further improved hunting habitat. It is generally recognised (Guthrie-Smith 1927, Stead 1932, Oliver 1955, Turbott 1967) that European settlement which brought about the clearing of large tracts of forest for pasture and the introduction of several species of small mammals enabled the Australasian harrier population to increase greatly. However this increase has been said to most closely parallel that of the rabbit (*Oryctolagus cuniculus*) which became very numerous and was not brought under control until the 1950's. Since rabbits have been effectively controlled throughout New Zealand the Australasian harriers' population density may have also decreased (Watson 1954, Turbott 1967).

There is no doubt that rabbit numbers were formerly very high in the sand country. For example, Wilson (1958) stated that on an area of 970 hectares, 5,000, 2,500, 1,000 and 500 rabbits were poisoned annually between 1920 and 1923. About 50 rabbits would live in the same area of sand country around Pukepuke Lagoon today (N. Bowick *pers. comm.*). Australasian harriers were also probably more abundant in the sand country prior to the 1950's for Wilson (1958) stated, "In 1922 Edgar Stead called up hawks by imitating a wounded duck and he and Bob Levin shot 52 in about an hour and a half." It would be most unusual to encounter such numbers of Australasian harriers at one lake in the sand country today.

Between 1950 and 1970 DDT was used extensively in New Zealand. Since 1970 it has been restricted to about 1% of its former use (Lock and Solly 1976). Fox (1977) concluded that although there was a considerable amount of variability between species in the levels of DDT and DDE (the breakdown product of DDT) that were lethal, in general wet weight levels of 30 - 80 ppm DDE in whole carcasses of raptors were lethal.

Lock and Solly (1976) analysed tissues of 27 Australasian harriers collected during the period of peak DDT use in New Zealand. They found them to contain an average of 30.13 ppm wet weight total DDT (Range: 0.81 - 191.68 ppm). These were the highest residues found in the tissues of any of the 61 species of birds and 16 species of mammals they analysed. They concluded that although Australasian harriers were most at risk from the effects of DDT it was not known whether it had affected reproduction or mortality in the species. Juveniles comprised 75% of the birds I trapped (Table 2.1). This would indicate that reproductive success of the species was more than adequate six years after the use of DDT was restricted.

Thus, although the evidence is not conclusive, it would appear that a decline in the Australasian harrier population density in New Zealand has occurred since the late 1940's as suggested by Turbott (1967). There may, however, have been reasons for this decline other than the decrease in density of the New Zealand rabbit population.

PART TWO : METHODOLOGY

A. Division of labour and materials

Between February 1976 and July 1977 I spent an average of four days a week at Pukepuke Lagoon. This meant that during the breeding season about 200 hours per month were occupied with field-work. About one quarter of this time was spent inspecting traps and marking birds. Most of the other 150 hours per month were spent in either a permanent hide, a portable hide or on dune ridges. From these I recorded hunting behaviour data and noted territory boundaries and observations of individually marked birds on a map of the study area (Figure 2.2). I also made observations of social interactions, nest sites and the communal roost. Observations were usually made from a distance of 100 m or more from nest sites and birds. About five hours per month

were involved in collecting pellets and prey remains. There was a similar division of labour between trapping and general observations during the non-breeding season, but fewer daylight hours limited field-work to about 140 hours per month.

In addition to the intensive field study outlined above I made fortnightly checks on individually marked pairs of Australasian harriers at Pukepuke Lagoon from August 1977 until February 1978. These checks were made to record whether adults present in the 1976-77 breeding season returned and established the same territories, paired with the same mates and had a similar fledging success in the 1977-78 breeding season, for data on these subjects had not previously been recorded for the Australasian harrier.

During the first 14 months field-work I used a shooters' hut owned by the Department of Lands and Survey for accommodation and for the last four months I used accommodation provided by the New Zealand Wildlife Service.

A permanent hide was erected on one of the highest dunes (20 m above sea level) which gave a commanding view of Pukepuke Lagoon and most of the study area. I also made a portable hide. A Honda C.T. 90 motorbike with reduction gearing was used for transport between Palmerston North and Pukepuke Lagoon. The motorbike enabled me to travel over the sand dunes and check the traps that were evenly spaced over the 12 km² study area.

B. Traps

The traps included: six cage traps (Plate 2.3), three automatic bownets (Plate 2.4) and two bal-chatris. The cage traps were adapted from those made by Hollom (1950). They measured 2 m square x 1.3 m high. They were made from number four gauge wire rods welded into rectangular gates and covered with 3 cm gauge wire netting. The gates were lashed together and could be unlashd and stacked flat for easy transportation. A wire netting floor prevented most mammalian carnivores from entering the traps. Trapped birds were recovered through a door (1.3 m x 0.6 m) in one of the rectangular gates. A post which protruded about 30 cm above the trap was tied to the side for the Australasian harriers to perch on. This introduced the birds to the trap entrance more readily. The circular trap entrance in the centre of the top of the cage trap was

PLATE 2.3: CAGE TRAP



PLATE 2.4: AUTOMATIC BOWNET



45 cm in diameter. From the circumference of the trap entrance hung 45 cm long wire droppers spaced 5 cm apart. These droppers were laced together 25 cm from their base to form an entrance "funnel". The lacing also prevented the droppers from making a metallic clinking on windy days.

Rabbits shot by the Manawatu Pest Destruction Council were used as bait. These were cut open and staked directly below the trap entrance. Unless the bait was staked firmly to the ground a bird would often drag it to the side of the cage trap and other Australasian harriers were then less likely to enter the trap.

The advantages of cage traps over automatic bownets and bal-chatris were: (i) more than one Australasian harrier could be caught at a time and a trapped bird acted as a decoy for others (as many as six birds were caught in one trap); (ii) they required less maintenance and needed checking only twice a day as they allowed the birds considerable freedom; (iii) they were less prone to damage and bait robbing by mammalian carnivores.

The disadvantages of cage traps were: (i) they were only effective from mid-February until the end of October; (ii) they were likely to be crushed by inquisitive cattle (*Bos* sp.); (iii) they were not as easily transported as other traps.

The three automatic bownet traps I made were similar to those of Tordoff (1954) and Mollison (1957). These traps enabled me to continue trapping Australasian harriers in summer. I trapped only two Australasian harriers with the bal-chatris I made so these traps were not used extensively. They were modelled on bal-chatris made by Berger and Mueller (1959) and Ward and Martin (1968).

C. Sexing and aging

Between August 1976 and July 1977 I banded 212 Australasian harriers with individually numbered stainless steel rings supplied by the Wildlife Service. Sexing was done by weighing the birds and examination and measurement of their legs and feet which are considerably more massive in the female than the male. There was little overlap between the sexes for these measurements (Fox 1977b). The reliability of this method was confirmed by dissecting and sexing ten birds and by examination and measurement of specimen skins from the Dominion Museum.

Birds were aged as adults or juveniles. The age classes most easily confused were juvenile and young adult females. However, prior to the post-juvenile moult, juvenile females had buff and brown rather than white and brown upper tail coverts and their plumage was much darker than that of adults. The juveniles' retrices often contained stress marks (Hamerstrom 1967) which also served to distinguish age classes.

D. Tagging

All trapped Australasian harriers were fitted with brightly coloured "saflag" wing tags (Plate 2.5). These were colour-coded so that a bird could be individually recognised and its sex and age recorded in the field. The wing tags were modelled on those made by Fitzner (1975). I found "saflag" wing tags had a useful field life of about two years. The sex and age of a marked bird could usually be identified at distances of 1.2 km or greater with the aid of 7 x 50 binoculars. Birds were often individually identified at distances of up to 0.8 km. During the last three months of trapping, juveniles were fitted with wing tags colour-coded for sex and age only. Therefore the percentage of juveniles resighted was calculated only from birds banded and individually marked prior to this time.

E. Morphometric data

From each trapped bird 17 morphometric measurements were taken. All linear measurements were taken according to the guidelines provided by Gurr (1947). Wing areas were recorded in the field by tracing outlines of opened wings onto sheets of stiff paper. These were later cut out and passed through a leaf area index machine which measured the area in square centimeters. Weights were obtained by placing the bird in a bag and suspending this from a spring balance accurate to 5 g. For each bird the estimated weight of its crop contents was subtracted on the basis that 120 g was the weight of a full crop. Two of ten dissected birds had 100 g of food in their stomachs but I was unable to correct this source of error in the field. Crop weight estimates were based on the knowledge gained from feeding captive birds known weights of meat. The weight of a bird was recorded at each recapture, but if it was trapped more than once in 30 days then an average weight was calculated and only this was used in the final analysis and presentation

PLATE 2.5: ADULT MALE WITH WING TAGS
AND JUVENILE FEMALE



of the data. This was because a few birds were trapped as often as six times in a month and could therefore have biased the data. Wing loadings were calculated using Brown and Amadons' (1968) formula:

$$\text{Wing loading} = \frac{\text{Weight}}{\text{Wing area}}$$

F. Moult data and colour of soft parts

Moult data were recorded using the system developed by Hamerstrom (1971). For each age and sex class the percentage of primary remiges and retrices that were newly moulted per month were calculated. No moult data were recorded for either juvenile sex in May, June and July. This was because the juveniles of the previous year were considered to be adults when they had completed their first post-nuptial moult by the end of April. In August the juveniles of that year began to moult their central retrices and data were collected from these birds. The colours of the plumage, tarsus, cere, eye-ring and eye were recorded for each bird.

METHODOLOGY : RESULTS

A. Trapping data

Of the 212 birds trapped, 19 (9.0%) were adult males, 81 (38.2%) juvenile males, 34 (16.0%) adult females and 78 (36.8%) juvenile females. Seventy-six (26.4%) of these birds were recaptured a total of 220 times (Table 2.1). A similar percentage of birds were resighted after banding and individual marking. Males were recaptured and resighted significantly more often than females ($\chi^2 = 5.54$; $P < 0.02$).

B. Morphometric data

A total of 3,452 morphometric measurements are recorded in Tables 2.2 and 2.3. There are no significant differences between adult and juvenile males for wing area, wing loading and all linear measurements (Table 2.2). However adult males were on average significantly heavier than juveniles (Table 2.5).

The length of the adult females' tarsi and toes were significantly greater than those of juvenile females ($t = 2.67 - 6.50$; $P < 0.01$) (Table 2.3). Adult females also had a significantly higher wing loading than juvenile females ($t = 3.60$; $P < 0.001$) and were significantly heavier in all seasons (Table 2.5). The female age classes had similar values for wing area and all other linear measurements.

Table 2.1: Number of Australasian harriers banded, individually marked, retrapped and resighted

	Number banded	Number retrapped	Percent retrapped	Total retraps	Number sighted	Percent sighted	Total sightings
Adult male	19	10	34.5	31	10	34.5	131
Juvenile male	81	34	29.6	89	20	29.8	61
Adult female	34	9	20.9	27	11	24.4	81
Juvenile female	78	23	22.8	73	15	22.3	46
Total	212	76	26.4	220	56	27.0	319

Table 2.2: Male Australasian harrier morphological data

	Number of specimens			Mean			Standard deviation			Range		
	Adult Male	Juvenile Male	Total Male	Adult Male	Juvenile Male	Total Male	Adult Male	Juvenile Male	Total Male	Adult Male	Juvenile Male	Total Male
Length exposed culmen (mm)	17	79	96	32.8	33.1	33.1	1.3	1.6	1.5	31.5-35.2	29.8-35.9	29.8-35.9
Length minus cere (mm)	17	79	96	22.2	22.1	22.1	0.8	0.9	0.9	21.5-23.8	20.0-25.1	20.0-25.1
Culmen width (mm)	17	79	96	28.7	29.2	29.2	1.1	1.5	1.5	26.6-30.1	27.0-32.0	26.6-32.0
Culmen depth (mm)	17	79	96	20.2	20.0	20.1	1.2	0.9	1.0	17.7-22.5	18.0-22.7	17.7-22.7
Tarsus (mm)	17	79	96	91.0	90.8	90.9	2.0	2.9	2.7	88.1-94.5	85.3-95.7	85.3-95.7
Toes: hallux (mm)	18	80	98	20.7	21.1	21.0	1.6	1.3	1.4	18.3-23.6	18.0-24.0	18.0-24.0
two (mm)	14	78	92	28.3	27.7	27.8	1.7	1.3	1.4	27.7-31.0	24.5-31.0	24.5-31.0
three (mm)	13	61	74	42.0	42.0	42.0	1.4	1.9	1.8	39.5-44.5	38.3-45.3	38.3-45.3
four (mm)	12	60	72	33.8	33.2	33.4	1.7	1.7	1.7	30.8-35.6	29.8-36.2	29.8-36.2
Claws: hallux (mm)	18	77	95	21.4	21.5	21.5	1.1	0.8	0.8	19.6-23.0	19.5-23.0	19.5-23.0
two (mm)	19	77	96	21.0	21.1	21.1	0.7	0.6	0.6	20.0-22.4	19.5-22.5	19.5-22.5
three (mm)	17	71	88	18.9	19.2	19.2	0.8	0.7	0.7	17.6-20.6	17.9-20.9	17.6-20.9
four (mm)	17	76	93	15.6	15.9	15.9	0.7	0.6	0.7	14.5-17.0	14.4-17.4	14.4-17.4
Tail (mm)	16	79	95	226	224	225	10.0	8.6	8.7	207-245	195-240	195-245
Wing length (mm)	16	79	95	408	403	404	9.3	7.4	7.9	391-425	385-421	385-425
Wing area (cm ²)	15	41	56	1,802	1,780	1,786	47.4	52.8	51.3	1,674-1,998	1,614-1,998	1,614-1,998
Weight (g)	54	111	165	640	615	625	50.7	51.4	52.3	520-720	505-710	505-720
Wing loading (g/cm ²)	15	41	56	0.345	0.340	0.34	0.02	0.03	0.03	0.30-0.39	0.27-0.42	0.27-0.42

Table 2.3: Female Australasian harrier morphological data

	Number of specimens			Mean			Standard deviation			Range		
	Adult Female	Juvenile Female	Total Female	Adult Female	Juvenile Female	Total Female	Adult Female	Juvenile Female	Total Female	Adult Female	Juvenile Female	Total Female
Length exposed culmen (mm)	34	74	108	37.2	36.0	36.4	1.9	1.1	1.2	34.9-40.4	34.0-39.1	34.0-40.4
Length minus cere (mm)	34	74	108	25.2	24.4	24.5	1.1	1.3	1.1	22.9-28.2	22.0-27.3	22.0-28.2
Culmen width (mm)	34	74	108	32.0	32.1	32.1	1.2	1.6	1.5	30.4-34.2	28.8-35.0	28.8-35.0
Culmen depth (mm)	34	74	108	22.4	22.0	22.1	0.8	0.8	0.8	20.7-23.8	20.0-23.4	20.0-23.8
Tarsus (mm)	34	74	108	97.9	96.7	97.1	2.4	3.1	3.0	94.2-103.9	90.0-102.9	90.0-103.9
Toes: hallux (mm)	33	75	108	24.9	24.5	24.6	1.8	1.9	1.9	21.9-29.0	21.5-30.1	21.5-30.1
two (mm)	26	66	92	33.2	30.9	31.5	1.9	2.3	2.4	29.8-36.0	28.6-36.0	28.6-36.0
three (mm)	17	56	73	47.6	46.0	46.4	1.7	1.4	1.6	44.0-50.1	42.6-49.5	42.6-50.1
four (mm)	21	61	82	38.3	37.4	37.6	1.8	1.6	1.7	34.1-41.0	34.9-40.8	34.1-41.0
Claw: hallux (mm)	34	78	112	24.3	24.1	24.2	0.9	0.9	0.9	22.7-26.5	22.7-26.4	22.7-26.5
two (mm)	33	78	111	23.8	23.6	23.7	0.8	0.8	0.8	22.2-25.0	22.0-25.5	22.0-25.5
three (mm)	34	78	112	21.1	21.2	21.2	0.9	1.0	1.0	19.4-22.8	18.9-23.2	18.9-23.2
four (mm)	34	78	112	17.5	17.6	17.6	0.6	0.8	0.7	16.4-19.1	15.5-19.4	15.5-19.4
Tail (mm)	33	74	107	239	235	236	8.9	6.9	7.8	215-257	214-247	214-257
Wing length (mm)	33	74	107	427	422	423	9.2	8.8	9.2	415-440	400-440	400-440
Wing area (cm ²)	16	46	62	2,066	2,035	2,043	72.3	65.6	67.1	1,808-2,352	1,804-2,358	1,804-2,358
Weight (g)	66	113	179	870	810	835	64.9	55.5	65.1	700-1,035	680-995	680-1,035
Wing loading (g/cm ²)	16	46	62	0.411	0.389	0.39	0.03	0.03	0.03	0.35-0.46	0.33-0.47	0.33-0.47

Table 2.4: Seasonal weight changes

	Adult male			Juvenile male			Adult female			Juvenile female		
	Mean weight (g)	Number weighed	Percent change	Mean weight (g)	Number weighed	Percent change	Mean weight (g)	Number weighed	Percent change	Mean weight (g)	Number weighed	Percent change
Summer (Dec-Feb)	600	9	-1.7	605	12	+1.7	865	13	+1.7	800	25	+0.6
Autumn (March-May)	640	22	+6.7	615	34	+1.6	875	13	+1.1	805	42	+0.6
Winter (June-Aug)	660	19	+3.1	630	44	+1.6	880	23	+0.6	850	29	+5.2
Spring (Sept-Nov)	610	4	-7.6	595	21	-5.5	850	17	-3.4	795	17	-6.5
Total	640	54	9.1	615	111	5.5	870	66	3.4	810	113	6.5

Table 2.5: Comparison of seasonal differences in weight

	Adult male v juvenile male	Adult female v juvenile female
Summer (Dec-Feb)	t = 0.20; N.S.	t = 5.22; P<0.001
Autumn (March-May)	t = 3.32; P<0.001	t = 5.70; P<0.001
Winter (June-Aug)	t = 3.61; P<0.001	t = 2.30; P<0.02
Spring (Sept-Nov)	t = 1.20; N.S.	t = 4.06; P<0.001
Total	t = 4.03; P<0.001	t = 8.28; P<0.001

Females were significantly larger than males for all measurements at the 0.1% probability level ($P < 0.001$) except for wing length ($t = 2.23$; $P < 0.05$) and tail length ($t = 1.34$; N.S.). Males were only 74.8% and 87.4% of the size of females by weight and wing area, respectively, but were 95.5% and 95.3% of female size by wing length and tail length. The measured ranges for males and females overlapped least for weight (7.5%), hallux claw length (4.3%) and exposed culmen length (9.2%).

Seasonal weight changes and differences between the age and sex classes are presented in greater detail in Table 2.4, and the levels of significance for differences between the classes are recorded in Table 2.5. All birds were heaviest in winter and all except adult males were lightest in spring. Adult males were lightest in summer. The season of greatest gains in weight was autumn. All birds lost most weight in spring. Juvenile males were slightly heavier than adult males in summer but were significantly lighter in autumn and winter. Adult females were significantly heavier than juvenile females in all seasons.

C. Moult

The juveniles underwent a post-juvenile body moult between April and July. The plumage colour changes that occurred in this moult have been recorded by Oliver (1955). Their central or deck retrices were moulted between August and November (Table 2.6). These central retrices were the last to be moulted at the end of the first post-nuptial moult the following March and April. For juvenile females their first post-nuptial moult began in November and continued for five months until the end of March. The juvenile males' first post-nuptial moult also continued for five months but began in December and finished at the end of April. The underwing barring typical of adult males became conspicuous during this moult (Plate 2.11).

Adult females began their post-nuptial moult in December when their nestlings were about a week old and continued moulting for six months until the end of May. Adult males continued moulting for the same length of time but began and finished their post-nuptial moult a month later. Unlike juveniles, the adults' central retrices were the first to be moulted in the post-nuptial moult.

Table 2.6: Molt data from trapped Australasian harriers

	Adult male			Juvenile male			Adult female			Juvenile female		
	Number of birds	% remiges moulted	% retrices moulted	Number of birds	% remiges moulted	% retrices moulted	Number of birds	% remiges moulted	% retrices moulted	Number of birds	% remiges moulted	% retrices moulted
January	4	20	6	2	50	58	8	39	20	4	54	73
February	3	37	25	0			3	57	56	3	53	89
March	0			1	80	92	4	85	87	1	80	84
April	2	85	100	3	90	94	2	98	98	1	100	100
May	1	80	100				8	93	95			
June	7	91	97				7	98	100			
July	4	93	100				2	0	0			
August	7	0	0	11	0	7	4	0	0	5	0	8
September	1	0	0	4	0	10	11	0	0	2	0	16
October	2	0	0	5	0	13	7	0	2	6	0	18
November	1	0	0	5	0	7	2	0	0	3	10	14
December	1	0	0	3	35	39	3	27	17	3	37	47

Table 2.7: Seasonal changes in colour of the cere, eye-ring and feet of Australasian harriers

	Non-breeding season		Breeding season	
	Cere and eye-ring	Feet	Cere and eye-ring	Feet
Adult male	Pale yellow	Lemon yellow	Yellow	Yellow-orange
Juvenile male	Pale yellow	Yellow	Yellow	Dark yellow
Adult female	Pale yellow	Yellow	Yellow	Dark yellow
Juvenile female	Pale yellow	Pale yellow	Yellow	Yellow

PLATE 2.6: FEMALE AGED 3 MONTHS



PLATE 2.7: FEMALE AGED 18 MONTHS



PLATE 2.8: ADULT FEMALE



PLATE 2.9: ADULT FEMALE



PLATE 2.10: MALE AGED 3 MONTHS



PLATE 2.11: MALE AGED 12 MONTHS



PLATE 2.12: MALE AGED 18 MONTHS



PLATE 2.13: ADULT MALE



D. Soft parts colour changes

Juvenile females had dark chocolate brown irises (Plate 2.6) which in most birds changed to mid-brown by the end of their first post-nuptial moult during their second winter (Plate 2.7). Thereafter the rate of change of their iris colour is not known, but as found in other studies (Redhead 1968a, Fox 1977b), appears very variable. I observed all combinations of iris colour from 80% brown with 20% yellow specks (Plate 2.8), to pale sulphur yellow with a thin black outer ring (Plate 2.9).

At fledging, males' mid-brown irises had a dorsal grey cast (Plate 2.10). Their iris colour changed to light brown by April, to brown with about 30% yellow specks by September (Plate 2.11) and to golden yellow by the end of their first post-nuptial moult (Plate 2.12). The rate of change was variable. Most adult males had a pale sulphur yellow iris with a thin black outer ring which contrasted strongly with their yellow eye-ring (Plate 2.13), but it is not known how old adult males were when their irises changed to this colour.

The cere and eye-ring of all age and sex classes changed from pale yellow to yellow during the breeding season. Whether this was due to gonad or diet changes is not known. Of all the classes, adult males had the most conspicuously coloured feet. These changed from lemon yellow to bright orange-yellow during the breeding season (Table 2.7).

METHODOLOGY : DISCUSSION

The 751 recordings of individually marked Australasian harriers obtained through initial banding, retrapping and resighting data in Table 2.1 provided the means by which the morphometric, moult and soft parts data were able to be collected. Table 2.1 is further discussed as the basis of the breeding and non-breeding biology observations in Chapters 3 and 4.

A. Morphometric data

The three measurements I took of Australasian harriers that had the lowest percent overlap (weight, hallux claw length and exposed culmen length) are all relatively easy measurements for a field worker to take. Furthermore, no sexed bird overlapped in all three measurements with the measured range of the other sex; so these should provide a comprehensive set of measurements for sexing birds in the field.

Redhead (1969) concluded that apart from dissection the next most effective method of determining the sex of trapped Australasian harriers was by plumage colour or weight differences. After the post-juvenile moult, I was unable to detect any difference between the plumage colour of juveniles and young adult females. I trapped two adult females that were as pale as adult males. Therefore I do not think that plumage colour is a reliable field sexing technique.

The morphometric data present some significant differences between the age and sex classes. While male Australasian harriers with an average wing loading of 0.34 g/cm^2 were similar to the European subspecies of *C. aeruginosus* (0.30 g/cm^2 , sex not recorded), adult females (0.41 g/cm^2) had a wing loading that lies within the known range for buzzards ($0.40 - 0.45 \text{ g/cm}^2$) (Brown and Amadon 1968). Buzzards have broader more rounded wings than harriers and they often have a short tail. Brown and Amadon (1968) equated these characteristics with reduced agility. Female Australasian harriers had a comparatively larger wing area to wing length than males. This suggests that females have broader more buteonine wings. They also possessed relatively shorter tails than males because they were significantly larger than males for all measurements except tail length. Nieboer (1973, cited by Schipper 1973) concluded that harrier species with longer tails in relation to their average body weight were more agile. Thus by measurement male Australasian harriers were more agile than females.

I think juvenile males were significantly lighter than adult males in autumn and winter because they were less experienced hunters and made significantly fewer prey captures (Table 6.2). The seasonal weight differences were not due to an overall size difference because the juveniles were on average slightly heavier than adults in summer and there were no significant differences between the age classes for all linear measurements. This is supported by Redhead's (1968a) data which showed for a nestling male reared in captivity that growth was complete at about 10 weeks, so the juveniles were not lighter because they had not reached adult size. Differences in stages of moult would not account for the significant differences in weight.

In contrast to the lack of difference between linear measurements of adult and juvenile males, juvenile females had on average significantly smaller prey catching apparatus than adult females. They also had a

significantly lower wing loading which was a direct consequence of their being significantly lighter. Although juvenile females were probably lighter than adult females because they were significantly less successful hunters (Table 6.2), this does not account for the difference in size of prey catching apparatus.

Fox (1977b) suggested that both juvenile sexes were not only lighter but were smaller than adults. However his data, like mine, showed that it was only juvenile females that were smaller than adult females. More data for all sex and age classes, particularly from museum specimens, would be required before I could conclude that ecological factors are selecting for larger size in female Australasian harriers.

It appears incongruous that all birds were most readily trapped in autumn and winter when they were gaining weight. Two possible reasons for this are that Australasian harriers developed a strong search image (Tinbergen 1960, Croze 1970) for carrion which comprised an increasing proportion of their diet in these seasons (Table 5.7), and they were therefore more readily attracted to the carrion in the traps. A second possibility is that the birds faced a pronounced feast or famine situation; particularly in winter when a large food item such as a sheep carcass may have provided several birds with food for three or four days. As the birds gained weight their wing loading would have increased and their agility decreased. Their ability to catch agile adult prey would also have decreased. If they did not catch any prey or locate another carrion item in the one or two days after the food had been consumed they may have lost little weight but they may have been hungry and therefore more readily trapped. Mueller and Berger (1970) demonstrated that hungry sharp-shinned hawks (*Accipiter striatus*) were most easily trapped. In spring and summer the Australasian harriers' search image probably changed and the birds no longer faced a feast or famine situation for they caught more small live prey (Table 5.4).

It seems entirely at odds with the morphometric data that the most agile adult males lost relatively more weight than the other classes did in spring when live prey availability was increasing (Chapter 5). In this season the average weight of adult females which were producing eggs decreased least. In Chapter 3 it was shown that at this time courtship feeding of the adult female by the adult male was a regular occurrence.

Thus the adult females' energy reserves were supplemented at the immediate expense of the adult males'. This trend continued into summer when the adult male fed the adult female and their young and lost more weight. Furthermore, territory defence and reproductive behaviour would have meant the adults, and particularly the adult male, had less time for hunting. With only themselves to feed and no territory to defend, the average weight of juvenile males increased in summer; more so than the average weight of juvenile females.

Carroll (1970) recorded similar seasonal weight changes for Australasian harriers but did not attempt to explain the trends. The average weights obtained in this study were similar to those recorded by Redhead (1969), Carroll (1970) and Fox (1977b).

The wing loadings calculated by Fox (1977b) for the Australasian harrier sexes were higher than those I obtained. He trapped all birds in autumn and winter when they were heaviest. Also, 80% (40) of the birds he trapped were adults which in these seasons were significantly heavier than juveniles.

B. Moult

All Australasian harriers moulted their primaries from the carpal flexure outwards as recorded for the hen harrier (*Circus cyaneus*) by Schmutz and Schmutz (1975). Because the adult Australasian harriers' moult lasted for one month longer than that of the juveniles, the adults would have had a smaller gap in their wings at any given stage of their moult. This could be correlated with the extra hunting efficiency that was demanded of the adults which were feeding nestlings as well as themselves. The adults' moult seemed to fit their seasonal energy budget well. Adult females began their post-nuptial moult when they were still being fed by the male, but after the eggs were laid, which suggests that there was a priority between energy needed for egg production and moult. Adult males, on the other hand, did not commence moulting until the young were ready to fledge, by which time their parental labours were almost completed.

As early as four months before their first post-nuptial moult began, the juveniles moulted their central retrices. These may have had a signalling function in breeding behaviour because the banding on the newly moulted retrices was similar to that of the adults' and much more conspicuous than that of their unmoulted retrices.

CHAPTER THREE

THE BREEDING BIOLOGY OF THE AUSTRALASIAN HARRIER

A. TERRITORIES AND HOME RANGES

Odum and Kuenzler (1955) noted that, "Examination of the voluminous literature on territorialism in birds reveals that many qualitative details have been worked out. The "kinds" of territory have been classified, and the means of establishment and defence of the territory area have been described for many species. On the other hand, many quantitative aspects of territorialism have scarcely been considered." Furthermore, numerous theories have been advanced to explain the significance of territories (Nice 1941, Lack 1954, Hinde 1956, Wynne-Edwards 1959, Brown 1969). I do not intend to review the substantial amount of literature on territories, but rather to record the data I collected relating to the territories of the Australasian harrier and discuss this in the light of other published work.

I have followed Newton's (1976) guidelines and have used the term "nest site" to describe the situation of the nest, "territory" for the area around the nest that was defended, and "home range" for the area that included the territory and hunting areas of the pair.

A.i. Territory and home range parameters

There were ten territories (Figure 3.1) in the 12 km² study area in both the 1976-77 and 1977-78 breeding seasons. For the two breeding seasons combined, the average distance between each nest site and its nearest neighbour was 910 m (Range = 300 - 1,600 m; N = 19 nests).

Territory size was gauged from observations of evictions of intruders, interactions between rivals along territory boundaries and border patrols (Section A.ii). In the 1976-77 breeding season I calculated the size of seven territories owned by paired adults and one defended by a juvenile male. Paired birds' territories averaged 31 ha (Range = 18 - 55 ha). Two of these decreased in size by about 20% after the young hatched during November, so that average territory size was then 27 ha (Range = 18 - 42 ha). Neighbouring males then hunted but did not defend the areas that the former territory owners had ceased to defend. The area above

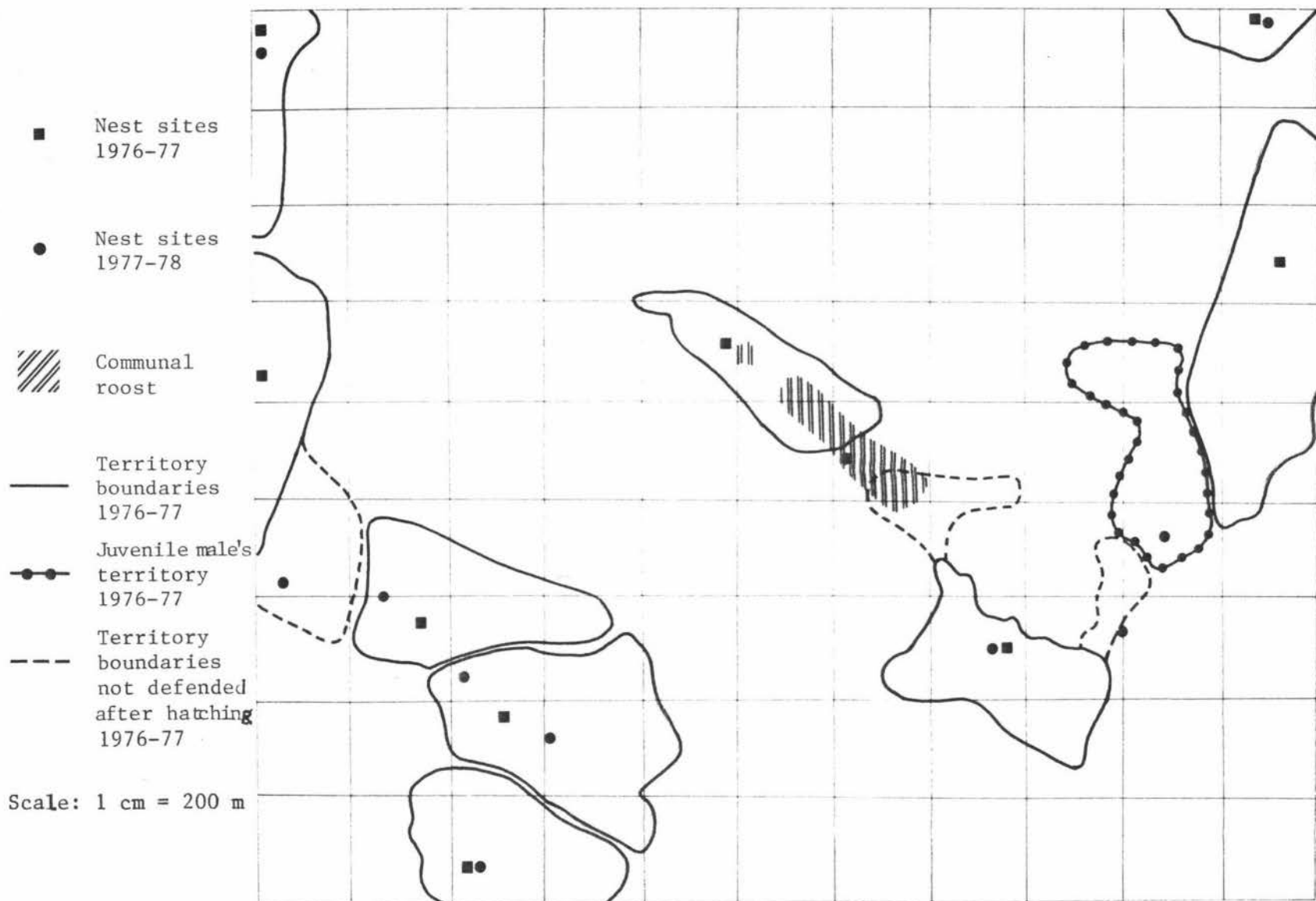


FIGURE 3.1: TERRITORIES AND NEST SITES

the territory was defended to a height of about 20 m at the boundary and 20 - 30 m over the nest site. Territory boundaries frequently occurred along dune ridges or ecotones such as that between raupo swamp and farmland. All regions of the territory were defended with equal vigour. Males and females defended the same territory except in cases where polygyny occurred. In the latter case females defended about half the area defended by males. Neighbouring Australasian harriers influenced the size and shape of each others territories through boundary displays and border patrols. Other birds such as white-backed magpies (*Gymnorhina tibicen*) did not affect territory size and shape.

Juveniles did not normally establish territories. However, a juvenile male established a small (12.5 ha) territory in August 1976 but this was abandoned three months later. This bird returned the following year and established a larger territory encompassing its former territory and bred successfully. In September 1977 a juvenile male was observed in the north-eastern corner of the study area as a territory owner paired with an adult female. A nest was built by the female but this was abandoned in early November. The juvenile male left the area at about the same time. In the 1977-78 breeding season, a female which I banded early in 1977 as a juvenile mated with an adult male whose mate of the previous season had failed to return. This pair fledged one nestling.

Breeding season home range sizes were determined from records of those individually marked birds most frequently retrapped and sighted. For example an adult male and female were sighted 39 and 32 times and retrapped seven and five times respectively. I calculated that the home ranges of Australasian harriers in the sand country were 9 km². Within this 9 km² were the pairs' favourite hunting areas which covered an area of about 3 km². In covering their home ranges no birds were forced to fly over other birds' territories.

Juveniles' daily home ranges were similar in size to the adults' favourite hunting areas but their total ranges during the breeding season were much larger. Individually marked juveniles were usually observed hunting for one to eight weeks and then they left the study area. After three or more months absence several of these birds were recorded (26.7%) in the study area once again. I was uncertain how far they ranged during the interval between recordings, but reported observations of

individually marked birds outside the study area and ringing returns (Tables 4.2 and 4.3) indicated that usually they did not leave the sand country. This extends about 40 km north and south and 15 km east of Pukepuke Lagoon (Figure 2.1).

During the two breeding seasons there was an average of 18 breeding birds and six juveniles in the study area. This gave a population density of about one bird per 50 ha. Although the home ranges and favourite hunting areas of most of these birds extended outside the study area they still overlapped with those of their neighbours. Different pairs' home ranges overlapped by about 70% but their favourite hunting areas overlapped by only about 10%. Juveniles were occasionally evicted from an area that was regularly hunted by an adult, but because each pair had its favourite hunting areas, birds from different pairs were rarely seen in the same area at the same time.

Discussion. One of the factors that limited the density of breeding birds at Pukepuke Lagoon was nest site or nesting habitat availability. This resulted in a random spacing of nest sites which meant that territories were not evenly spaced throughout the study area. Nest site availability was discussed by Hickey (1969) who demonstrated that the peregrine (*Falco peregrinus*) was also nest site limited and spacing of nest sites was random. Fox (1977) found the New Zealand falcon was not nest site limited and nest site spacing was non-random.

Food abundance and availability, degree of territoriality and the type of habitats available also influence breeding density in raptors (Moore 1957, Southern and Lowe 1968, Newton 1976). Because there was considerably more nesting and preferred hunting habitat available at Pukepuke Lagoon than further inland where drainage and grazing intensity has been greater (Cowie *et al.* 1967), I anticipate that breeding density would be much lower in inland areas.

Territoriality would have limited the breeding density of Australasian harriers more than hen harriers and Montagu's harriers because the Australasian harrier does not nest socially like these species (Balfour 1962, Bannerman 1956).

The home range of Australasian harriers in sand country (9 km²) was similar to the home range (8.8 km²) of a pair of breeding marsh hawks (*Circus cyaneus*) calculated by Hamerstrom and Wilde (1973). These

workers used radio-telemetry techniques. Craighead and Craighead (1956) calculated a smaller home range of 5.5 km^2 for the marsh hawk while Breckenridge (1935) estimated the area an adult male marsh hawk was seen regularly hunting to be about 2.6 km^2 . I was unable to find any data on home range of *Circus aeruginosus* in the literature.

A.ii Territory formation and maintenance

Homing. In 1977 the dispersal phase (described in Chapter 4) ended in May when several of the 17 adults that had been in the study area the previous breeding season began to return and hunt their former home ranges. Fifteen of the 17 adults were individually marked. Ten (66.7%) of these marked birds returned to re-establish territories and eight (53.3%) of them became resident in their former territories. Six (40.0%) paired with their mate of the previous breeding season.

Homing, or returning to a native locality (Mayr 1963: 569), has also been recorded for *Circus cyaneus* (Balfour 1962, Hamerstrom 1969). Homing would conserve time and energy in the various steps of the breeding cycle because a bird would return to familiar hunting areas, territory boundaries, neighbours, nest sites and possibly mates. There was no correlation between previous nesting success and returning to the study area as Hamerstrom (1969) recorded for the marsh hawk.

Displays. One week after the first adults returned the first evictions of intruders by adults from incipient territories were seen, and in mid-July the first territorial displays were observed. These coincided with the first courtship display diving of the breeding season.

Territorial displays by rival males involved both birds flying in the same direction on either side of the territory boundary about 10 m apart and at a height of about 15 m. They flew with their wings at an exaggeratedly high angle and with their bright orange-yellow tarsi thrust straight down. Their flight was slow with very few flaps and their pale ventral surfaces and dark underwing barring were conspicuous. Fox (1977b) recorded underwing barring as being particularly noticeable in adult males. Territorial displays were usually silent although the male's courtship call was occasionally heard at the end of a display flight. At the end of the territory display flight both birds usually landed on prominent trees or knolls within their respective territories.

They remained there for about five minutes and then usually left the area and began hunting.

Early in the breeding season there was a considerable amount of ambivalence exhibited in displays at territory boundaries. Boundaries were not well defined until about mid-September. Territory display flights, which were seen up to six times a day, decreased in frequency as the breeding season progressed and were replaced by border patrolling. For example, of two neighbouring adult males, one was seen to patrol their mutual territory boundary 12 times and the other six times in one afternoon in December. Females were only seen to make territory display flights and border patrols twice. This occurred after they had built nests in October.

With nest building initiated, the rate of observed evictions of intruders from territories increased markedly from two per 100 hours observation (total of 300 hours observation) in August and September to 20 per 100 hours observation (total of 450 hours observation) from October through until the end of December. Up until the time the nest was built adult males and females usually only evicted birds of their own sex, but after this time they were indiscriminate in their evictions. Prior to the female commencing incubation, adult males and females successfully evicted all intruders. After this period females were unsuccessful on four (16.0%) occasions whereas males were still always successful. Adult males were twice seen to rake with their talons intruders that were slow to leave. A few of the intruders' body feathers were dislodged on these occasions.

Eviction of intruders involved the defending bird flying fast, low and directly at the intruder. The intruder was attacked or pursued closely in a fast chase until such time as it either crossed the territory boundary or climbed to a height of at least 20 m. Once the intruder was above this height female territory owners usually returned to the centre of the territory whereas males "escorted" the intruder to the boundary. This escorting flight involved the male flying below and often ahead of the intruder which followed to the boundary. The male frequently thrust its tarsi down when it reached the boundary and flew along it for a short way before returning to the centre of the territory or continuing hunting. Watson and Dickson (1972) described a similar

escorting flight in hen harriers as a mild form of defensive behaviour shown by males, chiefly to other males.

A.iii Interspecific territory defence

Australasian harriers readily desert their eggs and young if flushed from the nest by man (Sharland 1932, Stead 1932, Soper 1958). I visited two nests before fledging took place but only when the female had begun hunting regularly. I found that some adults left the area as soon as I entered their territory while others circled overhead at a height of about 30 m and gave threat calls. These were accompanied by a shallow wing flutter.

Nest defence against potential avian predators was much stronger. On different occasions an adult male and female were observed threat calling and stooping at a bittern (*Botaurus poiciloptilus*). On both occasions the bittern was forced to leave the territory. Magpies usually had no difficulty evicting Australasian harriers from an area, but where the territories of the two species overlapped magpies were unable to evict them despite repeated attacks.

I learnt that an Australasian harrier's nest was very difficult to find in a large swamp with few landmarks and where the vegetation towered above the searcher's head; this was even after the female had been seen descending into a specific area of raupo on several occasions. Such a nest would be well hidden from the eyes of most mammalian predators but not from aerial predators which Australasian harriers attacked strongly. Watson (1977) attributed the vigorous attacks on man and other mammals by hen harriers and pied harriers (*Circus melanoleucus*) but not Montagu's and marsh harriers to the need of the former two species to protect their more open nest sites from mammalian predators and the trampling feet of herbivores. He found that hen harriers nesting in dense conifer forests were noticeably less aggressive towards man than those nesting in open moorland.

B. VOICE

The Australasian harrier was generally silent outside the breeding season. I noted several calls, each linked with distinct situations.

Courtship call. The male called a short plaintive 'kee-a' during courtship display (Section C.i), when soaring over the territory and when calling the female to accept prey at the "cock nest" (Section C.ii). This call was occasionally heard at the end of a territory display flight by rival males (Section A.ii).

Nest inspection call. A short 'see-o' was repeated about ten times in as many seconds by the male during nest inspection behaviour (Section D.i). This call was only given when the male was perched.

Food provision call. The male called the female from the nest to receive prey with a quiet 'chuck-chuck-chuck' (Section C.iv).

Soliciting call. The female called a high pitched 'seee-uh' during courtship display (Section C.i), when soliciting prey from her mate (Section C.iv), prior to copulation (Section C.iii), when attacked over the territory by magpies, and when she had difficulty evicting intruding Australasian harriers from the territory. Juveniles also gave this call when soliciting food from adults (Section E.iii).

Threat call. A loud sharp 'chit-chit-chit' was voiced by adults and juveniles during aggressive interspecific encounters (Section A.iii).

Fear call. Adults and juveniles gave a loud 'cheeeet' call when startled by man or struck by the talons of another Australasian harrier.

C. PAIR FORMATION AND MAINTENANCE

C.i Courtship display

During June pairs of Australasian harriers were observed together with increasing frequency as they soared on the same thermal. The male was often the higher of the two soaring birds. Perhaps the reason for this was that it enabled him to display his pale ventral surface to the female more often. When Australasian harriers soared in display their wings were raised high and bent slightly back. Occasionally the male stooped close to the female. She in turn flipped over and thrust her tarsi at the male in a manoeuvre reminiscent of the aerial food pass seen later in the breeding season (Section C.iv). When the male stooped at the female during chasing flights she also thrust her tarsi at him. Chasing flights usually lasted about 30 seconds. The male flew slightly higher as he chased the female. Soaring and chasing by pairs was most often seen late on warm sunny mornings when thermal production would have been highest.

Soaring frequently preceded display diving. In July the first shallow undulating display flights were performed by the male and the male's courtship call was heard. These rapidly progressed into the spectacular diving display which was performed by both sexes but most frequently by the male. The diving display consisted of a series of U shaped dives at heights varying from 50 - 200 m above the ground. The displaying bird flew with deep exaggerated wing beats reminiscent of the flight of a spur-winged plover (*Lobibyx novaehollandiae*). It dived steeply for about 25 m and then climbed out of the dive and performed a full or half roll like a wing-nut on a bolt as Breckenridge (1935) described for *Circus cyaneus*. At this point the bird usually gave the courtship call. If the female was soaring with the male prior to his diving display she either descended slowly with her wings held high and landed in the swamp vegetation or left the area and began hunting. If the female landed the male continued diving and eventually alighted beside her. On the two occasions I observed when the birds did not land out of sight in the tall vegetation the male alighted for about 30 seconds and then left the area and began hunting. Soaring, calling and display diving probably does not have a territorial function as well as a pair formation function because a third bird was seen to join a soaring pair on seven occasions. No overt aggression was shown towards the intruder. Sharland (1932) described numerous Australasian harriers display diving over the same swamp. Stead (1932) described similar courtship behaviour to that which I observed.

C.ii Courtship feeding

Courtship feeding took place on the "cock nest" built by the male. The male flew to the "cock nest" with prey, raised his wings high to expose the pale ventral surface and underwing barring and gave the courtship call. The female, which was usually perched on a cabbage tree nearby, then flew to the "cock nest" and took the prey. As the female landed the male left and perched nearby. The female fed at the "cock nest".

Courtship feeding was frequently observed and probably took place daily from mid-September until incubation began about the end of October. Because courtship feeding was a regular occurrence this behaviour may have had an important function in terms of higher egg production. If the

primary function of courtship feeding is to promote production of young, then Royama's (1966) term "production feeding" may be a more appropriate description of the behaviour. Witherby *et al.* (1943) described a similar sequence of events during courtship feeding by the marsh harrier. They stated that courtship feeding at a "cock nest" took place with absolute regularity until the last egg was laid.

C.iii Copulation

I observed copulation on three occasions, but none of them took place at "cock nests" where Witherby *et al.* (1943) assumed marsh harriers copulated. All copulations took place in October. On two occasions the female was soaring high over the territory when the male caught a frog in a farm drain. The female began a diving display descent and landed about 2 m from the male. The male flew 20 m away with the frog and continued feeding. The female's soliciting call was heard as she once again flew to the male. This time the male left the frog and flew about 3 m away. He stood side on to the female with his wings raised. The female was in a crouched posture facing the male and the soliciting call was again given as she pecked at the frog. The male then flew and alighted on her back. Copulation was completed in a few seconds as the male flapped to maintain his balance. The male then flew about 30 m away and began preening. The female completed her meal and then bathed in the farm drain. The average time taken from the beginning of the female's descent to the completion of copulation on the two occasions was four minutes. The third copulation observed was essentially the same except the male flew into the territory and presented the female with a small prey item before copulation.

C.iv Incubation and the aerial food pass

From Soper's (1958) data incubation begins about ten weeks before fledging takes place. From the fledging dates I recorded (Section E.iii) most birds started incubating eggs at Pukepuke Lagoon around the beginning of November. Male Australasian harriers were not seen to land at the nest once incubation began. This is in contrast to several records cited by Witherby *et al.* (1943) of male marsh harriers, the Australasian harriers' conspecific, being flushed from eggs.

Once incubation began the aerial food pass was the only observed mode of transfer of prey from male to female. Small prey about the size of a mouse (*Mus musculus*) were transferred about three times a day. Although aerial food passes varied they commonly consisted of the male flying slightly above and ahead of the female and then dropping the prey 2 m or so to her. The female flipped over to catch the prey with one or both of her feet. On three occasions I observed passes made from talon to talon. After the pass the female flew to eat the prey at a plucking station, a regularly used area of dry ground about 30 m from the nest. Once the prey was consumed, the female returned to the nest; often with nest material. Occasionally she made a brief flight before returning to incubate.

After delivering the prey the male frequently perched on a cabbage tree or prominent knoll about 100 m from the nest site for periods of up to 30 minutes. He then left to continue hunting. On six occasions when males were seen to return without prey and perch in the territory the female left the nest and stooped at the male. This forced him to leave the area and begin hunting. Females involved in polygynous relationships stooped at their mates more often, presumably because they received less food from their mates and were therefore more often hungry.

C.v Polygyny

I observed one case of polygyny in each of the two breeding seasons. Three of the four females and both of the males involved were individually marked. One male had two territories. The distance between nest sites was 1.3 km. The second male had one territory and the nest sites were 350 m apart. In the latter case the females both defended a territory within the male's territory. One of these females began nest building about one month after the other and received less food from the male. The favoured female fledged two young while the less favoured female and both the other females that were involved in the polygynous relationship during the previous breeding season failed to fledge any young. This gave an average reproductive success of 0.5 young fledged per female involved in polygynous matings. This was not significantly ($\chi^2 = 0.95$) lower than the 1.2 young fledged per female (N = 15) involved in monogamous matings.

Four other males were seen to display dive when unmated adult females entered their territories. These males all had mates that were incubating eggs. This indicates that males would probably form polygynous relationships readily if females co-operated. Females involved in polygynous relationships were also seen display diving on two occasions when adult males intruded on their territories.

Polygyny has been recorded for the marsh harrier (Hosking 1943, Axell 1964), hen harrier and marsh hawk (Yocom 1944, Hecht 1951, Balfour 1957, Hamerstrom 1969) and Montagu's harrier (Dent 1939).

Orians' (1969) theory on the evolution of mating systems predicted that a species would be likely to exhibit polygyny if it nested in marshes and early successional habitats and had widespread feeding areas but restricted nest sites. The Australasian harrier fits this model well. His model also predicted that there should be a positive correlation between average reproductive success per female and the number of females mated with a given male, since females are assumed to enter polygynous matings only when it is advantageous for them to do so. My data does not support this prediction, but Brown (1976) cited evidence that showed bigamous marsh harriers had higher nesting success than monogamous pairs. Furthermore, a male hen harrier can support four females and their broods satisfactorily; breeding success in such territories being higher than those where there were two or three females (Brown 1976).

For polygyny to occur an uneven sex ratio is not required (Orians 1969, Newton 1976). I found no evidence of an uneven sex ratio in the Australasian harrier population. I trapped approximately equal numbers of juvenile males and females (Table 2.1). Although more adult females were trapped than males this was probably due to greater mobility of the females during winter and spring when several previously untrapped females passed through the area (see Chapter 4). This contention is supported by the data in Table 2.1 which shows that approximately equal numbers of adult males and females were retrapped and sighted after ringing and individual marking.

D. NESTS

D.i Nest inspection and nest building

Nest inspection behaviour in September involved the pair flying low over the territory and while one bird landed the other continued to soar at a low altitude. The roles were then reversed. When landed the male

frequently gave the nest inspection call,

In mid-September males were seen carrying nest material. I found three unlined platforms or "cock nests" that had been built by males within 50 m of the sites where the female later built a nest.

Females began nest building in late September and early October. Nests took about four weeks to complete. Stead (1932) stated two weeks and Haddon (1969) four to six weeks as the time taken from the start of nest building to the laying of the first egg. Nest building was carried out in an unobtrusive manner as the female flew low for short distances from the nest site to gather nest material. Nest material was carried in either the beak or talons.

D.ii Nest parameters

Of the 19 nests built in the study area during the two breeding seasons, 11 were in dune hollow swamps that had been fenced to keep domestic stock out and eight were in raupo swamp. All were between 3 and 8 m above sea level.

Ten nests were examined after the young had fledged. The oval nests commonly consisted of a sturdy base of lupin, thistle, toe toe and flax stems with cabbage tree leaves, marram and other grasses forming a lining. The ten nests averaged 80 x 50 cm with the base of the cup 40 cm above ground or water level.

All seven nests that I examined in dune hollow vegetation were built on red rushes with a toe toe growing beside and to the west of the nest. The three nests examined in raupo were built on sedges (*Carex* sp.). All ten nests were surrounded by tall vegetation on three sides with an opening to the east. Thus they were protected from the potentially strong rain-bearing westerly winds. Mosher and White (1976) and Balgooyen (1976) also recorded that raptor nest aspects were influenced by prevailing weather conditions.

D.iii Conservatism and traditionalism in nesting habitat

The Australasian harrier was conservative in its choice of nesting habitat because only two (dune and raupo swampland) of the six major habitats (Figure 2.2) were nested in. The birds also exercised considerable traditionalism, for of the ten individually marked adults

that returned to Pukepuke Lagoon, nine nested in the same habitat as the previous season. One female changed from raupo to dune swamp. Only one nest was reused during the second breeding season. Although I did not investigate all nests I was able to ascertain from map records that all nine other nests were built at least 50 m from the nest of the previous season. Similarly Fox (1977) recorded a high degree of nest site conservatism and traditionalism for the New Zealand falcon (*Falco novaeseelandiae*).

E. HATCHING TO DISPERSAL

E.i Post-hatching behaviour

A change in the female's behaviour in early December indicated that hatching had occurred. She no longer took prey to the plucking station but returned to the nest with the prey immediately after an aerial pass. When the nestlings were about one week old the female began to spend long periods perched about 20 m from the nest. When it rained she returned to the nest to cover the young.

The male's behaviour also changed. He no longer perched in the territory after passing prey to the female but usually left the area and continued hunting. At the most closely observed nest, from which two young were fledged, the frequency with which the male returned with prey increased from an average of 3.2 prey items per 14 hour day during incubation, to 6.6 prey items per day after hatching took place.

From about the time nest inspection behaviour was first observed until at least two weeks after hatching took place, a period of about 12 weeks, all females observed generally remained within the pairs' territory. When not incubating they were frequently seen perched on prominent cabbage trees for periods of up to an hour or soaring over their territories. The males were away hunting for most of this time. Two weeks after hatching occurred a male was seen to land at a nest with prey for the first time. On this occasion and for the next few days the female closely pursued the male giving the soliciting call but he did not pass the prey to her. This action may have precipitated the female's renewed interest in hunting as her hunger forced her to hunt for herself and secondarily the nestlings. I saw males land at, or very near, four of the five successful nests during the 1976-77 breeding season, but only

after the nestlings were at least two weeks old. Most visits to the nest site by males were for less than 30 seconds, but one male stayed at the nest for up to three minutes on several occasions. Soper (1958) stated that he never saw a male alight at any of the 15 nests he observed for varying periods of time.

Where three, two or one young were fledged from a nest the female began hunting as regularly as the male when the young were about two, four and six weeks old respectively. I weighed three nestlings (2 females and 1 male; 2 weeks old) at one nest site and two nestlings (1 female and 1 male; 4 weeks old) at another when the females began hunting regularly. The average summer weights of an adult male and an adult female (Table 2.4) were added to the combined weight of the nestlings from each nest site. At the time the female began hunting regularly the combined weight of the families that fledged three and two young were 2,705 g and 2,475 g respectively. Six weeks after hatching took place and regular hunting by the female began, the combined weight of a family that fledged one female nestling would have been about 2,265 g. This figure is calculated from Redhead's (1968a) data on the growth of a nestling Australasian harrier and from Table 2.4. The mean weight of all families when the female began regular hunting was 2,480 g. Thus a combined family weight of about 2,480 g was the most a male Australasian harrier was able to support at Pukepuke Lagoon during the 1976-77 breeding season when unaided by the female.

Soper (1958) stated that the female was away from the nest for the greater part of the day once the nestlings were about five days old. If not hunting she was perched near the nest for hours at a stretch. I observed similar behaviour but did not classify very brief hunting trips, soaring over the territory and perching for hours at a stretch as regular hunting.

E.ii Nesting success

I was confident that I accounted for all the pairs, whether successful or unsuccessful at fledging young from the study area, during both breeding seasons. No young were fledged from four of the nine nests in the 1976-77 breeding season. Nine young were fledged from five nests giving an average fledging success rate of 1.8 young per successful nest or 1.0 young per nest site. Eleven young were fledged from six of the ten nest sites the following year giving the same (1.8) average fledging success

rate for successful pairs and 1.1 young fledged per nest site. Again four pairs failed to fledge any young.

Breeding success was high among those adults that returned. Of the ten adults that returned, six (60%) had successfully fledged young the previous breeding season but nine (90%) were successful in the second breeding season they were observed in the study area. Only five (50%) of the ten new birds in the study area fledged young during the 1977-78 breeding season. New arrivals were significantly less successful ($\chi^2 = 6.67, P < 0.01$).

There are no data on fledging success of the Australasian harrier with which to compare my data. Brown (1976) stated that the average number of young fledged by marsh harriers in Britain has been recorded as 2.3 from all nests and 3.0 from 57 successful nests. Marsh harriers nesting in Europe were similarly successful. However in the Camargue, which is ideal marsh harrier habitat, breeding success was much lower with 1.5 young reared per successful nest and 0.8 per pair, although clutch size was no different. In the Camargue there was a capacity population present including a very large proportion (70%) of non-breeding subadults and immatures (Brown 1976).

The high Australasian harrier population density at Pukepuke Lagoon (1 bird/50 ha) probably influenced fledging success. I have mentioned how territorial evictions of intruders occurred about three times a day border patrols between rival males occurred as frequently as 18 times in an afternoon. These would represent an important incursion into the available hunting time; particularly as most of these activities were carried out by the male.

The high population density may have also resulted in decreased food availability and this may have decreased overall breeding success. Balfour (1957) found that the average number of young hen harriers fledged decreased as adult population density increased. He attributed this decline to either a decline in food availability or an increase in polygamous relationships.

Like many raptors the Australasian harrier lays its eggs at irregular intervals, though usually on alternate days (Soper 1958). Hence there is usually a considerable size difference between the oldest and youngest nestling and it is not unusual for the youngest of a brood of harriers to

die and be eaten by its siblings in times of food shortage (Redhead 1969, Balfour and MacDonald 1970, Watson 1977).

Disturbance from other Australasian harriers probably caused at least two pairs to abandon their territories. In both breeding seasons pairs established territories in the same area as the communal roost (Figure 3.1 and Chapter 4) which was used throughout the year. These pairs were unable to evict the birds that came to the roost in the evening although the males spent about an hour each evening trying to do so.

The 1976-77 breeding season was unusually wet (N.Z.D.S.I.R. meteorological records). At first I thought rain may have increased nestling mortality and decreased overall fledging success as Australasian harriers were not observed hunting during continuous rain. Rain may also have chilled the nestlings if they were inadequately covered by the female. However the 1977-78 breeding season was unusually dry and the same average fledging success rate was obtained as in the previous breeding season.

High pesticide levels have been recorded in Australasian harriers (Lock and Solly 1976), but they were probably not a major factor affecting breeding success at Pukepuke Lagoon. Only six (16.7%) of the 36 adults failed to successfully fledge young in one of the two breeding seasons. Of these, one pair established a territory in the communal roost site and another pair abandoned their nest when a large area of raupo was cut from around it. The two other birds were individually marked females that did not return but whose former mates successfully fledged young the following breeding season. High pesticide levels probably stop harriers from breeding rather than reduce the number of young fledged per pair, for Hamerstrom (1969) found that the number of nests built by marsh hawks in her North American study area decreased by 87% when pesticide levels in the population were high.

I therefore believe that the most probable cause of the low breeding success at Pukepuke Lagoon was the high population density. This resulted in frequent territorial interactions and may have decreased food availability.

E.iii Sex ratio

There were six females and three males fledged during the 1976-77 breeding season giving a two to one sex ratio in favour of females.

Fledglings were not trapped during the 1977-78 breeding season. Balgooyen (1976), quoting several authors, stated that there was evidence both for and against an unbalanced sex ratio favouring females in raptors generally. However, if data are collected over several years, sex ratio imbalances may even out for Scharf and Balfour (1971) found that 18 male and 30 female hen harriers were fledged from nest sites in their study area in 1967, but 24 males and 14 females were fledged in 1968.

E.iv Fledging

Australasian harriers fledge about six weeks after hatching (Soper 1958). The mean fledging dates I recorded were 13 and 18 January (Range = 1 - 27 January). For the first week after the fledglings left the nest they remained within their parents' territory and perched close together on prominent bushes. Males were more precocious and accomplished most activities such as leaving the nest site and making their first flight outside the territory about a day before their larger sisters. One week after fledging, the young flew strongly after their parents and gave the soliciting call. The adults usually dropped prey and the fledglings all dived to catch it before it hit the ground. The first fledgling to sight the adult returning to the territory usually secured the food item.

After the young fledged two adult males were seen less often over their territories but continued to hunt in their home ranges. In these cases the females continued feeding the fledglings alone. At all other successful nests both parents fed the fledglings at about the same rate until about three weeks after fledging. At this time females were seen up to 2.5 km from the nest site on five occasions whereas prior to their young fledging they were not observed more than 1 km from the nest site.

Four weeks after fledging, individually marked fledglings were seen 2 km from the territory but they returned to roost near the nest site in the evenings. During this period they were seen to make their first successful captures of insect prey and were not seen to be fed by their parents although I could not be sure this did not occur.

There was a general dispersal of the young away from the study area about six weeks after they fledged. This took place in February and early March. Most of the adults that had successfully fledged young left the study area in March. Their departure was preceded by that of the

unsuccessful adult females which left in December and early January. The adult males that had failed to fledge young left with the successful adults in March. Presumably the unsuccessful adult females were not as familiar with the pair's home range as the males, and when they no longer received food from the male they left in search of areas where food was more readily available.

I do not think any birds were fed by their parents after they left the study area because the adults left about a week after the young birds. Furthermore, none of the numerous juveniles that passed through the study area in the ensuing weeks were seen flying near adults or soliciting prey from them.

F. CALENDAR OF EVENTS

May. The adults began to return to Pukepuke Lagoon and the first aggressive chasing and evictions of intruders from incipient territories was observed.

June. Courtship soaring and chasing by pairs took place over their incipient territories.

July. Territory display flights by rival males and courtship diving displays were seen for the first time.

August. The female spent about half the day perched or soaring over the pair's territory. A few evictions of intruding birds of the same sex took place.

September. The female spent most of the day in the pair's territory. Nest inspection behaviour and nest building occurred. Courtship feeding at "cock nests" took place, probably once or twice daily.

October. Copulation was observed on three occasions. The eviction rate increased markedly. Intruders were evicted regardless of their sex. Some females began incubating eggs at the end of the month.

November. Most females were incubating eggs. Food was transferred from the male to the female by an aerial pass.

December. Most young hatched early in the month. Females began hunting two or more weeks after their young hatched and some males landed at the nest with prey after this time. Those females that had failed to hatch young left the study area at about the end of the month.

January. All young were fledged. Fledglings made their first flights outside the territory.

February. The young ranged widely but returned to roost near the nest site in the evening. Most young dispersed from the area at the end of the month.

March. The adults also dispersed. Numerous unmarked juveniles and a few unmarked adults passed through the area.

April. Unmarked birds continued to pass through the study area.

CHAPTER FOUR

THE NON-BREEDING BIOLOGY OF THE AUSTRALASIAN HARRIER

INTRODUCTION

"What little is known of raptors in winter suggests that their dispersion and density are no less related to food supply than while breeding. Nesting sites are irrelevant and roosting sites are likely to be important only in open country, devoid of trees and crags. Harriers are unusual in roosting on the ground." (Newton 1976).

The non-breeding biology of the Australasian harrier is also largely unstudied. In this chapter data are presented and discussed on dispersion, density, home range size and communal roosting.

A. THE DISPERSAL PHASE AND SEASONAL MOVEMENTS

I observed that all individually marked juveniles and all except one adult dispersed from Pukepuke Lagoon in February and March 1977 and were not sighted or retrapped in the area for three months. One individually marked adult male was seen once in April 1977. Most of the adults began to return in mid-May as related in Chapter 3. A similar dispersion from the area was recorded in February 1978. Hugh Robertson (*pers comm*) informed me that two individually marked adult males were observed at Pukepuke Lagoon during March and April 1978.

Table 4.1 is a summary of the movements of birds as recorded from ringing, retrapping and sightings. The number of birds that were ringed each season are classified according to whether they: (i) became permanent residents, (ii) were resident in the area for at least one month and then left, (iii) were trapped and then after periods varying from one week to a month left the area and then returned after an absence of at least three months but did not become permanent residents, and (iv) were trapped once only and were not seen again. Australasian harriers were considered permanent residents if they were seen and/or retrapped regularly for nine months.

All the adult males that were trapped but were not permanent residents passed through the study area during the autumn and early

Table 4.1: Australasian harriers ringed per season and subsequent movements

Season	Adult male				Juvenile male				Adult female				Juvenile female																
	Number ringed	Percent ringed	Number ringed	Percent ringed	Number ringed	Percent ringed	Number ringed	Percent ringed	Number ringed	Percent ringed	Number ringed	Percent ringed	Number ringed	Percent ringed	Number ringed	Percent ringed													
Summer	2	100	0	0	0	0	3	25	5	41.7	4	33.3	2	40	1	20	0	0	2	40	0	0	5	27.8	4	22.2	9	50	
Autumn	0	0	0	0	1	2.9	4	11.8	1	2.9	28	82.3	0	0	0	0	0	0	6	100	2	5.5	7	19.4	1	2.8	26	72.2	
Winter	6	54.5	1	9.1	3	12	10	40	5	20	7	28	2	16.7	1	8.3	2	16.7	7	58.3	3	1	5.5	3	16.7	2	11.1	12	66.7
Spring	2	100	0	0	1	10	6	60	2	20	1	10	4	36.4	0	0	1	9.1	6	54.5	0	0	0	0	1	16.7	5	83.3	
Total	10	52.6	1	5.3	5	6.2	23	28.4	13	16	40	49.4	8	23.5	2	5.9	3	8.8	21	61.8	3	3.8	15	19.2	8	10.3	52	66.7	

winter dispersal phase. One was trapped on 28/4/77 and killed by a car 35 km north of Pukepuke Lagoon at Turakina on 18/5/77 (Table 4.2). I do not know how far the birds usually travelled during the dispersal phase. An indication of the possible distances travelled is given in the data of Watson (1954) who trapped an adult bird (unsexed) on 4/4/52. This bird was killed on 10/5/52 near Lake Waitaki, Otago, 740 km south-west of his Hawkes Bay trapping station. Adult males that were permanent residents at Pukepuke Lagoon were all trapped during late winter, spring and summer.

Few juvenile males were permanent residents, but about half of those trapped other than during the dispersal phase were observed hunting established home ranges for at least a month. A much higher percentage (40.4% v 11.8%) of juvenile males trapped in these three seasons returned to hunt their former home ranges after an absence of three months or more. The ringing returns show that three others returned to establish home ranges in the sand country less than 5 km from Pukepuke Lagoon (Table 4.2). Most juvenile males (82.2%) that passed through the study area during the dispersal phase were not seen again. Those that did establish home ranges during this period probably did so because there were very few adults present to compete with.

Although juvenile males were more sedentary after the dispersal phase, some birds continued to disperse widely in late winter, spring and summer. For example a bird ringed on 24/9/76 was resighted twice in October and was then killed by a car 85 km south-east of Pukepuke Lagoon near Masterton on 4/12/76 (Table 4.2). Another bird ringed as a nestling on 21/12/76 left during the dispersal phase, was retrapped on 29/7/77 and then sighted on 18/8/77 250 km south-west at Taylor's Pass, Marlborough (Table 4.3).

The timing of the juvenile females' dispersal phase was similar to that of the juvenile males. However a greater percentage of females were trapped once only and were not seen again. This greater mobility of the females was most evident during late winter and spring when they were possibly searching for a mate. I recorded one female breeding successfully when less than one year old whereas males were not recorded breeding successfully until after their second winter (Chapter 3).

Table 4.2: Ringing returns

Ring number	Sex and age	Date ringed	Retraps and sightings	Date deceased	Location	Cause of death	Distance
L-15277	Juvenile male	31/7/76	(26/8/76-2/12/76) x 10	23/3/77	Pukepuke Lagoon	Unknown	0 km
L-15289	Juvenile male	19/8/76	(27/8/76-14/10/76) x 6	25/10/76	Pukepuke Lagoon	Hit power lines	0 km
L-14406	Juvenile male	24/9/76	20/10/76, 28/10/76	4/12/76	Masterton	Killed by car	85 km
L-16585	Juvenile male	4/11/76		15/2/78	Oroua Downs	Caught in fence	5 km
L-17034	Juvenile male	25/2/77		31/8/77	Pukepuke Lagoon	Unknown	0 km
L-17048	Juvenile male	23/3/77		17/6/77	Lake Kaikokopu	Shot	5 km
L-11806	Juvenile male	30/3/77	(6/4/77-26/7/77) x 11	27/7/77	Pukepuke Lagoon	Unknown	0 km
L-17913	Juvenile male	2/6/77	31/7/77	2/2/78	Oroua Downs	Killed by car	5 km
L-17948	Juvenile male	29/7/77	31/7/77	20/2/78	Pukepuke Lagoon	Unknown	0 km
L-15189	Juvenile female	19/11/76		8/8/77	Rongotea	Shot	15 km
L-17016	Juvenile female	13/1/77		27/1/77	Pukepuke Lagoon	Drowned	0 km
L-11848	Juvenile female	26/5/77		19/11/77	Bulls	Shot	20 km
L-11826	Adult male	28/4/77	2/5/77	18/5/77	Turakina	Killed by car	35 km

Included in those juveniles, of both sexes, that returned after an absence of three months or longer were four of the nine birds that were fledged from the study area during the 1976-77 breeding season.

Like adult males, adult females were clearly divided into two major groups: those that were permanent residents and those that were trapped only once. All birds trapped during the general dispersal phase were not seen again. However, unlike adult males, a large proportion (56.5%) of the adult females trapped in late winter and spring were trapped once only. I assumed that like juvenile females, these were birds that were searching for a mate with a suitable territory but did not find one at Pukepuke Lagoon. An individually marked adult female that bred successfully in the 1976-77 breeding season was observed on numerous occasions during the winter of 1977 by R. Honeyfield on his farm 95 km north-west of Pukepuke Lagoon near Patea (Table 4.3). This bird did not return until early November and by then its mate of the previous season had already mated with another bird. The adult female that returned late entered into a polygynous relationship with these birds but received less food from the male and was the only adult that returned and failed to fledge any young.

Discussion

Although the Australasian harrier regularly migrates from Tasmania to the Australian mainland in February and returns in July and August (Sharland 1958, Hobbs 1959), it has not been recognised that all sex and age classes regularly disperse at about the same time in New Zealand. Several authors (Fleming 1939, Hindwood 1940, Gwynn 1953) noted that the Australasian harrier regularly visits islands up to 1,050 km from the New Zealand mainland. Oliver (1955) stated that it left New Zealand for the Kermadecs, 950 km distant from North Cape, at about the end of March and returned in September. Watson (1954) conducted a ringing study in Hawkes Bay and concluded that although juveniles moved about in autumn and early winter, adults remained within 8 km of the trapping area.

In summary, my results show that all sex and age classes dispersed from the trapping area during autumn and early winter and that other birds passed through the area. Most of the adults that were permanent residents returned after the dispersal phase. For several females the dispersal phase continued through winter and into spring. Juveniles were not

Table 4.3: Distant sightings of wing-tagged Australasian harriers

Sex and age	Date sighted	Location	Distance	Observer
Juvenile male	24/3/77	Foxton	10 km	P. Barber
Juvenile female	24/7/77	Foxton	10 km	L. Davies
Juvenile male	24/7/77	Foxton	10 km	L. Davies
Juvenile female	31/7/77	Foxton	10 km	H. Robertson
Juvenile female	31/7/77	Foxton	10 km	M. Dennison
Adult female	2/8/77	Patea	95 km	R. Honeyfield
Juvenile male	18/8/77	Taylor's Pass Marlborough	250 km	W. Brown
Juvenile male	16/11/77	Kowhai River Kaikoura	225 km	P. Moors
Juvenile male	27/11/77	Sanson	15 km	S. Lawrence
Juvenile female	3/12/77	Manakau	40 km	A. Walters
Juvenile male	3/2/78	Lake Grassmere	150 km	H. Robertson and M. Dennison

Table 4.5: Communal roost data

Month	Number of watches	Average number of birds/watch	Average roosting time	Average departure time
January	7	4.0	19.46	
February	4	0.7	19.45	6.17
March	9	1.4	18.25	6.54
April	11	1.4	17.54	7.04
May	7	2.0	17.25	7.26
June	17	4.4	17.16	7.16
July	17	6.3	17.28	7.06
August	4	10.0	17.50	7.00
September	6	5.2	18.29	6.10
October	11	6.4	18.51	5.33
November	12	8.1	19.23	5.03
December	5	3.5	19.45	4.46

usually permanent residents but those that established home ranges in the study area after the dispersal phase were likely to return after an absence of three or more months.

B. HOME RANGE SIZE AND POPULATION DENSITY

B.i Home range size

From trapping data and observations of individually marked birds during autumn and winter I estimated the home range of individual Australasian harriers in the sand country to be about 9 km². This was the same size as the home ranges of pairs during the breeding season.

The Wildlife Service kindly allowed me to use the radio-telemetry equipment at Pukepuke Lagoon to record home range size more accurately. On 26/6/77 a transmitter was placed on an adult female that had previously been trapped nine times and was frequently observed in the study area.

The receiver used had digital channel selection (100 channels) and was powered by a 12 volt dry cell. The channel had an average current drain of 0.16mA, which gave it a life of approximately 190 days from the battery source (2.8 v lithium cell). The lithium cells, weighed 9.5 g and had a nominal capacity of 750mA hours. They were 16.8 mm in diameter and 22.5 mm long. The transmitter operated at 160.36 MHz and had a line of sight range of at least 3 km. Total weight of the transmitter package (including harness) was 25 g. The transmitter had a flexible whip antenna about 20 cm long. I had available a hand-held two element yagi aerial, a motorbike mounted two element yagi and two huts with seven element yagis.

As soon as I released the Australasian harrier, with the transmitter attached, it flew approximately 4 km south-east and established a new home range in open farmland interspersed with pine plantations. From two weeks of intermittent contact I calculated the bird's home range to be 14 km². This was 35.7% larger than my field observations of individually marked birds had indicated but the adult female had moved into open farmland where the habitats available for hunting were not as suitable as those near Pukepuke Lagoon. Had the adult female remained at Pukepuke Lagoon its home range may have been similar to the 9 km² I calculated from field observations of other birds.

B.ii Population density

During the non-breeding season it was not unusual to trap as many as eight birds in one day. From trapping data, and field observations I calculated there were about 15 birds in the 12 km² study area or one bird per 80 ha. This represented a 37.5% decline in population density from that which existed during the breeding season. The road counts I made showed that most of the birds probably dispersed into more intensively farmed areas further inland. I travelled through 30 km of open farmland between Pukepuke Lagoon and Palmerston North each week and made 15 counts of Australasian harriers per season. There was a marked increase in the average number of birds recorded per trip during autumn and winter (Table 4.4).

Table 4.4: Average number of Australasian harriers counted per trip per season

Summer	Autumn	Winter	Spring
1.0	4.2	5.6	1.2

During the non-breeding season birds were not restricted to a limited area by a fixed nest site and would have been able to disperse inland and use the carrion there. Carrion formed an increasing proportion of the diet during autumn and winter (Table 5.7).

C. COMMUNAL ROOSTING

C.i Description of the roost

I made 94 evening and 16 morning observations of the communal roost at Pukepuke Lagoon (Figure 3.1). The roost, which was used throughout the year, was in swamp habitat which is a typical roost site (Gurr 1968), although Hedley (1976) observed a roost in a hay paddock near a large swamp. The Australasian harriers roosted in an area of about 4 hectares where the dominant vegetation was raupo, flax and cabbage trees. All birds perched on raupo that had been blown down to form a mat about 2m square and 20 cm above the water. This site was surrounded by 2 m high raupo and flax which sheltered the birds from the wind.

From observations of birds settling, it was clear that several birds often roosted in close proximity, though a few were sometimes widely

dispersed. Probably only one bird occupied each roost site because there was usually only one small area where down feathers, faeces and pellets were found. Gurr (1968) made a similar observation. No roosts showed signs of long continuous occupation since most contained only one pellet. A few had two, three or four pellets.

C.ii Arrival at the roost

All birds flew to the roost with a strong, direct, purposeful flight as reported by Stead (1932) and Gurr (1968). They usually arrived singly. The earliest an Australasian harrier arrived to soar over the roost was 72 minutes before the last bird landed in the roost when it was almost dark. On average the first bird arrived over the roost 31 minutes before the last bird landed, and the first bird landed 16 minutes before the last.

I took photometer readings near the roosting area. Light intensities were recorded in candles per square foot and multiplied by 43 to convert the readings to lux. Most birds arrived when the light was fading (774 lux) and landed about 15 minutes later (430 lux), about five minutes before it was dark. On three occasions birds probably landed when it was too dark to see them because extra birds were counted leaving the roost the next morning.

The average light intensities when the birds landed in summer, autumn, winter and spring were 537, 387, 365 and 408 lux respectively. These differences are not great for in the evening the light intensity faded from 537 to 365 lux in about 10 minutes.

On arrival 63% (260) of the birds soared and circled over the roost for several minutes and then either left the area or landed in the roost, 25% (104) landed in the roost without any preliminary soaring or perching and 12% (50) perched on posts or in open farmland just outside the roost. These results do not concur with those of Gurr (1968) and Hedley (1976) who claimed that almost all early arrivals settled outside the roost for several minutes. There was frequently a strong breeze blowing in the evening at Pukepuke Lagoon and this would have facilitated soaring. Perching outside the roost was most often seen on the few fine calm evenings, so perhaps differences in predominant weather conditions account for the different observations.

When soaring over the roost the birds flew at a height of about 20 m and often travelled in circles of about 100 m in diameter or soared and flapped the length of the swamp. Long gliding swoops were made over potential roosting sites. Over several minutes, the area soared over gradually decreased in size until the bird circled an area of about 20 m in diameter. Just prior to landing the birds flapped several times, glided 4-5 m and abruptly dropped from sight into the vegetation. As reported by Gurr (1968) and Hedley (1976), those birds that arrived at the roost near dark usually landed without any preliminary perching or soaring.

Rain precluded all soaring over the roost and as many as 11 birds were seen to land over a two minute interval just prior to the commencement of a heavy shower of rain. On windy nights birds occasionally settled in the roost and then flew up after a few minutes and landed at another site. Presumably the first site did not afford them sufficient protection.

C.iii Departure from the roost

Morning observations of Australasian harriers leaving the roost showed that 80% (36) left the area as soon as they rose from the roost and flew with a strong purposeful flight directly for distant hunting grounds. The other 20% (9) perched on posts just outside the roost for up to 20 minutes before departing. No birds soared over the roost before they left. The average light intensity (645 lux) was higher when the birds left the roost than when they landed in the evening. The average time between the first and last birds leaving the roost was 19 minutes. Heavy rain delayed the birds' departure one morning by about 30 minutes. Australasian harriers usually left the roost singly and frequently dropped their tarsi and defecated when they had flown about 100 m.

C.iv Seasonal interactions

During autumn and winter chasing for about 30 seconds and evictions of roosting birds were each seen on five occasions. In late winter the soliciting call was often voiced by a female perched outside the roost as other birds flew overhead. One evening in August 1976 I saw five birds perched for five minutes within 10 m of each other in open farmland. At least two of the birds gave the soliciting call several times before

the group disbanded. Display diving by adult males over the roost was observed on two spring evenings only.

Territory owners persistently tried to evict birds that arrived at the roost during spring as related in Chapter 3. However, territorial males were remarkably tolerant of each other when they roosted communally in summer; so much so that on a December evening six adult males soared together and then landed in an area about 10 m² and within two minutes of each other.

Although the amount of soaring over the roost at Pukepuke Lagoon was probably higher than that noted on Otago Peninsula by Gurr (1968), the number of birds and displays I recorded were considerably fewer. I observed a maximum of 20 birds whereas on one occasion there were more than 100 birds at the roost Gurr (1968) observed. The difference in the number of birds attending the roosts probably accounts for the behavioural differences recorded.

C.v Fluctuations in numbers at the roost

The number of birds attending the roost fluctuated markedly. It was therefore obvious that on a number of occasions most or all of the Australasian harriers in the study area roosted elsewhere. However the same individually marked birds were often seen at the roost for several nights in succession. On five evenings I saw one or two birds soar over the roost as the light began to fade. When no other birds arrived at the roost after about five minutes, these birds left and flapped steadily south for about 4 km in the direction of Lake Kaikokopu where I saw three birds roost together in July 1976. On several nights no birds landed at the roost. A maximum of 20 birds in August 1977 and an average of 4.2 birds from all observations was recorded. The roost was therefore much smaller than those described by Stead (1932), Middleditch (1949) and Gurr (1968), but similar in size to that observed by Hedley (1976).

More birds used the roost when winds were stronger than 15 km.p.h. The shelter provided by the tall swamp vegetation could be an attraction on such evenings. Windy conditions probably facilitated travel to the roost and certainly enhanced soaring over it.

Stead (1932) stated, "As soon as the nesting season is over harriers begin to collect on certain roosting grounds." The results of Gurr (1968)

and Hedley (1976) appear to support this statement. I found, however, that there was a marked decline in the number of birds at the roost after the adults dispersed from the area in late February and early March (Table 4.5). The birds that used the roost during autumn were a few unmarked adults that passed through the area and individually marked birds in their second autumn that briefly returned to Pukepuke Lagoon. Very few juveniles roosted communally during autumn. On two evenings in March 1977 the communal roost was not used even though there were an estimated 60 birds in the study area (see Chapter 5). Possibly these birds, nearly all of which were juveniles, did not roost communally because there were few adults present that they could observe travelling to the roost.

Only when the adults began to return in May did the number of adults and juveniles attending the roost begin to increase. The numbers reached a peak in late winter and early spring. During this period there was a noticeable segregation of the age groups using the roost. Adult males usually roosted together, approximately 300 m west of the juveniles. Adult females usually roosted between these two groups. The segregation was probably maintained by the adult males for on two occasions adult males evicted juvenile males from their area and pursued them until they were over the juveniles' roost site. Weiss (1923, cited by Watson and Dickson 1972) observed a similar segregation at communal roosts of Montagu's harriers.

In summer the roost was used by juveniles, and on windy nights by the individually marked adult males that held territories in the study area. Adult females did not roost communally during this season. They roosted at or near their nest sites.

From observations of individually marked birds I estimated that all the birds that used the roost hunted within about 4 km of the roost. Gurr (1968) estimated that some birds travelled up to 12 km to roost. However the Hooper's Inlet roost he observed was the only known roost on Otago Peninsula whereas there were several alternative sites in the sand country. Craighead and Craighead (1956) recorded marsh hawks flying 9 km from a communal roost to their hunting areas.

C.vi Reasons for the Australasian harrier roosting communally

Communal roosting by other harriers; hen, Montagu's, pallid, marsh, and long-winged (*Circus buffoni*), is well documented (Witherby *et al.* 1943, Weller *et al.* 1955, Bannerman 1956, Craighead and Craighead 1956, Meinertzhagen 1956, Jackson *et al.* 1972, Watson and Dickson 1972, Renssen 1973).

Although communal roosting is an adjunct to migration in some species of *Circus*, Gurr (1968) provided evidence demonstrating that this was not the case for the Australasian harrier. I found that some Australasian harriers roosted communally throughout the year so this is further evidence that communal roosting is not a preparation for dispersion or migration. For the same reason, communal roosts could not be viewed solely as places where normally solitary birds are able to meet mates.

Gurr (1968) contended that communal roosting by Australasian harriers has no protective function against predators for it is possible to approach within 2 m of a roosting bird at night before it will fly and then only the disturbed bird moves. However the waterlogged habitat and tall vegetation would afford the birds considerable protection from some predators, particularly mammalian predators.

Weller *et al.* (1955) and Gurr (1968) stated that communal roosting occurs when large numbers of harriers assemble in an area to take advantage of locally abundant prey. Gurr (1968) further suggested that because prey and Australasian harrier numbers were high throughout the year in New Zealand, there were sufficient birds present to elicit this response in many localities all year round. While large numbers of birds at a communal roost may be the result of large numbers gathered in an area, I do not believe that large numbers of Australasian harriers are required for, or cause, communal roosting. My results show that quite low numbers are capable of eliciting communal roosting throughout the year. When a large number of juveniles gathered at Pukepuke Lagoon to eat the rabbits shot by the Manawatu Pest Destruction Council there was no increase in numbers at the roost.

Ward and Zahavi (1973) viewed communal roosts as "information centres" for food finding. This would be most important for those birds that were inexperienced at utilising the food resources of a region. The crops of Australasian harriers that arrived at the roost well-fed, bulged noticeably. This could act as a cue to other birds that there

were good feeding areas in the region. However, only once did I see a bird follow another from the roost in the morning. Although Australasian harriers may use the communal roost as a staging point for food finding during their essentially nomadic existence in autumn and early winter, this does not explain why, in spring and summer, birds with established home ranges attended the roost or why adult males that held territories were observed at the roost on several evenings in these seasons. Further work noting the extent to which individually marked Australasian harrier's crops bulged when they arrived at the roost in the evening, the direction they came from, their behaviour at the roost, and the manner and direction in which they left the next morning could prove rewarding.

I think it is likely that communal roosting by the Australasian harrier has a primary social function and the roost may act as a centre providing information on the movements and density of a population and the resources of a region. The soaring over the roost on all except very wet evenings, displays and interactions, segregation of the age and sex classes during the breeding season, and assembly of most of the territory owning adult males at the roost on several evenings in spring and summer could be some of the ways in which this information is transmitted.

CHAPTER FIVE

THE DIET OF THE AUSTRALASIAN HARRIER AT PUKEPUKE LAGOON

INTRODUCTION

The initial aim of this section is to describe the prey and carrion eaten by Australasian harriers from Pukepuke Lagoon. The diet of Australasian harriers from a discrete area of the North Island has not previously been studied. Also, prior to this research, the influence of age and sex on diet has not been investigated. A secondary aim is for these diet data to provide the necessary information on which to base conclusions about hunting behaviour, predator-prey relationships and seasonal changes in activity of the Australasian harrier population.

The diet of Australasian harriers in New Zealand has also been recorded in four other qualitative studies. Carroll (1968) studied the food habits of 124 Australasian harriers collected over three years from a wide range of North and South Island localities. Redhead (1968b, 1969) made a similar study when he analysed the stomach contents of 129 Australasian harriers and 20 pellets collected from the south east of the South Island. In both these studies the age and sex of the corpses were recorded but these were not correlated with the food found therein. Douglas (1970) and Fox (1977), who collected pellets cast by Australasian harriers from eastern South Island hill country, analysed 99 and 18 pellets respectively.

I did not carry out feeding trials similar to those suggested by Lockie (1959) as being necessary for quantification of the diet. The data provided by a qualitative study were considered sufficient to satisfy the aims of this section. A similar approach has been adopted in most studies of harrier (*Circus* sp) diets. Two notable exceptions are the quantitative studies of Errington and Breckenridge (1936), and Schipper (1973). But even these concentrated on the breeding season when data on food habits can be readily obtained at nest sites.

I was unable, however, to use many of the techniques described in the literature for obtaining data on raptor diets because Australasian

harriers readily desert their nests at all stages of incubation and nestling development if disturbed (Stead 1932, Soper 1963).

METHODS

Between March 1976 and August 1977 a total of 344 pellets, (75 from the communal roost, 87 from nest sites, 182 from trapped birds) 120 prey remains, (from five nest sites) and the stomach contents of five male Australasian harriers were collected for analysis. During this time 64 successful attacks or instances of Australasian harriers feeding from carrion were also recorded and 65 road-killed animals were checked for sign of Australasian harriers having fed from them.

The results are presented as the frequency of occurrence of each food type in the total number of items identified. My analysis showed that a range of one to four prey species were to be found in pellets. However it is the prey within pellets and not the pellets alone that make up the Australasian harriers' diet. I therefore believe that the percent frequency of each food type with respect to the total number of items identified, rather than the total number of pellets, more accurately reflects the composition of the diet. The same method of presentation will be accurate where food items are monospecific as they were in prey remains, successful attacks and each instance of carrion use. The data from several sources can then be combined and a more comprehensible presentation derived. Schipper (1973) has demonstrated that such a combination is only permissible in a qualitative study.

Five analysis techniques were used in assessing the diet of Australasian harriers from Pukepuke Lagoon. In ascending order of importance to this study, they were: sign interpretation, stomach analysis, field observations, prey remains analysis and pellet analysis.

1. Sign interpretation: Numbers of road-killed carrion were checked for Australasian harrier feeding sign and recorded on 60 trips (fifteen, 30 km trips per season) between the Palmerston North city boundary and Pukepuke Lagoon. Small passerines were excluded from the counts because of the ease with which they could have been carried from the road by harriers.

By closely observing trap bait that Australasian harriers, black-backed gulls (*Larus dominicanus*), feral cats (*Felis cattus*) and ferrets

(*Mustela putorius furo*) had fed from I was able to distinguish Australasian harrier feeding sign. In general Australasian harriers were able to tear open the skin of a dead animal more readily than gulls. Having gained entry, usually via the flank or bottom lip of a mammal, they gleaned muscle tissue from bones rather than concentrating on soft tissues such as eyes and intestines as gulls were forced to do. Mammalian carnivores generally consumed small bones such as the ribs of lagomorph carrion while Australasian harriers left these intact.

Because the road kills I examined were outside my study area I have only used them as a reference source for comparing with seasonal observations of carrion use at Pukepuke Lagoon.

2. Stomach content analysis: The crop and stomach contents of five male Australasian harriers were analysed using the techniques described by Day (1966) and Redhead (1968a).

3. Field observations: Members of the New Zealand Wildlife Service and I noted successful attacks and instances of Australasian harriers feeding from carrion at Pukepuke Lagoon.

Incidental observations are often biased towards large and unusual prey and may be coloured by observer bias and hearsay. Mistaken prey identity may also be involved. For example, during this study I was informed by a trained observer that an adult female Australasian harrier had been seen to capture a live adult duck in shallow water. On checking I found that the prey was a 450 g carp (*Carassius* sp.).

4. Collection and identification of prey remains: I gathered most prey remains from five nest sites and their associated plucking stations, after fledging. Thus a bias in favour of prey taken during the latter half of the breeding season may exist. Two of the five nests were visited once to weigh the nestlings two weeks before fledging and I also collected prey remains then. Ten other collections were made from plucking stations near three other nest sites during incubation.

Computation of numbers of large prey found at nests such as rabbits (*Oryctolagus cuniculus*), hedgehogs (*Erinaceus europaeus*), ducks, pukekos (*Porphyrio melanotus*), was based on the number of individual skulls, legs or wings recovered. Adult and fledgling Passeriforme feathers were identified by comparing them with specimens from my reference collection. All specimens except the grey warbler

(*Gerygone igata*) and fantail (*Rhipidura fuliginosa*) were shot in the study area. I did not try to distinguish between the skylark (*Alauda arvensis*) and the New Zealand pipit (*Anthus novaeseelandiae*) in prey remains. I did not see any ciril buntings (*Emberiza cirilus*) during the study and therefore did not consider them when prey remains containing yellow passerine feathers were found. They are said to be uncommon in the Manawatu Sand Country (Falla 1957).

5. Pellet analysis: Australasian harrier pellets consist of the undigested residue of food from the stomach. Bone is readily dissolved by Australasian harrier digestive juices and the pellets consist largely of hair, feathers or chitinous insect parts. Vegetable matter is also often found in pellets. Balfour and MacDonald (1970), who observed hen harriers (*Circus cyaneus*) pulling shoots from bushes surrounding nest sites and swallowing them, suggest that vegetation may act as a digestive aid.

Misidentification of pellets was most unlikely because other raptors are uncommon in the Manawatu Sand Country (Falla 1957, Gill 1976). Australasian harrier pellets are also larger than those from the New Zealand falcon (*Falco novaeseelandiae*) (Fox 1977). Pellets cast by black-backed gulls in the nearby colony were smaller and differed in shape and texture from Australasian harrier pellets.

I soaked pellets in water overnight before analysing them and then teased them apart on a shallow white tray. Following macroscopic examination representative hairs or feathers, mounted in 70% alcohol, were examined microscopically. Failure to examine microscopically, every hair and feather from every pellet, probably resulted in a few omissions of prey present. Mounted hairs and feathers were identified using the key developed by Day (1966). His key identified mammalian hair to genus or species but feathers to family only. He did not separate hair and rabbit fur on microscopic structural differences. I examined 182 pellets known to contain fur from either hares or rabbits used as trap bait, and found pellets containing hare fur were markedly paler in colour. It was on this macroscopic characteristic that I distinguished the fur of these two lagomorphs in pellets. Because there is no key for differentiating microscopically between the feathers of different species of birds, those feathers I could not classify to species were grouped as unidentified Passeriformes or Anseriformes.

Another possible source of error includes stray hairs or feathers in pellets, for example down feathers from the lining of a nest clinging to eggs an Australasian harrier had eaten. Small insects such as ladybirds (*Coccinella* sp) were found only in pellets that also contained the remains of insectivorous birds, and therefore these insects were not recorded as occurring in the diet of the Australasian harrier.

I did not find evidence of nestling down in any pellets although remains of nestling and fledgling passerines were found at plucking stations and nest sites. I found these and other prey such as frogs and fish to be under-represented in pellets in relation to field observations. Brown (1976), in reference to this problem, has stated that prey such as frogs and fish are not readily found in pellets as they leave few indigestible remains.

A problem peculiar to this study was that most of the pellets from trapped birds contained fur from the lagomorphs used as bait. The percent frequency of occurrence of lagomorphs in the diet was therefore calculated only from communal roost and nest site pellets, prey remains, field observation and stomach analysis data.

The data of Glading *et al.* (1943) on food presented to captive hawks, including harriers (*Circus* sp), confirms that roughly, each species occurrence in a pellet corresponds to one prey item. I have followed their guideline in estimating numbers of prey in pellets unless numbers of identifiable parts indicated otherwise.

Bird prey counts. The number of terrestrial birds observed were recorded five times per season while I walked a 2.5 km transect which included approximately equal distances of open farmland, duneland, pines and raupo. The counts for raupo and pine habitats may have been less accurate than those for farmland and duneland due to increased cover concealing birds. This would have had little effect on seasonal trends however.

Prey and carrion in the diet. In the derivation of Table 5.7 all medium sized (75-200 g) and small (<75 g) birds, Australian green frogs (*Littoria aurea*), insects, mice (*Mus musculus*) and brown rats (*Rattus norvegicus*) were considered to be prey, while all sheep (*Ovis* sp), opossums (*Trichosurus vulpecula*) and prions (*Pachyptila* sp) were deemed

to be carrion. I found ten prions dead in the study area after a summer storm. The four prions in the summer diet were most likely found dead by Australasian harriers after this storm.

Opossums are generally nocturnal and are therefore not directly vulnerable to Australasian harrier predation. Sheep are too large to be considered prey although the occasional second-hand report of Australasian harriers attacking weak lambs has been recorded (Buller 1888, Oliver 1955).

All rabbits, hares (*Lepus europaeus*), hedgehogs, ducks, pheasants (*Phasianus colchicus*), pukekos and magpies (*Gymorhina tibicen*) in the diet were classified as of unknown origin. That is to say, I did not know whether they were prey or carrion unless I saw them taken as live prey or eaten as carrion.

Australasian harriers kill both adult and juvenile rabbits and hares (Buller 1888, Sharland 1932, Stead 1932, Douglas 1970) and I have also observed them eating lagomorph carrion.

I have placed hedgehogs in the unknown category for the following reasons: there are apparently few hedgehogs available as carrion during summer. This is deduced from Brockie's (1957) statement that there is evidence that most hedgehogs die during winter from diseases such as pneumonia or from drowning in their nests while hibernating. If the remains of 20 hedgehogs found at nest sites were not from animals that had died from natural causes then they were even less likely to have been road kills. This is because the home ranges of three pairs of Australasian harriers (18 hedgehogs at their nests) did not include any public roads, while secondary roads existed on the edges of the ranges of two other pairs (two hedgehogs). Skull measurements showed that 40% of these hedgehogs were juveniles; an age group that would have been more vulnerable to predation.

I have observed hedgehogs foraging during the day in all seasons except winter. I have also flushed an adult male Australasian harrier from beside two juvenile hedgehogs curled in defensive balls; so the activity rhythms of the two species coincide sometimes.

Although I was unable to find any evidence in the literature, other than hearsay, of Australasian harriers killing adult ducks, pheasants, pukekos or magpies I have seen Australasian harriers kill four month old

domestic hens (*Gallus domesticus*) weighing approximately the same as these species. This took place at Hunter's Poultry Farm where the hens had no cover they could escape into. However, even here, hens older than four months were generally immune from Australasian harrier predation.

I observed Australasian harriers flushing ducks, pheasants and pukekos on more than 60 occasions. In every case these birds either successfully defended themselves or evaded the Australasian harrier. However, Stead (1932) has stated that there can be no doubt that the presence of great numbers of Australasian harriers is one of the chief difficulties in the way of establishing game birds in open country. These large birds (>200 g) were therefore placed in the same unknown origin category as lagomorphs and hedgehogs.

Diet of the Australasian harrier ages and sexes. Field observations of feeding Australasian harriers of known age and sex provided one source of data for the analysis of the diet of the Australasian harrier ages and sexes while pellets from birds caught in cage traps provided the other. There were insufficient data collected from trapped birds for the analysis to be made in terms of adult male, adult female, juvenile male and juvenile female diet. Those pellets that could be classified in this way are recorded in Appendix A.12. There was often more than one bird in a cage trap. If for example one was an adult female and the other a juvenile female then a pellet cast in the trap could only be recorded as having come from a female Australasian harrier. Hence the data are classified in terms of adult, juvenile, male and female diet. All pellets from juveniles were from birds that were independent of their parents.

I hypothesised that the interacting variables of size, manoeuvrability, conspicuousness and experience of the four Australasian harrier age and sex classes were reflected in their diets. I therefore divided their respective diets according to the agility and size of the food items. Live prey were scaled with adult passerines being the most agile and insects the least agile. The relative proportions of live prey and carrion in the diet were also compared.

To investigate whether larger female Australasian harriers eat larger food items I compared the number of dietary items weighing more and less than 200 g. Because the remains of small food items were more

likely to have multiple occurrences in a single pellet than the remains of large food items were, the number of food items per pellet were also compared.

RESULTS

Field Observations. Of the 64 observations, 36 (56.3%) were of Australasian harriers taking identifiable prey and 28 (43.7%) were of them feeding from carrion. Four of these records were made by observers other than myself.

A summary of Table 5.1 shows that small birds (61.1%) were the most important prey. Seven (19.4%) of the prey were frogs, three (8.3%) were mammals, three were insects and one (2.7%) was a carp.

Adult males took 14 birds, five frogs, two juvenile rabbits and one mouse. Adult females captured seven birds, one frog and one carp. The difference between the prey taken by the sexes is not significant.

In Table 5.2, 17 (60.7%) large (>200 g) mammals, seven fish (25.0%) and four (14.3%) large birds were recorded as the carrion the Australasian harriers fed from. These results concur with the live prey and carrion classification I developed in Methods.

If the observations in Tables 5.1 and 5.2 are tested for seasonal differences in live prey and carrion use for later comparison with the pellet and prey remains data it is found that significantly more prey and fewer carrion items were eaten in spring and summer than in autumn and winter ($\chi^2 = 38.15$; $P < 0.001$).

Stomach analysis. Five male Australasian harriers collected during summer and autumn from Pukepuke Lagoon contained remains of two passerines, two opossums, one hedgehog and one brown rat. These results are recorded in Appendix A.11 and are included in Table 5.4.

Prey remains and pellet analysis. Of the 292 food items recorded in Table 5.3, 187 (64.0%) were identified in pellets and prey remains collected during summer from five nest sites and 105 (36.0%) were identified in 70 pellets collected from the communal roost during autumn, winter and spring.

Table 5.1: Successful attacks by Australasian harriers at Pukepuke Lagoon.

Prey	Date	Details
1. 1 Mallard duckling	22/9/76	Adult female caught duckling in reeds after hover and dive (W. Pengelly).
2. 1 Frog	24/9/76	Adult male - Hover at 3m. Farm swamp.
3. 1 Juvenile rabbit	2/10/76	Adult male → production feed adult female.
4. 1 Frog	14/10/76	Adult male - stooped from 3m to farm pond vegetation → fed to adult female.
5. 1 Frog	27/10/76	Adult male - hovered at 1m - stooped into drain vegetation - fed on post.
6. 1 Small bird	28/10/76	Adult male → adult female.
7. 1 Juvenile rabbit	17/11/76	Adult male → adult female.
8. 1 Bird pullus	17/11/76	Adult male → adult female.
9. 1 Small bird	18/11/76	Adult male → adult female.
10. 1 Bird pullus	18/11/76	Adult male → adult female.
11. 1 Fledgling) finch)	25/11/76	Adult female → nestlings.
12. 1 Fledgling) finch)		
		Same Brood
13. 1 Small bird	6/12/76	Adult male → adult female → nestlings.
14. 1 Fledgling) Hedgesparrow)	7/12/76	Adult male → adult female → nestlings.
15. 1 Fledgling) Hedgesparrow)		
		Same Brood
16. 1 Small bird	7/12/76	Adult female → nestlings.
17. 1 Small bird	8/12/76	Adult male → adult female → nestlings.
18. 1 Frog	8/12/76	Adult male → adult female → nestlings.
19. 1 Small bird	9/12/76	Adult male → adult female → nestlings.
20. 1 Small bird	9/12/76	Adult male → adult female → nestlings.
21. 1 Sparrows nest	18/12/76	Unmarked harrier extracted nest from tree and flew away with it.
22. 1 Mouse	4/1/77	Adult male → adult female → nestlings.
23. 1 Small bird	7/1/77	Adult female → nestlings.
24. 1 Small bird	7/1/77	Adult male → adult female → nestlings.
25. 3 Locusts	9/1/77	Unmarked juvenile caught 3 locusts from 7 attempts in long grass. Fed on post.

Table 5.1: Successful attacks by Australasian harriers
(continued) at Pukepuke Lagoon.

Prey	Date	Details
26. 1 Frog	9/1/77	Unmarked juvenile caught frog in farm drain vegetation. Fed on post.
27. 1 Frog	9/1/77	Adult male caught frog in raupo. Fed on cabbage tree branch.
28. 1 Small bird	13/1/77	Adult male → nestlings.
29. 1 Small bird	14/1/77	Adult male → nestlings.
30. 1 Frog	20/1/77	Adult female caught frog in farm drain vegetation. Prey eaten by following fledgling.
31. 1 Small bird	20/1/77	Adult female → fledglings.
32. 1 Small bird	25/1/77	Adult female → fledglings.
33. 1 Blackbird	26/1/77	Adult male stooped and dived into raupo from 5m (P. Moors).
34. 1 Carp	22/7/77	Adult female hovered and plucked 450g fish from shallow water (K. Potts).

Table 5.2: Carrion use by Australasian harriers at Pukepuke Lagoon

Carrion	Date	Details
1. 6 Rabbits	24/3/76	6 Harriers feeding from rabbits shot by Manawatu Pest Destruction Council
2. 1 Mallard duck	24/3/76	Unmarked juvenile Harrier
3. 1 Carp	25/8/76	Adult female feeding from 650 g carp (W. Pengelly)
4. 1 Lamb	15/9/76	Unmarked Harrier
5. 1 Lamb	26/10/76	Unmarked Harrier
6. 1 Lamb	27/10/76	Unmarked Harrier
7. 1 Sheep	8/1/77	Adult male
8. 1 Pukeko	14/1/77	Adult male
9. 1 Mallard duck	26/1/77	Unmarked juvenile
10. 1 Pukeko	23/2/77	Adult female
11. 1 Rabbit	26/2/77	Unmarked juvenile
12. 1 Pukeko	26/2/77	Adult female
13. 1 Rabbit	23/3/77	Juvenile female
14. 2 Rabbits	21/4/77	2 Unmarked juveniles. Rabbits shot by Manawatu Pest Destruction Council
15. 3 Rabbits	28/4/77	3 Unmarked juveniles. Rabbits shot by Manawatu Pest Destruction Council
16. 6 Eels	6/7/77	4 Unmarked Harriers, 2 juvenile females. Eels dredged up during mechanical drain clearing

In the summer diet 84 (45.0%) introduced passerines were the predominant avian prey. Of the 36 passerines identified in prey remains 20 (55.5%) were fledglings and nestlings. It is likely that a similar percentage of passerine remains in pellets were of fledglings and nestlings. Rabbits (13.9%), hedgehogs (9.1%) and mice (6.9%) were the most important mammalian foods. Skull measurements showed that 65.0% (15) of the rabbit remains and 40.0% (8) of the hedgehog remains at nest sites were of immature animals. These results clearly demonstrate the Australasian harriers' ability to exploit a vulnerable food source that became available during the breeding season. All 11 (5.9%) frogs, eels and carp were identified from prey remains rather than pellets. Large insects which were not abundant until late summer did not occur in nest site pellets or prey remains.

Although nesting success was on average low, with only 1.8 young fledged per successful nest, it was observed that some successful nests had a markedly higher fledging success rate than others. When the influence of diet on nesting success was considered I found that mammals comprised 36.6% of the food supplied to nestlings by three pairs of Australasian harriers that fledged on average 2.3 young per pair; while two other pairs supplied a diet consisting of 28.8% mammals and fledged only 1.0 young per pair (Appendix A.1 - A.5). This difference is not significant. However, those pairs that fledged more young took significantly more large (>200 g) mammals ($\chi^2 = 4.24$; $P < 0.05$). These results suggest that the supply of greater numbers of large mammals to nestlings will increase fledging success.

When nesting, Australasian harriers took more birds (53.5% v 20.1%) and aquatic prey (5.9% v 0%) and less mammals (34.2% v 64.7%) and insects (0% v 11.4%) than when roosting communally. This difference is significant ($\chi^2 = 60.5$; $P < 0.001$).

In the communal roost pellets, wool was identified in 22.9% of the remains of food items. This contrasts strongly with the low frequency of occurrence of wool (2.1%) in nest site pellets and prey remains collected during the summer. During summer there were fewer dead sheep available because lambing, with its associated high sheep mortality, ended in late spring.

Table 5.3: Seasonal diet of the Australasian harrier at Pukepuke Lagoon determined from nest site pellets and prey remains and communal roost pellets.

	Nest site pellets and prey remains		Communal roost pellets							
	Summer Dec-Feb		Autumn March-May		Winter June-Aug		Spring Sept-Nov		Communal Roost Total	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Rabbit	26	13.9	5	20.8	11	20.8	2	7.1	18	17.1
Hare	2	1.1	0	0	0	0	0	0	0	0
Hedgehog	17	9.1	1	4.2	7	13.2	2	7.1	10	9.5
Opossum	2	1.1	1	4.2	2	3.8	1	3.7	4	3.8
Sheep	4	2.1	2	8.3	10	18.9	12	42.9	24	22.9
Mouse	13	6.9	2	8.3	8	15.1	2	7.1	12	11.4
Total Mammals	64	34.2	11	45.8	38	71.7	19	67.9	68	64.7
Duck	5	2.7	1	4.2	2	3.8	2	7.1	5	4.8
Pheasant	4	2.1	1	4.2	0	0	2	7.1	3	2.9
Pukeko	3	1.6	0	0	0	0	0	0	0	0
Prion	4	2.1	0	0	0	0	0	0	0	0
Passerine	84	45.0	1	4.2	9	17.0	3	10.8	13	12.4
Total Birds	100	53.5	3	12.6	11	20.8	7	25.0	21	20.1
Total Eggs	12	6.4	0	0	2	3.8	2	7.1	4	3.8
Frog	3	1.6	0	0	0	0	0	0	0	0
Eel	6	3.2	0	0	0	0	0	0	0	0
Carp	2	1.1	0	0	0	0	0	0	0	0
Total Aquatic	11	5.9	0	0	0	0	0	0	0	0
Hemiptera	0	0	0	0	1	1.9	0	0	1	0.9
Orthoptera	0	0	10	41.6	1	1.9	0	0	11	10.5
Total Insects	0	0	10	41.6	2	3.8	0	0	12	11.4
TOTALS	187	100.0	24	100.0	53	100.1	28	100.0	105	100.0

Of the other important mammalian foods, highest percentages of rabbits and mice were identified in the autumn and winter diet, while most hedgehogs (13.2%) were eaten during the winter. Most autumn and winter occurrences of rabbit in the diet were probably from carrion. This conclusion is drawn from: 11 observations of the use of rabbit carrion following a rabbit shoot in the study area by the Manawatu Pest Destruction Council (M.P.D.C.) compared with two observations in spring and summer, the increased success in poisoning rabbits by the M.P.D.C. in winter when grass growth is least leading to greater numbers of rabbit carcasses (N. Bowick, pers. comm.), the more frequent use of road-killed lagomorphs during autumn and winter (Table 5.6), the finding of lead shot in two (11.0%) pellets from communal roosts that contained rabbit fur, and the belief that strong, experienced adult lagomorphs would be less vulnerable to Australasian harrier predation than juveniles would be in summer.

Opossums were identified infrequently in the diet in all seasons. Australasian harriers may find opossum carrion unpalatable. When fresh rabbit or hare and opossum were both placed in the same cage trap Australasian harriers invariably consumed the lagomorph only. Further evidence indicating a significant ($\chi^2 = 9.47$; $P < 0.01$) preference in favour of lagomorphs was obtained from road kills (Table 5.6). Here nine (70.0%) of 13 lagomorphs and only two (12.5%) of 16 opossums were eaten by Australasian harriers. Opossums have thicker and tougher skins than rabbits. However I do not think this accounted for the differences in the observations because I always sliced bait animals open to make them more attractive to Australasian harriers. The flesh of road-killed animals was also often exposed after vehicles had passed over them. Thus when trapping Australasian harriers, the use of rabbit or hare bait rather than opossum should improve trapping success.

Overall diet. The results of the nest site pellet and prey remains, communal roost pellet and trapped birds pellet analysis, together with the field observations and stomach analysis data are combined in Table 5.4. Only the trapped birds pellet analysis has not been considered so far. These results are discussed further in the section on the diet of the Australasian harrier ages and sexes (Table 5.9).

Of the 470 food items in Table 5.4, mammals were the principal food (46.4%). Birds (36.6%) were the next most important food, while eggs (4.8%), aquatic prey (4.6%) and insects (7.6%) were of approximately equal predominance.

The brown rat is the only mammal recorded in Table 5.4 and not in Table 5.3. Thirty two large (>200 g) birds including ducks, pheasants, pukekos and magpies comprised 6.9% of the annual diet. They were identified most frequently in the spring, summer and autumn diets. All 16 large birds in the summer diet were identified from prey remains. Fifteen (93.8%) were adults and one was a duckling.

Of the 138 (29.0%) passerines in the diet one (0.2%) was a large bird (>200 g), 12 (2.4%) were medium sized (75-200 g) birds and 125 (26.4%) were small (<75 g) birds. One hundred and seven of these passerines were taken during summer. This seasonal peak of passerines in the diet corresponds with the peak in passerine availability as determined from my terrestrial bird counts in Table 5.5. The number of passerines in the diet decreased through autumn and winter and rose again in spring. The average number of passerines in the bird count data so closely reflected the frequency of occurrence in the diet that a significant correlation ($r = 0.997$; $P < 0.05$) between the two sets of data is obtained. This strongly suggests that the Australasian harriers' diet was influenced by prey availability.

One species of medium sized passerine and four small species were commonly seen in the study area but occurred infrequently in the diet. They were: starlings (*Sturnus vulgaris*) (0.4%), waxeyes (*Zosterops lateralis*) (0.4%), grey warblers (0.2%), fantails (0%) and welcome swallows (*Hirundo tahitica*) (0%).

Twenty one of the 23 (4.8%) eggs were identified in the spring and summer diet. These included: five duck, two pheasant, two blackbird (*Turdus merula*), one hedge sparrow (*Prunella modularis*) and 11 unidentified eggs. Like the nine frogs that were caught during spring and summer, eggs were generally only available during these seasons. Three carp, and ten eels (*Anguilla* sp.) were recorded in the summer and winter diet. The insects in the diet were predominantly hemipterans (1.0%) and orthopterans (6.4%). These were taken when the adults emerged in late summer and autumn.

Table 5.4: Seasonal diet of the Australasian harrier at Pukepuke Lagoon.

	Summer Dec-Feb		Autumn March-May		Winter June-Aug		Spring Sept-Nov		Totals	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Rabbit	31	12.7	22	25.9	22	23.9	7	12.3	82	17.2
Hare	2	0.8	0	0	0	0	0	0	2	0.4
Hedgehog	20	8.2	10	11.8	12	13.0	3	5.3	45	9.4
Opossum	4	1.7	1	1.2	2	2.2	2	3.5	9	1.9
Sheep	5	2.0	3	3.5	11	12.0	19	33.3	38	8.0
Rat (Brown)	0	0	4	4.7	4	4.3	0	0	8	1.7
Mouse	15	6.2	6	7.0	14	15.2	2	3.5	37	7.8
Total Mammals	77	31.6	46	54.1	65	70.6	33	57.9	221	46.4
Duck	5	2.0	5	5.9	2	2.2	3	5.3	15	3.1
Pheasant	5	2.0	2	2.4	0	0	3	5.3	10	2.1
Pukeko	6	2.5	0	0	0	0	1	1.7	7	1.5
Prion	4	1.7	0	0	0	0	0	0	4	0.9
Magpie	1	0.4	0	0	0	0	0	0	1	0.2
Blackbird	6	2.5	1	1.2	2	2.2	1	1.7	10	2.1
Starling	2	0.8	0	0	0	0	0	0	2	0.4
Hedge Sparrow	19	7.8	0	0	1	1.1	2	3.6	22	4.6
House Sparrow	5	2.0	1	1.2	1	1.1	0	0	7	1.5
Skylark/NZ Pipit	5	2.0	0	0	0	0	1	1.7	6	1.3
Yellowhammer	14	5.8	0	0	3	3.3	2	3.6	19	4.0
Greenfinch	6	2.5	0	0	0	0	1	1.7	7	1.5
Chaffinch	4	1.7	0	0	0	0	0	0	4	0.8
Goldfinch	2	0.8	0	0	2	2.2	0	0	4	0.8
Waxeye	1	0.4	0	0	1	1.1	0	0	2	0.4
Greywarbler	1	0.4	0	0	0	0	0	0	1	0.2
Unidentified Passerines	43	17.8	4	7.0	5	5.3	1	1.7	53	11.2
Total Birds	129	53.1	6	17.7	17	18.5	15	26.3	174	36.6
Eggs	15	6.2	0	0	2	2.2	6	10.5	23	4.8
Frog	6	2.5	0	0	0	0	3	5.3	9	1.9
Carp	2	0.8	0	0	1	1.1	0	0	3	0.6
Eel	4	1.7	0	0	6	6.5	0	0	10	2.1
Total	12	5.0	0	0	7	7.6	3	5.3	22	4.6
Coleoptera	1	0.4	0	0	0	0	0	0	1	0.2
Hemiptera	3	1.2	1	1.2	1	1.1	0	0	5	1.0
Orthoptera	6	2.5	25	29.4	0	0	0	0	31	6.4
Total Insects	10	4.1	26	30.6	1	1.1	0	0	37	7.6
TOTALS	243	100.0	78	100.0	92	100.0	57	100.0	470	100.0

Table 5.5: Average number of birds counted seasonally per trip along 2.5 km transect.

Habitat and Bird Size	Summer Dec - Feb	Autumn March-May	Winter June-Aug	Spring Sept-Nov
Farmland				
Large	0	4.0	4.8	1.0
Medium	4.0	0.7	0.6	0
Small	1.0	12.0	4.8	12.0
Raupo				
Large	4.0	0.6	0.2	2.0
Medium	0	3.3	0.7	1.5
Small	11.0	3.0	8.4	2.0
Pines				
Large	8.0	4.6	2.0	3.5
Medium	3.0	0	2.3	3.5
Small	53.0	11.7	6.1	34.0
Duneland				
Large	7.0	4.9	5.5	7.5
Medium	12.0	6.3	7.6	3.5
Small	98.0	33.9	30.6	54.5
Total				
Large	19.0	16.1	12.5	25.0
Medium	19.0	9.9	11.0	8.5
Small	163.0	60.5	50.0	102.5

Bird size : small <75g, medium 75-200g, large >200g.

Table 5.6: Numbers of road-killed animals and the number eaten by Australasian harriers.

Carrion	Summer Dec - Feb			Autumn March-May			Winter June-Aug			Spring Sept-Nov			Totals		
	Number recorded	Number eaten	% eaten	Number recorded	Number eaten	% eaten	Number recorded	Number eaten	% eaten	Number recorded	Number eaten	% eaten	Number recorded	Number eaten	% eaten
Hedgehog	7	0	0	11	4	36.4	0	0	0	7	0	0	25	4	16
Rabbit	3	1	33.3	2	2	100	3	3	100	3	1	33.3	11	7	63.6
Opossum	2	0	0	5	2	40	2	0	0	7	0	0	16	2	12.5
Hare	0	0	0	0	0	0	2	2	100	0	0	0	2	2	100
Cat	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Total Mammals	12	1	8.3	19	8	42.1	8	6	75.0	17	1	5.9	55	15	27.3
Juvenile Magpie	2	0	0	0	0	0	0	0	0	4	0	0	6	0	0
Duck	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Pukeko	1	0	0	0	0	0	2	0	0	0	0	0	3	0	0
Total Birds	3	0	0	0	0	0	2	0	0	5	0	0	10	0	0
TOTAL	15	1	6.7	19	8	42.1	10	6	60.0	22	1	4.5	65	15	23.1

The seasonal changes in prey and carrion availability were reflected in seasonal changes in the diet. When the total numbers of mammals, birds, eggs, aquatic prey and insects are compared the seasonal diets differ significantly except those for winter and spring. However, significantly more sheep carrion and fewer mice, rabbits and hedgehogs were eaten in spring than in winter. The significance levels are recorded in Table 5.8.

Examples of carrion availability and use. Significantly more ($\chi^2 = 9.71$; $P < 0.01$) road-kills were eaten by Australasian harriers during autumn and winter than in spring and summer, although there were not more dead animals on the roads during the former seasons (Table 5.6). During spring and summer most Australasian harriers occupied territories in the sand country where nest sites were more numerous but roads were fewer than on the Kairanga Plains. Therefore road-kills were present in similar numbers during all seasons but geographically unavailable to many Australasian harriers during spring and summer.

During autumn and winter Australasian harriers made good use of distant food sources. For example, I estimated that there were about 60 Australasian harriers in the study area following a rabbit shoot by the M.P.D.C. in March 1977. This estimate was made after I had trapped 21 Australasian harriers, mainly previously untrapped juveniles, in the two days after the shoot and then resighted seven of these birds. I also counted 59 unmarked birds during the same two days. If a similar proportion (1/3) of these birds were resightings then the total number of Australasian harriers in the study area was about 60.

Live prey and carrion in the diet. Live prey (53.5%) was numerically the most important food in the diet. According to the criteria discussed in Methods, carrion accounted for 17.4% of the diet, whereas 29.1% of the food items could not be placed in either category. These results are presented in Table 5.7.

The frequency of occurrence of live prey in the annual diet was significantly greater than that of carrion ($\chi^2 = 96.8$; $P < 0.001$). There was significantly more live prey in the summer ($\chi^2 = 104.76$; $P < 0.001$) and autumn ($\chi^2 = 10.6$; $P < 0.01$) diets. Greatest use of carrion occurred during winter but the difference between carrion used and prey

Table 5.7: Live prey and carrion in the diet of the Australasian harrier.

Food	Summer Dec-Feb		Autumn March-May		Winter June-Aug		Spring Sept-Nov		Totals	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Live Prey	154	63.4	42	49.4	37	40.2	22	38.6	255	53.5
Carrion	18	7.4	17	20.0	27	29.4	21	36.6	83	17.4
Unknown	71	29.2	26	30.6	28	30.4	14	24.6	139	29.1
TOTAL	243	100.0	85	100.0	92	100.0	57	100.0	477	100.0

Table 5.8: Seasonal comparison of the proportion of mammals, birds, eggs, aquatic prey and insects in the diet of the Australasian harrier.

Season	χ^2	Probability Level
Summer : Spring	21.15	P<0.001
Summer : Autumn	94.13	P<0.001
Summer : Winter	48.92	P<0.001
Autumn : Winter	40.00	P<0.001
Autumn : Spring	37.81	P<0.001
Spring : Winter	19.9	P<0.001

Table 5.9: Diet of the Australasian harrier ages and sexes

Food items	Adult		Juvenile		Male		Female	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Mammals	20	39.2	38	46.9	32	42.6	34	52.3
Birds	20	39.2	15	18.7	25	33.4	17	26.1
Eggs	4	7.9	3	3.7	6	8.0	2	3.0
Frogs & Fish	7	13.7	2	2.5	4	5.3	3	4.6
Insects	0	0	23	28.4	8	10.6	9	13.9
>200g	24	47.1	39	48.1	32	42.7	43	66.2
<200g	27	52.9	42	51.9	43	57.3	22	33.8
Live Prey	29	56.9	46	56.8	46	61.3	29	44.6
Carrion	6	11.8	8	9.9	6	8.0	11	16.9
Unknown	16	31.3	27	33.3	23	30.7	25	38.5
TOTAL	51	100.0	81	100.0	75	100.0	65	100.0

Table 5.10: Number of food items per pellet.

	Adult		Juvenile		Male		Female	
	Number of pellets	% of total pellets	Number of pellets	% of total pellets	Number of pellets	% of total pellets	Number of pellets	% of total pellets
1 food item	14	43.8	38	50.7	25	46.3	35	53.0
2 food items	14	43.8	28	37.3	25	46.3	20	30.3
3 food items	4	12.4	7	9.3	3	5.6	9	13.6
4 food items	0	0	2	2.7	1	1.8	2	3.1
TOTAL	32	100.0	75	100.0	54	100.0	66	100.0

captured is not significant. Approximately equal numbers of food items in the spring diet were live prey or carrion and this reflects a period of pronounced change in the type of food available. In late spring this change was essentially from sheep carrion, provided during the lambing season, to newly available frogs, birds eggs and the young of passerines and rabbits. These results concur with those in Tables 5.1 and 5.2 on the observed use of live prey and carrion.

Diet of Australasian harrier ages and sexes. The data for the diet of the age and sex classes is recorded in Tables A.6 - A.12 of the appendices, included in Table 5.4 and summarised in Tables 5.9 and 5.10.

Adult Australasian harriers took significantly more birds and aquatic prey and fewer insects than juveniles did. This suggests that the Australasian harriers' hunting agility increased with experience because birds are considerably more agile prey than insects. However, similar frequencies of occurrence of live prey and carrion were identified in the adult and juvenile diets. Although adults took advantage of large carrion items which required no hunting agility, the important distinction here is that when carrion was not available they did not have to resort to less remunerative prey such as insects.

Age did not influence the size of food items Australasian harriers ate because adults and juveniles had similar numbers of large (>200 g) food items in their diet and similar numbers of food items per pellet.

It may be deduced that male Australasian harriers are more agile hunters than females because they ate significantly more live prey and fewer items of carrion ($\chi^2 = 3.84$; $P < 0.05$). Males also had more birds and fewer mammals in their diet, although this difference is not significant.

Because of their larger size, females were able to take significantly more large (>200 g) food items than males took ($\chi^2 = 6.47$; $P < 0.02$). Pellets from females also contained fewer food items per pellet although this difference is not significant.

DISCUSSION

Having considered the data on home ranges and population mobility in Chapters 3 and 4, I am confident that those food items identified in the winter, spring and summer diets were eaten in, or close to, the study

area. The same individually marked birds generally remained near Pukepuke Lagoon during these three seasons so the diet data collected from the communal roost, nest sites, trapped birds and field observations were all from the same population. Therefore these seasonal changes in the diet were not due to different hunting habits of seasonally different Australasian harrier populations. Despite the greater mobility of the population during autumn, I believe that the data indicate that most of the food items in the autumn diet had their origins in the Manawatu Sand Country, if not in the study area.

The Australasian harrier population at Pukepuke Lagoon drew its food from a wide range of natural prey and carrion items. Mammals (46.4%) were numerically the most important food items in the diet. Abundant species such as rabbits, hedgehogs, sheep and mice were eaten most frequently. Passerines were the most important bird food, especially during summer. Game birds in the diet included ducks, pheasants and pukekos and they were taken in similar overall frequency (6.7%) to birds eggs, aquatic prey and insects.

Passerines, and particularly introduced passerines, were the only common birds in the medium (75 - 200 g) and small (<75 g) size ranges at Pukepuke Lagoon. Their abundance was also noted by Falla (1957) who stated that introduced passerines, especially finches, are probably present in the Manawatu Sand Country in greater density than on any other terrain in New Zealand.

In all seasons these birds were taken in proportion to their availability for there was a significant correlation between the number of birds counted (Table 5.5) and the number occurring in the diet. Most passerines were taken during summer when the adults would have been more vulnerable as they were nest building, incubating, feeding nestlings and singing in their territories. However, approximately half of the passerine feathers identified at Australasian harrier nest sites were from nestlings and fledglings, indicating that Australasian harriers took advantage of this newly abundant and vulnerable food source. The same conclusion may be drawn from the data showing that nearly all the birds' eggs taken occurred in the spring and summer diets.

Of the common medium sized (75-200 g) and small (<75 g) passerines in the study area, only starlings, waxeyes, fantails, grey warblers and

welcome swallows occurred infrequently in the diet. Starlings often forage in open farmland from where an approaching Australasian harrier would readily be seen by these alert birds. However, Australasian harriers were not seen to hunt this habitat at Pukepuke Lagoon. When foraging in duneland starlings often moved in flocks which provide additional protection from predators (Tinbergen 1951). Waxeyes and grey warblers remain within or close to cover while foraging in shrubs. Soper (1963) described waxeyes as, "agile restless birds, never staying long in one place and when feeding will hover like grey warblers and hawk like fantails." This behaviour and the fact that they are rarely seen on the ground where the Australasian harrier takes most of its prey may make them difficult for Australasian harriers to catch. Fantails and welcome swallows forage on the wing and their flight is variable and unpredictable. These habits may in general preclude the predation of these passerines by Australasian harriers.

Approximately equal frequencies of occurrence of game birds in the diet were calculated for each season. During summer and autumn when water levels are lowest ducks often die following ingestion of lead shot (Bellrose 1951). This has been frequently recorded at Pukepuke Lagoon (Caithness 1974). This would have been one source of carrion. The shooting season which extended through autumn and winter would have resulted in even more carrion and wounded birds being available. During spring there are no major sources of game bird carrion so it is probable that some of the adults taken in this season were taken as live prey. These were probably morbid or nesting birds.

Of the mammalian foods in the diet, sheep carrion was readily available when others were not. This occurred during late winter and spring during the lambing season. Fifty percent of all wool was identified in pellets collected in spring while 29.0% was from winter pellets. The sex of the Australasian harriers that cast these pellets was generally not known because wool occurred mainly in pellets collected from the communal roost. However, this abundant food source would have been most important for adult female Australasian harriers which may have been in critical need of replenishing food reserves following overwintering, as they had to ultimately produce a clutch of eggs.

For all other mammals commonly identified in the diet, lowest frequencies of occurrence were in spring. These mammals included rabbits, hedgehogs, rats and mice. Their frequency of occurrence in the diet increased through summer and autumn to be highest in winter and this was paralleled by their changing availability.

Brown rat and house mouse population numbers increase from late summer through to winter (Daniel in press, Fitzgerald in press). This would in part account for their corresponding increase in frequency of occurrence in the diet. Other factors that would have rendered rodents more vulnerable would have been the loss of much ground cover as grazing pressure from domestic animals increased and the increase in hunting skill of the juvenile Australasian harriers.

Australasian harriers took advantage of the summer increase in the rabbit population for 65.0% of the rabbit remains at nest sites were of immature animals. While fewer young rabbits were available during autumn and winter the M.P.D.C. control operations were most intensive in and around the study area during these seasons. It has been demonstrated that Australasian harriers made good use of this carrion source.

Forty percent of hedgehog remains at Australasian harrier nest sites were of immature animals so they also took advantage of this food source when it became available. In autumn road-kills provided a substantial source of hedgehog carrion which Australasian harriers used. More hedgehog carrion may be available in winter for Brockie (1957) stated that there is evidence that most hedgehogs die during this season. However, whether they die in cover or in the open is not recorded.

Hares and opossums occurred infrequently in the diet. Hares were uncommon in the study area and were therefore not readily available. Opossums are mainly nocturnal and I considered those in the diet to be carrion for Australasian harrier and opossum activity rhythms do not generally coincide.

When adult hemipterans and orthopterans emerged in summer they became vulnerable. However only juveniles caught them while adults took more agile and remunerative prey. Most insects were taken during autumn when there were few adult Australasian harriers in the study area so in this season adults may have caught insects in other areas.

In summary, the seasonal trends seen in the diet data demonstrate a greater reliance on mammalian carrion during winter and early spring. This dietary emphasis then changed in summer to live prey; particularly passerines and their eggs and young, and to a lesser extent, insects and young rabbits.

Redhead (1969) explained this trend as a move from a staple mammalian diet to a preferred one and that birds, particularly passerines and their eggs were selected ahead of all other foods available at this time. I believe, however, that changes in prey density and vulnerability, together with changes in carrion availability, have been shown to be the major reason for changes in seasonal diets in this study.

Douglas (1970) provided some of the most convincing data that can be used against a palatability theory and in favour of availability. In his Harper-Avoca study area hare carrion was unusually abundant during the summer. In this season 75.5% (34) of the Australasian harriers' diet was mammalian and only 8.8% (4) was avian.

Schipper (1973) also made the conclusion that harriers prey where they find a particular prey species in its highest densities while Craighead and Craighead (1956:188) state that prey tend to be taken by predators generally in proportion to their relative densities.

The data of Carroll (1968), Redhead (1968b, 1969) Douglas (1970) and Fox (1977) indicate similar diets for Australasian harriers, from widespread New Zealand localities, to that found in this study. Differences between the studies in the consumption of particular foods are mainly due to variations in the types of prey and carrion available in the habitats sampled.

One aspect that I do not think was due to differences in food availability but rather to differences in sampling technique is the frequency of occurrence of aquatic prey in the diets. As in this study, no aquatic prey were identified in pellets by other workers, while a frequency of occurrence of 1.8% (9) for these prey was found by those workers carrying out stomach analyses (Carroll 1968, Redhead 1969).

In this study all 22 (4.6%) aquatic prey were either identified as remains at nest sites or seen taken as prey or carrion in the field. I saw five frogs caught during spring and summer only, although they were

also available during autumn. Carp were available throughout the year but were only seen taken during summer and winter. Besides the four eels at nest sites, six eels were recorded in the winter diet. The eels in the winter diet were carrion. They were dredged up and killed during mechanical drain clearing operations.

It is clear that aquatic prey, and particularly frogs, were under-represented in pellets and prey remains in relation to my field observations. I also found the pulli of Passeriformes to be under-represented in relation to field observations. Mice were under-represented in prey remains only. Schipper (1973) drew similar conclusions from his study.

Another interesting result that went unmentioned in other studies of the Australasian harriers' diet is that contrary to popular opinion, the Australasian harrier ate significantly greater numbers of live prey than carrion annually. I believe that the erroneous opinion that Australasian harriers are primarily consumers of carrion is based on the frequent autumn and winter sightings of Australasian harriers feeding on road-killed carrion; they are rarely seen taking live prey by the average observer.

I was unable to establish whether or not the hedgehogs in the diet were from carrion items only. As in this study, Douglas (1970) found hedgehog remains at Australasian harrier nest sites in a season when few hedgehogs die from natural causes (Brockie 1957). He also concluded that these hedgehogs were unlikely to be road-kills as the nearest back country road was 10 km away. During this study I placed four active adult hedgehogs in cage traps with Australasian harriers and left them together for 12 hours. Although no harm came to the hedgehogs the abnormality of the surroundings would probably have precluded any predatory activity and properly conducted trials are needed to establish whether or not Australasian harriers kill hedgehogs.

Diet and breeding success. The results obtained on the diet supplied to Australasian harrier nestlings and the resultant fledging success suggest that the supply of greater numbers of large mammals will increase fledging success. Five nests is a small sample size, but if this trend is a general one then because it was the number of large mammals and not the number of small prey supplied that influenced fledging success it may

be reasoned that total food biomass provided to the nestlings was most important.

No differences in the age and experience of the pairs were apparent. Even if there had been, the data on the influence of age and sex on the diet shows that age had no effect on the size of food items eaten. Also the pairs' territories and hunting ranges did not appear markedly different.

The only obvious difference between the more and less successful pairs was the stage of nestling development at which the females began hunting as regularly as their mates. It was shown in Chapter 3 that for those pairs that fledged three, two and one young, the female began hunting when the nestlings were on average two, four and six weeks old respectively. It is also pertinent to note that the same pair on the same territory that fledged one young in the 1976-77 season fledged three young in the 1977-78 season when the female began hunting two weeks after the nestlings hatched. In the 1976-77 breeding season she rarely hunted at all.

Female Australasian harriers ate significantly more large (>200 g) food items and more mammals than males did. Adult females were also as successful hunters as adult males (Table 6.2) so this would account for the greater number of large prey at the nest sites of those pairs that fledged more young. However it is impossible to assess without data on hatching success, whether the females of the more successful pairs began hunting earlier to feed their larger broods, or most broods were initially of a similar size and more survived from those that received extra food provided by the female earlier in the nesting period.

There are few diurnal predators in New Zealand capable of killing two week old Australasian harrier nestlings. At this age nestlings need less brooding and are capable of scrambling out of the nest and into cover (Soper 1958). There would therefore appear to be no major selection pressure against females beginning hunting at about two weeks after the young hatch and strong selection pressure in favour of this habit. Soper (1958) found that females may spend long periods off the nest as early as five days after the young have hatched but he did not record how much of this time was spent hunting or perched nearby. Five days after the young hatch is earlier than females of other races of *Circus aeruginosus* cease close brooding their nestlings (Brown and Amadon 1968:385). This would indicate that the habit of the New

Zealand population is an unusual one that is probably not selected against because there are few diurnal predators present.

No insects were found in any nest site pellets or prey remains. The taking of large numbers of small prey such as insects would not appear to improve nesting success for Schipper (1973) found that in Northern France, no young were reared by marsh harriers in nests where young were fed with prey of an exceptionally small size. Marples (1942) also stated that raptors in general take more remunerative prey during the breeding season. As in this study, Fox (1977) found a relationship between the frequency of occurrence of larger prey in the diet and nesting success. He found that for 19 pairs of New Zealand falcon, those that took more hares or rabbits had greater nesting success.

Age and sex. When intraspecific differential niche use has been studied it has been usual practice to investigate differences between males and females of sexually dimorphic species (Selander 1966). However this study has shown that age of Australasian harriers influenced reaction to prey as strongly as sex and size. Adults have had more experience in prey capture, suggesting that learning plays an important role in the development of hunting ability and prey preferences. The adults employed this experience in taking significantly more agile prey than did juveniles. This conclusion is supported by the hunting behaviour data which demonstrates that adults of both sexes were significantly more successful hunters than juveniles (Table 6.2).

The size of food items eaten by Australasian harriers was influenced by their sex only. Larger females took significantly more large (>200 g) food items and significantly fewer agile food items. Thus, from the diet data, adult males were the most agile hunters while juvenile females were the least agile. These results suggest that in studies of the effects of differential niche use on intraspecific competition, differences between adults and juveniles should be considered as well as those between males and females.

While I found no difference in the size of prey taken by adult and juvenile Australasian harriers, Mueller and Berger (1970) found that juvenile sharp-shinned hawks (*Accipiter striatus*) more frequently attacked inappropriately large prey than adults did. However, I believe that it is a mistake to assume that because juveniles attacked tethered large prey more often they would have been successful in catching these animals in the wild. That is, to assume that these inappropriately

large animals would have occurred in the juveniles' diet. Mueller and Berger (1970) also found that proportionally fewer males of both age groups struck large prey than did females. They concluded that age of sharp-shinned hawks influenced reaction to prey at least as strongly as sex.

The results from this study concur with those of Nieboer (1973) who concluded that due to structural and morphological differences, smaller male harriers should be more agile and manoeuvrable than females. Schipper (1973) who studied adult male and female harriers only, found differences between the diet of the sexes similar to those obtained in this study. He observed prey brought to nest sites by three sympatric species of harrier and found that males took more birds and fewer large prey than females captured. He also concluded that male harriers were more agile hunters than females.

The conclusions on the diet of the age and sex classes of Australasian harriers at Pukepuke Lagoon provide a basis for further study of their hunting agility and conspicuousness.

CHAPTER SIX

AUSTRALASIAN HARRIER HUNTING TECHNIQUES

INTRODUCTION

Harriers have low wing loadings (the ratio of body weight to the surface area of the wings) (Brown and Amadon 1968) and are therefore capable of making sustained slow flights in search of prey. Because of their low wing loading they are also particularly manoeuvrable (Brown 1976). Thus the Australasian harriers' morphology has a considerable influence on the type of searching and attacking techniques it employs. These techniques are discussed in this chapter along with other aspects of hunting behaviour.

Like most raptors the Australasian harrier is rarely observed capturing prey. Attacks are usually a short dive backwards or a hover and dive forwards to take prey on the ground. When compared with the searching phase of the hunt, attacks involve a minor expenditure of energy. Therefore I prefer Fox's (1977) broad definition of hunting behaviour: "when a bird of prey searches for, locates and attacks prey." Definitions such as that proposed by Rudebeck (1951): "when a bird of prey makes one or more attempts to kill or seize a specially selected quarry", place most emphasis on the attacking phase of the hunt and little on the searching phase.

METHODS

The descriptions of the techniques used by the Australasian harrier when hunting are based on my field observations at Pukepuke Lagoon and on references in the literature. In the discussion of these techniques and other factors influencing the degree of surprise attained when the predator and prey meet I have largely confined myself to the behaviour of the predator.

Attacks by the Australasian harrier. Ninety five attacks on prey (24 by adult males, 14 by adult females and 57 by juveniles) were recorded. For each attack I noted: the search technique used prior to the attack, the attack technique, the direction in which the Australasian harrier dived during the attack relative to its direction of travel while searching, the height the attack was initiated from, the success or

failure of the attack and when possible the prey species. Only completed attacks were recorded. Hesitations in flight were not considered to be attacks.

Because many attacks were made on prey in tall vegetation it was often not possible to identify the species of the prey. When the Australasian harrier remained out of sight in the vegetation for several minutes after an attack it may have been ground hunting, resting, or feeding from the prey it had caught. In such cases the success or failure of the attack could not be determined.

Attacks on the Australasian harrier. Attacks by other birds disrupted the Australasian harriers' hunting routine. I quantified the disruption for 155 attacks by recording: the duration of the attack in seconds, the distance travelled by the bird to attack the Australasian harrier, the distance the Australasian harrier was forced to fly from the area it was previously hunting and the number of birds involved in the attack.

Hunting in the daily cycle. Because of the undulating nature of the terrain in the study area, the Australasian harriers' very mobile method of hunting and its extensive home range, I was generally unable to follow individual birds for periods of longer than 15 minutes. The Australasian harriers' habit of perching on the ground out of sight made locating resting birds difficult. I was therefore unable to determine quantitatively the amount of time spent hunting on the wing, hunting on the ground and perching.

For the same reasons, all the birds in an area under observation could not be accounted for at any given time and therefore only general statements about the effects of season and atmospheric conditions on the daily hunting cycle have been made.

RESULTS

Seven search techniques and five attack techniques in the Australasian harriers' hunting strategies have been distinguished. These are discussed in what I consider to be their descending frequency of use.

A. Search techniques

1. Slow quartering
2. Soaring and prospecting
3. Listening
4. Ground hunting
5. Stooping to flush prey
6. Fast contour hunting
7. Still hunting

B. Attack techniques

1. Dive attack
2. Hover attack
3. Direct flying attack
4. Tail chasing and stooping
5. Glide attack

A. Search techniquesA.1 Slow quartering

The Australasian harrier was rarely observed using any search technique other than slow quartering when hunting lower than 9 m above vegetation. It generally flew a twisting path 2-7 m above the vegetation while searching the area immediately below and ahead. That this was the area searched is demonstrated by the low percentage (5.3%) of attacks made on prey to the side of its flight path (Table 6.2). So intent was the birds' search of the ground below that I twice saw hunting Australasian harriers fly into telephone wires in their path. While slow quartering they would usually flap into a head wind to gain height and then glide to a vegetation edge ahead so as to be in a position to surprise any prey immediately on the other side (Figure 6.1). There were many variations to this basic flight. These were largely dictated by weather conditions, terrain, vegetation structure and type of prey hunted. Thus on a calm day over swamp vegetation slow quartering flight often consisted of frequent flapping and few height changes.

The use of vegetation edges. The Australasian harrier used the technique described above when it approached a series of vegetation edges perpendicular to its direction of travel as shown in Figure 6.1. A slightly different technique was employed where a vegetation ecotone lay

FIGURE 6.1: SLOW QUARTERING

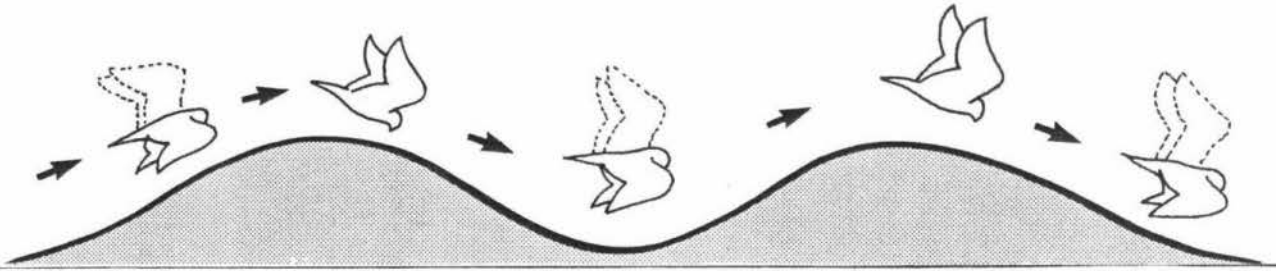
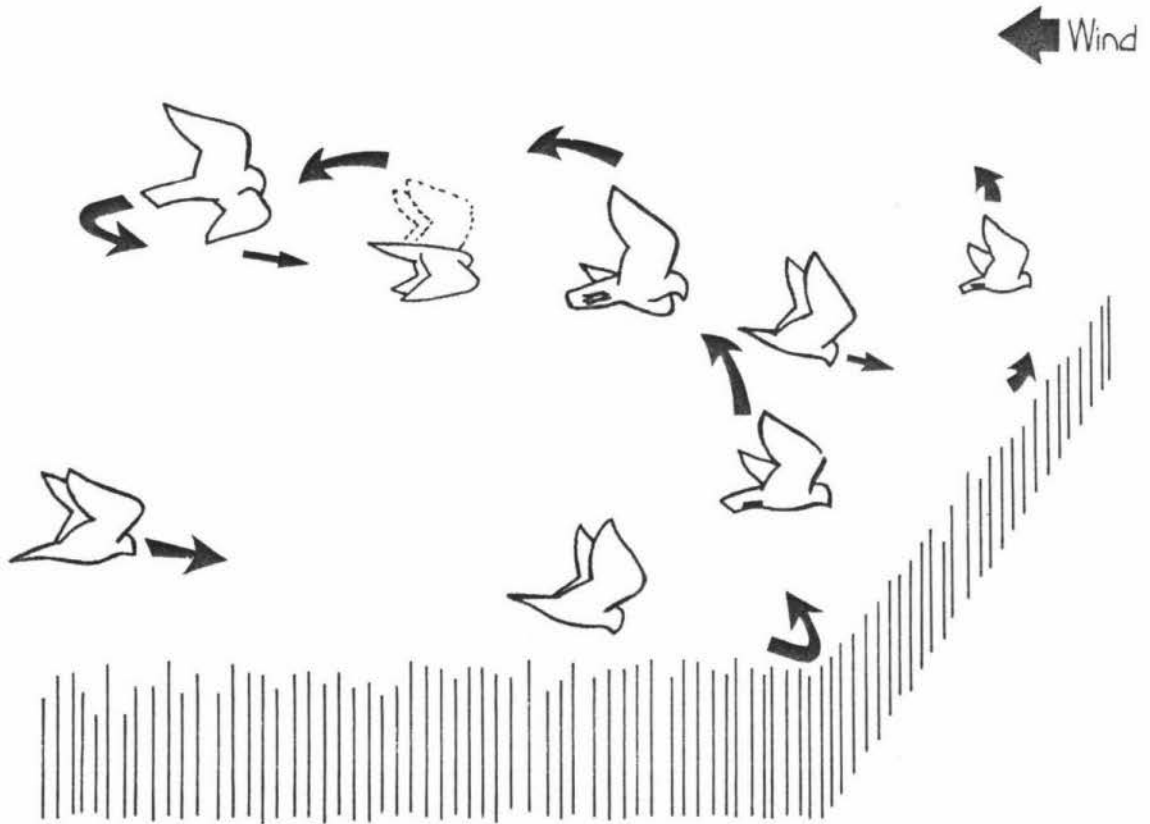


FIGURE 6.2: SLOW QUARTERING VERTICAL EDGES



perpendicular to the direction of the prevailing wind and parallel to the Australasian harriers' direction of travel. It would then approach the ecotone using flap and glide flight (Figure 6.1) and commence a zig-zag flight along the ecotone while facing into the wind at all times (Figure 6.2). This zig-zag flight was achieved by the Australasian harrier manoeuvring so that the wind struck its ventral surface and lifted it about 5 m above the vegetation and 1 m back from the ecotone. By raising its wingtip on the opposite side to its intended direction of travel it would sideslip about 7 m to arrive at a point 2 m above the vegetation and 3 m back from the ecotone. Here the bird would raise its lower wing through 90° and level out to approach the ecotone once again.

Another use of vertical vegetation edges was observed where the density of the cabbage trees would allow. Here the Australasian harrier occasionally flew below the cabbage tree canopy over the flax sub-canopy. In this way it was able to use tree trunks to conceal its approach and surprise prey by suddenly appearing from behind a tree. Similarly, taller lupin bushes and boxthorns were used to conceal its approach in dune habitat.

The effect of wind on slow quartering. The three most noticeable effects of moderate to strong winds (>18 km.p.h) on slow quartering flight were to increase: the number of aspect changes, the number and amplitude of height changes and the amount of poising on the wind.

In moderate to strong winds the Australasian harrier was buffeted so that each wing tip rotated through as much as 120° . These aspect changes did not appear to upset its hunting ability for the bird maintained its head in a fixed position relative to the vegetation it was searching while its wings and body moved. Aspect changes would have made it more conspicuous however.

The Australasian harrier often allowed moderate to strong winds to lift it from the end of a glide to 7-9 m above the vegetation prior to another gliding descent rather than to the more usual 3-5 m observed in light winds (<18 km.p.h). Thus the bird was able to use the extra height to maintain the length of its forward dive without having to expend extra energy flapping. Although this behaviour saved energy the Australasian harrier was more often in a less favourable position for launching an attack because higher flights gave prey more time to react.

Poising on a head wind is a form of very slow quartering. The average wind speed recorded when Australasian harriers were observed poising was 21 km.p.h (Range = 10-30 km.p.h). They were most frequently observed hunting in this manner on up-draughts where the wind travelled up and over an obstruction such as a dune ridge, a row of pine trees or a wall of raupo.

Poising flight allowed them to search a small area of vegetation very thoroughly. A bird would usually drift slowly sideways without flapping, often with its tarsi slightly lowered ready to pounce on prey. The stronger the wind the closer it held its wings to its body in order to maintain its stability and hunting position.

A.2 Soaring and prospecting

The Australasian harrier frequently soared on thermal streets (Pennycuik 1972) rising from areas of bare sand in the study area. The main characteristic of this search technique is the use of height from which a bird is able to search efficiently a large area of ground below. However little of the important element of surprise is retained unless the Australasian harrier can first descend undetected to a height from which it is capable of launching an attack. The maximum height from which I observed an Australasian harrier initiate a dive attack was 9 m. Therefore I assumed birds were soaring or prospecting when they were flying above this height with their heads angled down searching the vegetation below. This assumption was also supported by my observation that when flying higher than 9 m they did not consistently fly a twisting path with frequent height changes and did not follow terrain contours.

While birds were frequently seen soaring at heights of 30 m to 250 m and occasionally beyond my unaided vision, the reasons for such flights were not always obvious. Bouts of soaring often preceded courtship displays in spring and I saw territorial defence initiated by three soaring adult males on different occasions during the breeding season. A bird may also have been soaring for physiological reasons; for example to cool off, because soaring was most frequently observed during hot weather. It was probable therefore that diverse internal and external factors at times provided the motivational stimulus for soaring.

However there can be no doubt that soaring and prospecting flights were used as hunting tactics by the Australasian harrier. On four

occasions I observed Australasian harriers descend steeply from soaring flight and begin a fast direct flying attack on prey from dead ground. After four other descents a slow quartering approach was adopted. Of these eight attacks, only one involving a direct flying attack was successful. On numerous other occasions not individually recorded because attacks did not eventuate, Australasian harriers descended from soaring and prospecting flights and continued hunting at heights lower than 9 m.

Even when weather conditions did not favour production of thermals, Australasian harriers still regularly undertook high prospecting flights. These were particularly noticeable in winter when the birds flew at heights of 15-50 m with their heads directed down searching the terrain below. High flights may have been more energy demanding but they would have enabled the bird to search a much larger area. Large carrion items which were most frequently used in this season (Table 5.7) would have been more readily located by birds flying at greater heights.

A.3 Listening

Harriers have unusually keen hearing. This is facilitated by their partial facial discs and ears with large external openings and sometimes a pronounced conch. These are the same specialised auditory structures that are even more highly developed in some owls (Brown 1976).

Keen hearing would probably serve the Australasian harrier well when attempting to locate moving or calling prey in dense vegetation and would therefore be most frequently used in conjunction with other search techniques such as slow quartering. This however is generally difficult to prove in the field. I recorded one example of hunting by sound when observing four Australasian harriers hunting a dense 1 m high choumoellier crop. A blackbird burst into song from under the cover of the crop only 10 m from my hide. Two juvenile Australasian harriers, the nearest being 40 m away, immediately changed course and flew to hover over the area from where the blackbird had called. One landed on top of the crop and looked down and around while the other circled overhead. After two minutes of fruitless searching they left to continue slow quartering over the crop.

Stead (1932) cited a more graphic example. "If a gunner conceals himself thoroughly, and imitates the harriers' shrill staccato food call, interspersing it with the high-pitched alarm quack of a frightened grey

duck, any harrier that is within hearing will fly straight to the spot, and, if two or more are following one another, and the gunner does not show himself as he shoots the first the others will come straight on, taking no heed whatever of the report of the gun. I have shot many hundreds - probably thousands - in this way."

A.4 Ground hunting

Australasian harriers were most frequently observed ground hunting for frogs and tadpoles in temporary pond vegetation. Ground hunting birds were much less conspicuous than those flushing waterfowl or slow quartering. Despite this I saw about as many birds alongside drains and ponds as I observed stooping at waterfowl, and saw more attacks made by ground hunting (5) birds than birds flushing prey (2).

When ground hunting they usually stood on a tuft of vegetation searching or listening for movements with frequent twists of their heads. When a prey was sighted the Australasian harrier leapt into the air and with a few quick flaps was over the prey which it pounced on; sometimes with a resounding splash.

Stead (1932) recorded a similar mode of hunting after tadpoles. "Harriers walk in the slime, and, balancing themselves on one foot with the aid of their wings, catch with the other any tadpoles they may flush."

Although they were rarely seen ground hunting in habitats other than short temporary pond vegetation, a short period of stalking prey on the ground often followed an unsuccessful dive attack in other habitats. For example I observed a juvenile male make an unsuccessful dive attack on a frog resting on a raupo stem one meter from the ground just in front of my hide. The frog dived onto the bare mud below the raupo canopy. After peering into the foliage for about five seconds the Australasian harrier also hopped below the canopy. I watched the bird stalking between the raupo stems with its head twisting all the while as it searched for the frog for about a minute. It then flapped up through the vegetation and continued slow quartering before leaving the area.

A.5 Stooping to flush prey

While flying along the raupo-water ecotone Australasian harriers frequently accelerated towards groups of adult ducks or pukekos that were loafing and feeding. This conspicuous approach usually had the effect of flushing the prey and simultaneously alerting the Australasian

harrier to the presence of any unhealthy birds. If the prey had not flushed when the Australasian harrier was about 20 m from them it would commence a stoop in their direction. I recorded 45 such stoops at ducks, 16 at pukekos, three at female pheasants and two at shags. In only two instances did the Australasian harrier return to attack unsuccessfully waterfowl. The first attack was initiated against a mallard (*Anas platyrhynchos*) that had been shot and wounded but could still fly. The duck managed to escape into thick raupo. The second attack was on one pukeko in a flock of 12. This bird remained inactive with its feathers fluffed out while the other flock members had sleek plumage and were actively feeding. Although the juvenile Australasian harrier did not capture the unhealthy pukeko it returned eight times in the ensuing four hours to harry the flock and was later joined in the hunt by two other juveniles. Each time the juvenile returned, the pukekos, including the morbid bird, ran about 2 m to the cover of the raupo to escape from it.

A.6 Fast contour hunting

I observed four adult males and six unsexed birds fast contour hunting along dune ridges. In each case the bird was closely following terrain contours with a moderate (>18 km.p.h) tail wind, and flying with only a few flaps 1-3 m above marram grass. One of the adult males made two unsuccessful dive attacks on small passerines.

When fast contour hunting Australasian harriers searched a large area of duneland but this was covered much less thoroughly than when slow quartering. Because of the speed and height at which the bird travelled a greater degree of surprise would have been attained and provided it was sufficiently manoeuvrable, agile prey such as small birds would have been more readily captured by Australasian harriers hunting in this way.

A.7 Still hunting

Many raptors frequently still hunt the surrounding habitat visually and aurally while perched at a suitable vantage point (Brown and Amadon 1968:70). This, however, was an uncommon search technique for the Australasian harrier at Pukepuke Lagoon.

I saw an adult male and an adult female commence attacks from perches on fence posts alongside farm drains. In both cases the birds flew 3 m over the drain vegetation, hovered briefly, and then plunged

into the vegetation. These attacks, both unsuccessful, were probably directed against eels, frogs or tadpoles,

B. Attack techniques

B.1 Dive attack

Dive attacks were most frequently initiated by Australasian harriers when they were slow quartering. Although subject to considerable variation the basic attack was as follows: on sighting prey below, the Australasian harrier snapped into a full stall with its head uppermost, tail fully fanned and wings spread wide. It then pirouetted through 180° , half folded its wings and dived earthwards as shown in Figure 6.3. If the vegetation was at least 2 m high then it often plunged from sight while still in this dive position. If in duneland the Australasian harrier threw its wings back and thrust its tarsi forward for its talons to be in a grasping position as it entered the 1 m high marram grass. Most dive attacks were directed back at prey they had passed over. In 51 dive attacks Australasian harriers on 38 (74.5%) occasions dived backwards, on nine (17.6%) dived forwards and on four (7.9%) dived sideways (Table 6.2).

I was impressed by the speed, manoeuvrability and determination of Australasian harriers during dive attacks. These qualities distinguished genuine attacks from the more leisurely aerial stoops they made when flushing large birds (>200 g) in their search for wounded or unhealthy prey.

B.2 Hover attack

In this attack the Australasian harrier flapped vigorously and then either dived head first to the ground as in Figure 6.3, or descended more slowly while flapping and maintaining a hover position but with its tarsi lowered. Unlike dive attacks it had time to position itself for a hover attack and dropped or dived forward onto prey in 92.1% (35) of the observed attacks (Table 6.2). Hover attacks sometimes followed an unsuccessful dive attack but lacked the speed and resultant striking force of the latter.

Like dive attacks, most hover attacks were initiated by birds using the slow quartering search technique. All seven attacks made by ground hunting and still hunting birds involved hover attacks.

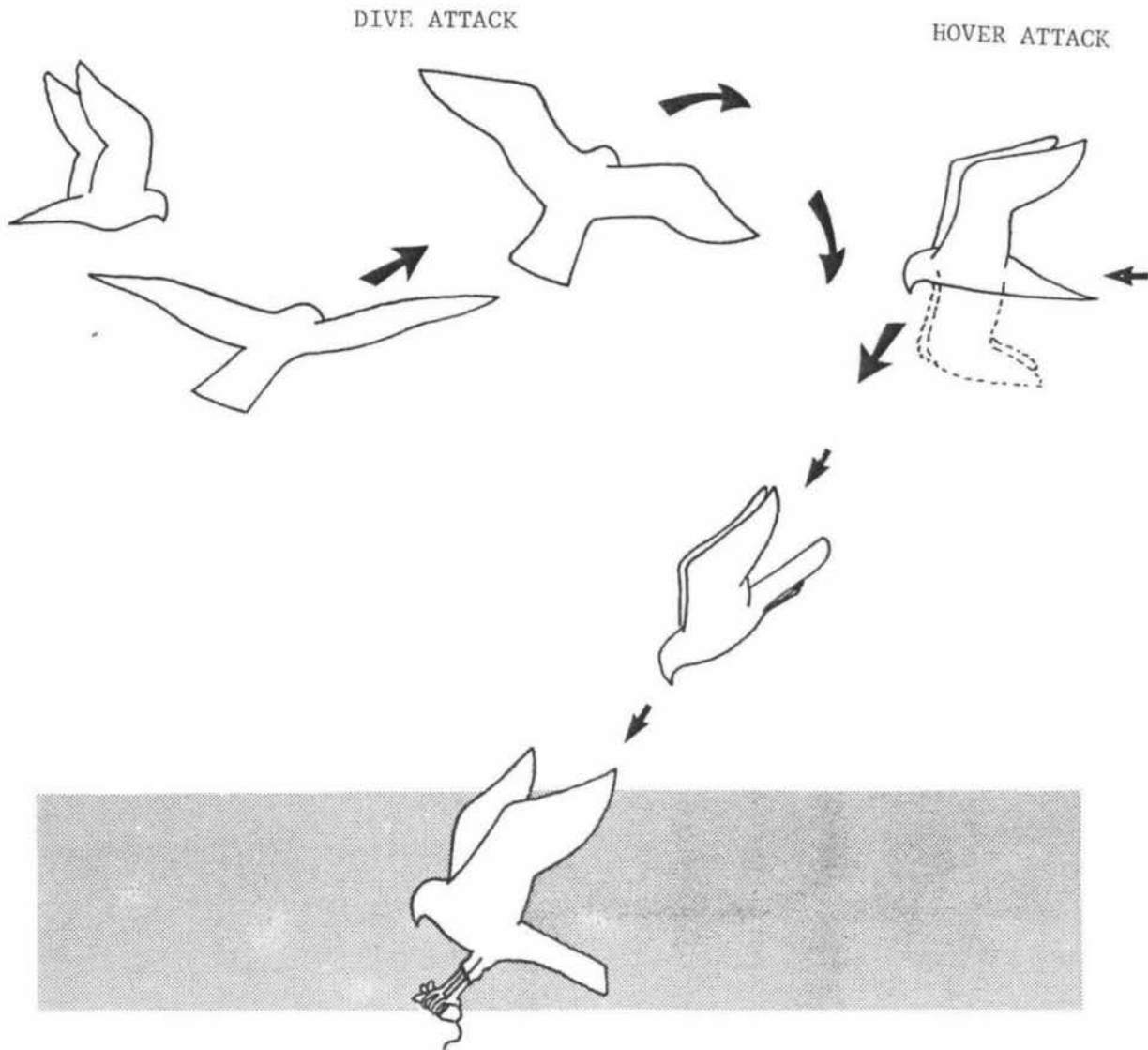


FIGURE 6.3

B.3 Direct flying attack

Three of the four direct flying attacks I observed were made by females on ducks. In these attacks they descended steeply from soaring flight and when 1 m above the vegetation began a direct flying attack by flapping hard and fast from dead ground in the direction of the prey. They suddenly appeared from over the raupo edge and dived head first with their wings half closed at the ducks at the waters edge. The ducks dived into deeper water to escape.

A juvenile female dived from a height of 5 m into vegetation bordering a farm drain in the only successful direct flying attack observed. I was unable to identify the prey it flew away with.

Stead (1932) recorded a similar attack strategy: "One day I watched a harrier beating (slow quartering) over a stubble field, when it flushed a skylark, which flew away some distance and settled. The harrier carefully marked the spot, and flew swift and low towards it (direct flying attack); saw the lark and struck at it on the ground. The lark dodged the blow, ducked out from behind the hawk, and settled again about two yards away; but the hawk, with a rapidity of movement with which one would scarcely have credited it, rose and swept back on its victim (dive attack) and flew off with it in its talons."

Although large (>200 g) mammals occurred frequently in the diet (Table 5.4) I did not see Australasian harriers attack any. Direct flying attacks have however been employed with success by Australasian harriers against large mammals. Sharland (1932) stated, "We were within ten paces of it (the young rabbit) when the harrier, skimming over the grasses from below a spreading tree, grasped it almost without a pause." Stead (1932) saw three Australasian harriers combine to kill a hare, and another kill an adult hare using a combination of direct flying attacks and dive attacks.

B.4 Tail chasing and stooping

Tail chasing attacks are more typical of falcons and accipiters and involve a raptor pursuing prey in the air and overhauling it. One or more stoops may then be made by the raptor in an attempt to seize or hit the prey with its feet.

On two occasions I saw juvenile Australasian harriers pursuing small birds for 20 m and 30 m. The prey easily eluded them and I concluded that they were inexperienced hunters.

Other observers have recorded more closely contested aerial pursuits of prey. From a car Stead (1932) observed an Australasian harrier chasing a blackbird (*Turdus merula*) at a measured speed of 40 m.p.h (64 km.p.h). The blackbird was forced to seek refuge under a small rush and was possibly saved by the observer's intrusion. Because the blackbird that Gibb (1970) saw chased had strayed from cover it was captured when it landed in open sand country. Buller (1888), who observed an Australasian harrier tail chasing and stooping at a small bird, stated that it was a mode of chase that he had never observed before during a very long acquaintance with the species. Oliver (1955) stated that the Australasian harrier has been recorded catching small birds on the wing by flying underneath them and so forcing them upwards until there is an opportunity to strike.

B.5 Glide attack

I did not observe any glide attacks at Pukepuke Lagoon. However Fox (1977) saw Australasian harriers make glide attacks on small birds in hill country on two occasions, but concluded this was an uncommon attack strategy for them. He described a glide attack as: "when a raptor slips off the perch without a single wingbeat and glides in a fairly flat trajectory straight towards an already located prey. As the flying speed increases the raptor closes its wings until the last few meters, then it quickly opens its wings and tail to reduce speed and may rock from side to side."

C.1 Search and attack techniques and their rate of success

All attacks made by Australasian harriers that could be identified with respect to age and sex have been recorded in detail in Tables A.13 - A.15 of the appendices. These results are summarised in Table 6.1 and 6.2.

The high percentage (80.0%) of attacks that were made by birds that were slow quartering emphasises the importance of this search technique. Soaring (8.0%) and ground hunting (5.0%) were the next most important search techniques.

Ninety three (97.9%) of the 95 attacks were made on prey on the ground or on water. Dive attacks and hover attacks together comprised 93.7% of the attacks. Direct flying attacks (4.2%) and tail chasing attacks (2.1%) were uncommon.

Table 6.1: Search techniques used prior to observed attacks by Australasian harriers.

	Slow quartering	Soaring	Listening	Ground hunting	Contour hunting	Flushing	Still hunting
<u>Adult male</u>							
number	21	0	0	0	2	0	1
percent	87.5	0	0	0	8.3	0	4.2
<u>Adult female</u>							
number	10	4	0	2	0	0	1
percent	58.8	23.5	0	11.8	0	0	5.9
<u>Juvenile</u>							
number	49	4	1	3	0	2	0
percent	83.1	6.8	1.7	5.1	0	3.4	0
<u>Total</u>							
number	80	8	1	5	2	2	2
percent	80.0	8.0	1.0	5.0	2.0	2.0	2.0

Table 6.2: Observed Australasian harrier attack techniques

	Dive attack	Hover attack	Direct flying attack	Tail chase attack	Average height (m)	Dive attack direction			Hover attack direction			Success		
						Back	Forward	Side	Back	Forward	Side	✓	x	?
<u>Adult male</u>														
number	16	8	0	0	3.2	13	3	0	1	6	1	7	15	2
percent	66.7	33.3	0	0		82.2	18.8	0	12.5	75.0	12.5	29.2	62.5	8.3
<u>Adult female</u>														
number	6	6	2	0	3.3	5	1	0	0	6	0	4	10	0
percent	42.9	42.9	14.2	0		83.3	16.7		0	100.0	0	28.6	71.4	0
<u>Juvenile</u>														
number	29	24	2	2	3.3	20	5	4	1	23	0	4	47	6
percent	50.9	42.1	3.5	3.5		69.0	17.2	13.8	4.2	95.8	0	7.0	82.5	10.0
<u>Total</u>														
number	51	38	4	2	3.3	38	9	4	2	35	1	15	72	8
percent	53.7	40.0	4.2	2.1		74.5	17.6	7.9	5.3	92.1	2.6	15.8	75.8	8.4

From the previous descriptions it may be stated that dive, tail chasing and direct flying attacks required greater manoeuvrability of the Australasian harrier than hover attacks. The use of the former techniques would have made success more likely when hunting agile prey. Thus 90.5% (19) of the observed attacks on small passerines were either dive attacks (17) or tail chasing attacks (2). Conversely, hover attacks were frequently initiated against less agile or unhealthy prey, prey in or on water, or prey concealed in tall vegetation. It was unlikely that unidentified prey in tall vegetation were small passerines however, for these birds always flew to escape. Thus 92.1% (35) of hover attacks were made on frogs, ducklings on water, insects, an unhealthy pukeko and unidentified prey.

Fifteen (15.8%) attacks were successful, 72 (75.8%) were unsuccessful and I was unable to determine the success of 8 (8.4%) attacks. Of the two most important attack techniques, dive attacks (19.6%) were more successful than hover attacks (10.5%) but the difference is not significant.

C.2 Influence of sex and age on attacks

The observed searching techniques can be readily divided into two categories: (i) searching flights close to the ground such as slow quartering, listening, contour hunting and flushing and (ii) high searching flights and hunting while perched. The searching techniques in the latter category are frequently used by buzzards (De Vries 1976, Brown and Amadon 1968, Weir and Picozzi (1975)). Adult females used buteonine (buzzard-like) searching techniques significantly more often than adult males ($\chi^2 = 8.76$; $P < 0.01$) and juveniles ($\chi^2 = 5.35$; $P < 0.05$). Although juveniles used buteonine searching techniques relatively more often than adult males the difference is not significant.

On average adult males made more attacks requiring greater manoeuvrability and from a lower height (3.2 m) than adult females and juveniles (3.3 m) did. Hover attacks required less manoeuvrability of the Australasian harrier than dive, direct flying and tail chasing attacks. Although adult males (33.3%) made relatively fewer hover attacks than adult females (42.8%) and juveniles (42.1%) did, the difference is not significant.

Adult males (29.2%) and adult females (28.6%) had similar rates of success from their attacks. Juveniles made only four (7.0%) successful attacks. They were significantly less successful than adults ($\chi^2 = 6.42$; $P < 0.02$).

C.3 Qualitative differences in hunting techniques

Although there were quantitative differences in hunting techniques employed by adult males and adult females in Tables 6.1 and 6.2, these were not readily apparent during field observations. In contrast, juveniles displayed some repeated examples of their inexperience as hunters. These were most noticeable during the juveniles' first four months of independence.

Both juvenile males and juvenile females tended to show an interest in most potential prey whether the prey were alert or not. They were often seen to hover over large alert prey such as pukekos and ducks for as long as two minutes. On three occasions they circled at between 15 and 20 m above a flock of alarmed chattering house sparrows (*Passer domesticus*) and twice landed on a very dense 3 m high boxthorn which several small passerines had taken refuge in. In each case their chances of catching the prey were practically nil. When they were not within one or two meters of a bird, adults passed on as soon as it was alerted to their presence and they were twice seen to accelerate past alert small birds towards a feeding non-alert one.

I recorded another possible instance of juvenile hunting inexperience in March 1977 when I caught a juvenile male that was unable to fly because its feathers were coated with mud. I reasoned that the bird had probably made an inappropriate dive attack on prey on deep mud or in shallow water, rather than the more usual hover attack.

C.4 Co-operative hunting

Juveniles were more frequently seen hunting in pairs or trios than adults. There were, however, fewer opportunities to observe adults hunting in teams for during the breeding season most adults would usually not tolerate any Australasian harrier other than its mate in the same hunting area. Further, at the end of the breeding season in mid-February most adults left the study area and did not return until mid-May.

The 30 Australasian harriers observed hunting co-operatively in 12 pairs and two trios were: 11 individually marked juvenile females, two adult females and 17 unmarked birds with dark plumage that could have been either adult females, juvenile females or juvenile males. They were seen hunting in this manner in all seasons of the year.

When hunting co-operatively they flew 10-100 m apart, followed the same general direction and occasionally crossed paths. When one hunting area had been searched the birds then progressed as a group to the next hunting area. In November 1976 I observed three Australasian harriers, two individually marked juvenile females, and one unmarked bird, hunting together on four consecutive days in this manner. If one of the members of the team launched an attack or hovered over prey the others immediately flew into the area to join the attacking bird.

In the same month I twice saw adult females following their mates at a distance and height of 20 m. The females were probably not hunting but waiting for the males to catch prey, for when one of the males caught an eel the following female stooped and took it in a talon-to-talon pass. This possibly represents a more unusual case of courtship feeding for the Australasian harrier.

D. Hunting in the daily cycle

While some raptors which take large prey in relation to their body size may only hunt in the early morning and again in the evening (Brown and Amadon 1968: 47), the Australasian harrier was observed to spread its hunting over a longer period. Given favourable weather conditions it was observed hunting during every hour of the day. However, there were some periods in which hunting activity was more noticeable than in others. During all seasons there was a hunting activity peak from the time the birds left their roosts shortly after dawn until mid to late morning about four hours later. A slack period when fewer birds were seen flying then occurred. This lasted for up to eight hours, but with progressively fewer daylight hours this slack period was reduced by half to about four hours by mid-winter. Finally the birds were often seen hunting, throughout the year, in the three hours prior to roosting at dusk.

Rain, low temperatures, overcast skies and low wind velocities were noticeable inhibitors of hunting. Persistent heavy rain provided the

greatest single disruption to the daily hunting cycle. If heavy rain prevented Australasian harriers from hunting for most of a morning then hunting usually took place throughout the afternoon if it was fine. Although I did not make any observations when it rained heavily all day, if intermittent heavy showers continued to fall throughout the day birds were frequently seen hunting during light showers but always landed when the rain became heavy. However this may not invariably occur for Buller (1888) recorded an Australasian harrier hunting during a heavy shower without any apparent inconvenience.

Fog was only present during a few early morning observations and, like rain, it delayed the birds' departure from the roost by about 30 minutes.

E. Interspecific attacks on the Australasian harrier

Details of 155 interspecific attacks on Australasian harriers are summarised in Table 6.3. One hundred and twenty-three (79.4%) attacks were made by magpies. Although magpies were not as persistent in their attacks as were black-backed gulls (*Larus deminicanus*) (9.0%) or spur-winged plovers (*Libinia novaehollandiae*) (6.5%), they were considerably more abundant and during their breeding season they maintained territories that they defended fiercely. On average attacks by magpies lasted only 16 seconds while they chased Australasian harriers about 30 meters. In this respect they caused only a minor disruption to hunting.

Magpies and Australasian harriers most frequently came into conflict over open farmland where the magpies preferred to forage. However, open farmland with grass less than 10 cm high was not hunted by Australasian harriers at Pukepuke Lagoon. Because they were most frequently attacked by magpies when travelling from one hunting area to another or when hunting adjacent habitats with taller vegetation, actual hunting disruption was minimal. Attacks by species other than magpies were infrequent and they had little disruptive effect on hunting.

Seasonal differences in the number of attacks and their duration were not marked although more (36.8%) took place in spring when birds had dependent young than in the other seasons.

Table 6.3: Observed attacks on Australasian harriers by other species

	Summer Dec - Feb			Autumn March-May			Winter June-Aug			Spring Sept-Nov			Total												
	Total number attacks	Average number birds	Average time (sec)	Average distance to attack (m)	Total number attacks	Average number birds	Average time (sec)	Average distance to attack (m)	Total number attacks	Average number birds	Average time (sec)	Average distance to attack (m)	Total number attacks	Average number birds	Average time (sec)	Average distance to attack (m)	Average chase distance (m)								
Magpie	23	1.8	16	23	28	36	2.2	16	22	29	23	1.5	16	27	29	41	1.2	17	31	36	123	1.7	16	26	31
Blackbacked gull	4	1.5	15	10	35	0					2	1.0	10	10	30	8	1.4	36	26	86	14	1.4	26	19	64
Spur-winged plover	2	2.0	30	35	75	2	2.5	20	30	60	1	2.0	20	40	50	5	1.8	24	40	128	10	1.9	24	37	96
Pukeko	0					0					0					3	2.3	16	10	5	3	2.3	17	10	5
Pied stilt	2	15	15	5	5	0					0					0					2	15	15	15	5
Mallard duck	1	1	60	5	5	0					0					0					1	1	60	5	5
Starling	0					2	150	20	15	0	0					2	150	20	15	0	2	150	20	15	0

The extent of the magpies' hostility occasionally went beyond mere disruption of hunting when an Australasian harrier was grounded by two or more attacking magpies. I saw magpies force two juveniles that were wet from bathing and another juvenile that had just been released from a trap to land. Stead (1932) stated that an Australasian harrier caught in such a position would be lucky to escape alive. However I observed that magpies attacked flying Australasian harriers more fiercely than perched or grounded birds. They mobbed and dive-bombed grounded or perched birds but provided they did not attempt to fly they stopped their attacks within two or three minutes.

F. Prey escape tactics

I was frequently alerted to the presence of an Australasian harrier I had not seen by the alarm call of a magpie or other bird. Small passerines flew and called when Australasian harriers were at least 20 m from them. I noticed that the early warning of an Australasian harrier's approach achieved by flocks of small passerines played an important role in preventing its near approach and the possibility of its surprising an unwary bird. This may have been an important factor in the decline of small passerines in the Australasian harriers' diet during autumn and winter when passerines were generally in flocks. Adult ducks normally flew to escape but if surprised while on water they would dive like ducklings. Ducklings and pukekos usually sought the sanctuary of raupo when they saw an Australasian harrier approaching. If caught away from cover adult pukekos would band together and hop off the ground and peck at the Australasian harrier hovering above them.

The only non-avian prey reaction observed was that on several occasions all the frogs croaking in a small pond fell silent when an Australasian harrier flew overhead.

G. Behaviour at carrion

Davies and Davis' (1973) description of how location of carrion by soaring red kites (*Milvus milvus*) was followed by tighter circling overhead, with gradual loss of altitude, and the bird eventually settling on the ground or on a perch at some distance from the food before approaching it, could be readily applied to the Australasian harriers' behaviour under the same circumstances.

Although only one Australasian harrier was ever observed feeding from an item of carrion at any one time, as many as five others were seen perched on knolls or fence posts 10-50 m from the feeding bird waiting for it to be satiated. Frequently one of those not feeding would carry out a direct flying attack on the feeding bird in an attempt to displace it from the carrion. The feeding bird would either mantle the carrion, take no notice, or fly into the air and strike up at the attacking bird with its talons and then return to the carrion. In only one of 23 attacks during 12 observations was the feeding Australasian harrier displaced. This took place during the breeding season when an adult male evicted an unmarked Australasian harrier from a dead sheep that it had been feeding from for 15 minutes near the adult male's territory boundary. On two other occasions, however, territory owning adult males tried unsuccessfully to displace intruding females from rabbit carrion that I had placed in their territories.

Individuals were seen to remain at carrion for up to 40 minutes. During this time most of the waiting birds left the area to continue hunting. From individually marked birds it was determined that those Australasian harriers initially in attendance would often return after 20 minutes or more and again attack the feeding bird or perch nearby.

From only 12 observations of two or more Australasian harriers competing for a single item of carrion I was unable to draw any conclusions about which ages or sexes, if any, had preference when the feeding bird left the carrion.

H. Interspecific competition for carrion

The Australasian harrier had few other species to compete with for carrion at Pukepuke Lagoon. Feral cats and ferrets were observed eating rabbit bait in the cage traps during winter and would have provided some competition for carrion during this season. During spring and summer when black-backed gulls from the colony on the southwestern edge of the study area were foraging for their chicks I trapped 42 of these birds in automatic bownet traps baited with rabbit. The Australasian harriers' strongest interspecific competition for carrion would certainly have come from the birds in this colony which I estimated to contain about 200 pairs. Although black-backed gulls attacked

Australasian harriers when they were flying, I observed six unsuccessful attempts by gulls to displace them from carrion. When on five occasions black-backed gulls were observed feeding from carrion and Australasian harriers flew overhead they did not attempt to displace the gulls, so it appeared that the first bird of either species to find the carrion had preference.

Black-backed gulls, however, had a distinct competitive advantage during wet squally weather when they continued to fly while Australasian harriers remained grounded.

DISCUSSION

Superficially the hunting techniques employed by harriers are similar. As for the Australasian harrier, slow quartering is the most commonly used search technique with ground hunting, still hunting from low perches and fast contour hunting less frequently used by other harriers (Trautman 1944, Craighead and Craighead 1956, Brown and Amadon 1968, Dickson 1974, Schipper *et al.* 1975, Watson 1977). Similarly dive and hover attacks are commonly employed while direct flying attacks and tail chasing attacks are less frequently recorded (Cooch 1946, Dickson 1974, Watson 1977).

It was calculated in Chapter 2 that the Australasian harrier has a wing loading of 0.34 gm/cm^2 (males) and 0.39 gm/cm^2 (females) which would suggest that it is less manoeuvrable than other harriers. For example, Montagus' (*Circus pygargus*), hen and marsh harriers have wing loadings of 0.21, 0.25 and 0.30 gm/cm^2 respectively (Brown and Amadon 1968). However 44.9% of the Australasian harriers' summer diet was passerines of which approximately half were adults (Table 5.4). That the Australasian harrier is able to take agile prey such as adult passerines, despite its higher wing loading, suggests that it may have evolved a more accipitrine (Accipiter-like) wing shape along similar lines to those suggested by Schipper (1973) for the hen harrier. He found that the hen harrier takes comparatively more birds than Montagus' harrier which has a lower wing loading. Unfortunately I do not have any wing measurements of these harriers with which to compare those I took of the Australasian harrier.

The Australasian harrier hunts most of a similar range of habitats to those hunted individually by hen, marsh and Montagus' harriers in Europe. Also it is able to take prey from the entire range of sizes and agilities that Schipper (1973) has shown to occur to different degrees in the diets of these three European species. Unlike the hen harrier, the Australasian harrier was not observed hunting over open farmland with grass shorter than 10 cm. Presumably surprising adult passerines in vegetation of this height or lower is too demanding of the Australasian harriers' manoeuvrability. I did not observe any other potential prey in this habitat so it would have had little other reason for hunting there.

It is also unlikely that the Australasian harrier is often able to catch flying adult passerines as Watson (1977) stated the hen harrier has been seen to do. Oliver's (1955) record of the Australasian harrier catching small birds on the wing would indicate that it is capable of much greater manoeuvrability and speed in the air than other references in the literature and my observations would suggest. Perhaps the method of attack described by Oliver (1955) was derived from an attack made on a fledgling or weak and unhealthy bird; or it is an extrapolation of Buller's (1888) very similar account of an unsuccessful attack by an Australasian harrier. Like other harriers, the Australasian harrier generally takes its prey on the ground or from shallow water.

In New Zealand the only diurnal raptor that is a potential competitor of the Australasian harrier is the New Zealand falcon which Fox (1977) has shown to have very different ecological requirements and hunting behaviour. The morepork's (*Ninox novaeseelandiae*) diet consists largely of invertebrates and it is mainly confined to woodland (Cunningham 1948, Lindsay and Ordish 1964). The little owl (*Athene noctua*) is also mainly an invertebrate feeder although it takes more vertebrates during the breeding season (Marples 1942). These two nocturnal owls are not considered to be significant competitors capable of influencing the hunting behaviour of the Australasian harrier.

Schipper (1973) and Schipper *et al.* (1975) explained the observed differences in food composition between hen, marsh and Montagus' harriers with reference to predation differences in time and habitat and to

predation differences directly related to intrinsic, morphological and structural properties maintained through interspecific competition.

The marsh hawk (*Circus cyaneus hudsonius*), unlike its Eurasian conspecific does not have any other species of harrier to compete with in North America and therefore hunts both open grassland and marshland (Craighead and Craighead 1956). It also depends on carrion during severe winter weather (Errington and Breckenridge 1936). However both the marsh hawk and the hen harrier at times experience intense competition from the short-eared owl (*Asio flammeus*) which also has a low wing loading, is diurnal, hunts open grassland and marshland and occurs in about 94% of the range of both harrier subspecies (Clark and Ward 1974). Other potential competitors of both the marsh hawk and the hen harrier include several species of *Buteo* which are efficient soaring raptors with wing loadings of 0.40 - 0.45 gm/cm² (Brown and Amadon 1968). Thus the ranges of hunting behaviour of all the species of harrier considered are much more severely limited by those of other raptors that are phylogenetically or ecologically closely related to them than is the hunting behaviour of the Australasian harrier.

A number of land birds have broader niches or feeding stations on islands than they have on continents (Lack 1969). It may be reasoned that the same birds would exhibit a broader range of hunting behaviour. Thus in the absence of strong competition from other birds of prey the Australasian harrier has evolved a wider range of hunting techniques than have been recorded for Eurasian and North American harriers.

Buteonine hunting techniques. Buzzards (*Buteo* sp) frequently use high soaring and prospecting flights as a search technique, while glide attacks and direct flying attacks are not uncommon (Pinowski and Ryszkowski 1962, Brown and Amadon 1968, De Vries 1976, Weir and Picozzi 1975). While these hunting techniques have been employed to some degree by all Australasian harrier sex and age classes, adult females, which have a significantly higher wing loading that lies within the known range for buzzards, made significantly greater use of buteonine hunting techniques. Adult males on the other hand, made greatest use of traditionally circinine (harrier-like) hunting techniques.

An advantage of soaring and high prospecting flights during autumn and winter would have been that they enabled the Australasian harrier to

observe readily both carrion and the movement of other birds into areas where food was unusually abundant. Several authors have noted concentrations of Australasian harriers similar to that which I observed following a rabbit shoot at Pukepuke Lagoon by the Manawatu Pest Destruction Council. Buller (1888) recorded as many as 70 Australasian harriers hovering in one area over White Island which is 47 km from the mainland. They were catching kiore (*Rattus exulans*) that had been forced from cracks in the rocks when the island was erupting in 1884. Stead (1932) noted a large concentration of Australasian harriers and gulls which had gathered to feed on imprisoned fish when the Selwyn River was drying up and Ryder (1948) observed large numbers of Australasian harriers in the Kaiangaroa pine forest during winter when cullers had left numerous deer and pig carcasses lying about.

Glide attacks by Australasian harriers have only been recorded in hill country. It may well be that there are more suitable perches to still hunt and launch a downhill glide attack from in hill country than in the lowland study area I used. Because there is little east-west movement between hill country and lowland by the Australasian harrier population in New Zealand (Watson 1954) and the adults are philopatric, the possibility that the population in the hill country has evolved more buteonine hunting techniques than the lowland population should not be discounted. However the marked seasonal dispersal of the population from Pukepuke Lagoon would argue against this suggestion.

Co-operative hunting. Another aspect of the Australasian harriers' hunting behaviour that distinguishes it from other harriers' is co-operative hunting. I believe that a reason for the lack of this type of hunting by other harriers is that they have a low frequency of occurrence in their diet of animals large enough to provide sufficient food for the whole group.

The female and male Australasian harriers that I kept in captivity for a short period could in one meal eat 150 g of meat. My observations also show that the first bird to a food item is unlikely to be displaced until it is satiated. Thus only food items weighing more than about 200 g would contain sufficient tissue for more than one Australasian harrier meal.

The frequency of occurrence of food items weighing more than 200 g was significantly greater in the female Australasian harriers' diet (66.2%) than in the males' (42.7%) (Table 5.9). It follows from a consideration of the Eltonian pyramid of numbers which predicts that there are fewer large animals than small, that females would encounter fewer food items in their optimal food item size range than males would. By hunting co-operatively individual females would increase their numbers of encounters with the numerically fewer large (>200 g) food items. Males would more frequently consume all of the significantly smaller food items in their diet and would therefore gain less from co-operative hunting.

From Schipper's (1973) data I have calculated that approximately 35% of the number of prey taken by the marsh harrier weighed more than 200 g while 13.6% of male and 19.5% of female marsh hawks' prey weighed more than 125 g in Clark and Wards' (1974) data. This would suggest that there is a paucity of food items in their diets with sufficient tissue to provide a meal for more than one harrier. These two species would therefore gain less from co-operative hunting than both male and female Australasian harriers do.

Provided there is sufficient food for more than one meal the food need not be a single item but may be several closely grouped items such as the eggs in a duck's nest or a newly fledged brood of small birds. There would be similar advantages for both sexes and all species that hunted co-operatively for this type of food which is most abundant in spring and summer. However breeding activities precluded co-operative hunting by most adult Australasian harriers during these seasons.

In spring and summer juveniles were usually in the study area for one to three weeks and then they moved on. Therefore, unlike adults, they were not exploiting a familiar area and would have been at a disadvantage. By hunting co-operatively a pair of juveniles would have been more likely to discover by chance those areas of high prey concentration that the adults had become familiar with.

As with food items weighing more than 200 g, several closely grouped small items would be unlikely to provide a meal for more than two or three Australasian harriers, so greater numbers of birds than these are unlikely to be seen hunting co-operatively. Also, two or three

Australasian harriers would be all that were needed to subdue a large animal that one could not. It may be no coincidence that Buller (1888) and Stead (1932) both cited examples of three Australasian harriers hunting co-operatively. In the attack witnessed by Stead (1932) an adult hare was killed while Buller (1888) recorded that they killed an adult turkey (*Meleagris gallopavo*).

Thus co-operative hunting would have more advantages for pairs or trios of adult females and the juveniles of both sexes than for adult males which were never observed hunting in this manner. Juvenile females which were most frequently observed hunting this way would gain most from co-operative hunting.

Hunting success. The Australasian harriers' average rate of hunting success calculated during this study (15.8%) was significantly higher ($\chi^2 = 4.22$; $P < 0.05$) than that found for hen harrier males (6.0%) and combined juveniles and females (8.5%) by Schipper *et al.* (1975). They stated that their findings did not differ materially from those of Rudebeck (1951) who observed low rates of hunting success for raptors that actively pursue avian prey including the peregrine (*Falco peregrinus*) (7.5%), merlin (*Falco columbarius*) (4.5%) and sparrow hawk (*Accipiter nisus*) (11.0%).

However, Schipper *et al.* (1975) included hesitations as well as dives in their definition of an attack whereas Rudebeck (1951) determined hunting success from completed attempts to kill or seize quarry only. Therefore the hunting success rate of the hen harrier would have been much closer to that found for the Australasian harrier in this study if hunting success had been calculated from completed attacks.

Brown and Amadon (1968) considered that a success rate of 5% was too low for most raptors and that probably one in four attacks were successful. The rate of success of adult males (29.2%) and adult females (28.6%) at Pukepuke Lagoon agree very closely with this estimate. However much higher rates of success have been recorded for other raptors. For example Jenkins (1970) and Balgooyen (1976) recorded success rates of 40% and 70% respectively for male American kestrels (*Falco sparverius*), while Lambert (1943) and Ueoka and Koplín (1973) recorded success rates of 90% and 82% for Ospreys (*Pandion haliaetus*). The rate of success of juvenile Australasian harriers (7.0%) was

significantly lower than the adults' and similar to those obtained by Rudebeck (1951). In this respect it would be interesting to know the ages of the migrating raptors that Rudebeck (1951) observed hunting. Unfortunately the sex and age of the raptors were infrequently recorded.

No significant differences between adults and juveniles in the degree to which different searching and attacking techniques were used could be found to account for their different rates of hunting success. However juveniles were frequently seen to show an interest in inappropriately large prey and their attacks included 17 (29.8%) on adult ducks and an adult pukeko and 19 (33.3%) on unknown prey, some of which may have included inappropriately large prey in tall vegetation. Similarly, Mueller and Berger (1970) found from their study of sharp-shinned hawks (*Accipiter striatus*) that adults were less likely to attack inappropriately large animals than juveniles were.

That the ability to obtain food improves with age and experience in birds has been demonstrated for little blue herons (*Florida caerulea*) (Recher and Recher 1969), brown pelicans (*Pelecanus occidentalis*) (Orians 1969), oystercatchers (*Haematopus ostralegus*) (Norton-Griffiths 1968) and sandwich terns (*Sterna sandvicensis*) (Dunn 1971). These birds take from six months to three years depending on their species to become as efficient foragers as adults. As for raptors, the hunting methods of these birds demand careful judgement and co-ordination. It may be anticipated therefore that the Australasian harrier's hunting techniques would require a protracted period of learning in early life and that juveniles would be less successful hunters than adults. It has been pointed out that bird hunting hawks generally have longer periods of fledgling dependence than hawks that hunt less agile prey such as small mammals. For those raptors concentrating on invertebrates the development of hunting skills is also a fairly slow process (Snyder and Wiley 1976).

Reduced hunting success by juvenile Australasian harriers would be critically important during long periods of wet weather when they may be grounded and unable to hunt. As noted in this study, the marsh hawk and hen harrier (Craighead and Craighead 1956, Dickson 1974) spent longer periods on the ground during wet weather while Schipper (1973) found that rain reduced the supply of prey to nests for all three harrier species

he studied. In this respect the Australasian harrier is like other harriers despite its exhibiting a wider range of hunting techniques than other members of the genus *Circus*.

CHAPTER SEVEN

THE AUSTRALASIAN HARRIERS' HUNTING BEHAVIOUR ;
AN INTRASPECIFIC COMPARISON

INTRODUCTION

Nieboer (1973) made an intraspecific and interspecific morphological comparison between the members of the genus *Circus* and concluded that male harriers of all the species he studied were more manoeuvrable than females. He also considered adult male harriers to be less conspicuous than other birds because their light colour contrasted less against the sky.

The aim in this chapter is to field test Nieboer's (1973) laboratory findings by carrying out an intraspecific comparison of the Australasian harriers' hunting behaviour. Because the searching phase is very important and most amenable to study I have concentrated on this aspect of hunting in my study of the effect of age and sex on hunting behaviour.

Schipper *et al.* (1975) noted differences between male and "female" hunting behaviour when they studied two sympatric species of harrier in Holland and France. However, they were unable to distinguish between adult female, juvenile male and juvenile female harriers of the same species. They classed all these birds as "females", but stated that had they been able to distinguish between these classes the differences found would have been greater. It is possible, however, that the differences they recorded were due to the influence of age and experience rather than to morphological differences between the sexes. To eliminate that possibility from this study I collected data only from individually marked birds of known age and sex.

HYPOTHESIS

The components of hunting behaviour that I quantified were influenced by the working hypothesis that for optimum surprise and hunting success Australasian harriers should fly as low and as fast as possible to minimise the distance between themselves and prey. Lower and faster flights lead to more sudden confrontations with prey which require

greater manoeuvrability of the predator. This manoeuvrability is naturally limited and as vegetation height and density increases so they must fly either higher or slower if they are to maintain sufficient time to halt their forward momentum on sighting prey and dive to the ground. The use of wind may also increase the Australasian harriers' manoeuvrability. Flying into a head wind would enable them to fly lower and faster as the increased braking effect from such a wind would halt the birds' forward momentum more rapidly.

The number of flaps per minute and the number of height changes per minute are also important hunting behaviour parameters because they influence hunting efficiency and conspicuousness. For optimum hunting efficiency Australasian harriers should flap as infrequently as possible and change height as often as possible. This is because besides requiring more energy than gliding, flapping flight renders the bird more conspicuous. A flying technique employing frequent height changes, on the other hand, would require less energy than direct flapping flight. Through frequent height changes Australasian harriers may also use vegetation edges to conceal their approach and so increase the element of surprise during confrontations with prey.

METHODS

Between September 1976 and August 1977 I collected data from individually marked Australasian harriers while they hunted on the wing. Total times recorded were: 5,058 seconds for adult males, 3,574 seconds for adult females and 4,185 seconds for juveniles. With these data I investigated differences between hunting efficiency, manoeuvrability, conspicuousness and experience of the age and sex classes.

While they hunted the following data were dictated into a portable tape recorder: the height flown above the vegetation, the flying speed, the wind direction relative to the Australasian harriers' flying direction, the number of flaps and height changes and the type of habitat hunted. This was then replayed and entered onto a record sheet (Figure 7.1). During the replay the times taken for the above activities were recorded with a stop-watch.

Harrier Age	Sex	Individual	Date	Time	Wind Speed	Temperature	Rain			Fine	Cloud x/10										
							Light	Med.	Heavy												
Adult	Male	B-9	15-2-77	09.25	11 km.p.h/N.W	11°C				✓	2/10										
Area Habitat	Wind Direction			Harrier Speed				Height changes and height (m)	Flaps	Time (sec)											
	Circle	Head Wind	Cross Wind	Tail Wind	Poise	Hover	Slow				Normal	Fast									
K-2 Dune		✓						✓													
		✓		✓				✓													
		✓		✓				✓													
		✓						✓													
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		✓						✓													
		✓						✓													
		✓						✓													
	K-3 Raupo		✓						✓												
		✓						✓													
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		✓						✓													

Figure 7.1

The data collected contained four variables and were grouped under three classifications.

1. Classifications

1.i Age and sex

- a) adult male
- b) adult female
- c) juveniles, both sexes combined

1.ii Flying speed and wind direction relative to the flying direction

- a) head wind, speed slow
- b) head wind, speed normal
- c) head wind, poising
- d) head wind, hovering
- e) cross wind, speed normal
- f) tail wind, speed normal
- g) tail wind, speed fast
- h) circling, speed normal

1.iii <u>Habitat and vegetation height</u>	<u>Height</u>	<u>Plate</u>
a) open farmland	: <0.1 m	7.1
b) farm drain and temporary pond vegetation:	0.1-0.5 m	7.2
c) dune grasses and lupins	: approx. 1.0 m	7.3
d) raupo	: approx. 2.0 m	7.4
e) cabbage trees and flax	: approx. 6.0 m	7.5
f) pine plantations	: >10.0 m	7.6

2. Variables

- a) wind speed
- b) average height
- c) number of flaps per minute (average flaps)
- d) number of height changes per minute (average height changes)

1.i Age and sex. Data were collected from equal numbers of juvenile males and females so no bias in favour of either sex should exist in the data for this age class. There were insufficient data to include juvenile males and juvenile females as separate sub-classifications.

PLATE 7.1: OPEN FARMLAND



PLATE 7.2: FARM DRAIN



PLATE 7.3: DUNES



PLATE 7.4: RAUPO SWAMP



PLATE 7.5: CABBAGE TREES AND FLAX



PLATE 7.6: PINE PLANTATIONS



1.ii Flying speed and wind direction relative to the flying direction. For hunting Australasian harriers I distinguished slow (about 20 km.p.h), normal (about 30 km.p.h) and fast (about 40 km.p.h and faster) flying speeds. These categories were developed from a synthesis of speedometer readings and field observations. Hunting speeds were noted while I rode a motorbike and maintained a constant distance from Australasian harriers hunting over long roadside grass or nearby crops along a course parallel with mine. While some error in defining hunting speeds in kilometers per hour was probably incurred, it was readily apparent after several months observation whether a bird was hunting at a speed that was slow, normal or fast for the species.

Because insufficient data for statistical analysis were collected from birds poising on a head wind, hunting fast with a tail wind and circling, these data, comprising 3.7% of the total collected, were omitted.

1.iii Habitats. The habitats in the study area were divided into six distinct categories according to vegetation density and height. These categories were distinguished firstly to establish which habitats Australasian harriers preferred to hunt and secondly to determine whether adult male, adult female and juvenile birds hunted over the habitats in different ways and to different degrees.

Australasian harriers were not seen hunting over open farmland and very few observations were made of adult females and juveniles over pine plantations, so these habitats were excluded from the calculations of the influence of habitat on the three dependent variables (average height, average flaps and average height changes). These comprised 2.8% of the total data collected.

Although the data collected from birds as they hunted over the remaining four habitats were used in the calculation of the influence of habitat on the three dependent variables, they were not suitable for determining the degree to which the different sex and age classes hunted the habitats. This was because they contained continuous observations of hunting over a series of habitats where an observation of an Australasian harrier over one habitat was not necessarily independent of the next. Hence a chi-square test could not be used. However,

individually marked birds were frequently observed hunting for short periods when hunting behaviour was not being recorded. In these cases the habitat hunted over was recorded in my field notes. These data complied with the requirement of independence of observations necessary for a chi-square test to be made.

2. The variables. After each hunt wind speed was measured with an anemometer held 2 m above ground level. Solitary trees of known height provided the basis for estimates of hunting height. For increased clarity I divided hunting height into 2 m intervals (1, 3, 5, 7 and 9 m) above the vegetation. Similarly, only height changes greater than 2 m were recorded.

3.1 Biometrical considerations. The following procedure was adopted during the statistical analysis of the data with an IBM 1620 computer. The arithmetic means and standard deviations were calculated and regressed for each of the four variables. The regressions were tested for significance (Figures 7.2.a-d). There was a significant correlation between the arithmetic means and standard deviations of the data for average flaps and average height so these variables were transformed to logarithms in an attempt to remove the correlations. When a significant correlation remained, a calculated constant was added to the transformed variables. For each regression equation ($Y = MX + c$), a value for X when $Y = 0$ was calculated and used as the constant (Bliss 1967: 179).

For average height the regression equation was: $Y = 0.223X + 2.579$ so that ($\frac{C}{M} = 13$), while for average flaps the regression equation was $Y = 0.2039X + 24.352$ ($\frac{C}{M} = 120$). These means and standard deviations of the transformed variables, plus their constants ($\log(Y + 13)$ and $\log(Y + 120)$) were then regressed and no significant correlation remained (Figures 7.2.c and d).

The data were then sorted according to the first classification: age and sex. An analysis of variance was carried out and the individual group regressions calculated and graphed (Figures 7.3.a-i). The levels of significance for each within group correlation between the pairs of variables were also calculated.

FIGURE 7.2.a

$$Y = 0.117X + 5.85$$
$$r = 0.119; \quad P = \text{NS}$$

FIGURE 7.2.b

$$Y = 0.056X + 4.07$$
$$r = 0.1398; \quad P = \text{NS}$$

FIGURE 7.2.c

$$Y = 0.224X + 2.58$$
$$r = 0.7341; \quad P < 0.001$$
$$Y = 0.042X + 3.15$$
$$r = 0.2087; \quad P = \text{NS}$$

FIGURE 7.2.d

$$Y = 0.204X + 24.35$$
$$r = 0.8300; \quad P < 0.001$$
$$Y = 0.002X + 7.94$$
$$r = 0.0160; \quad P = \text{NS}$$

Fig 72 a Arithmetic Means v Standard Deviations for Average Height Changes

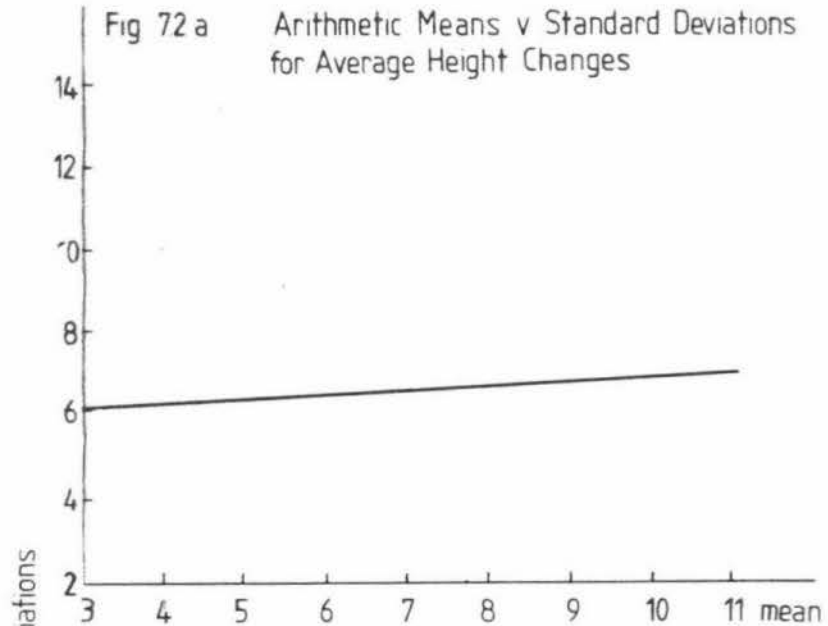


Fig 72 b

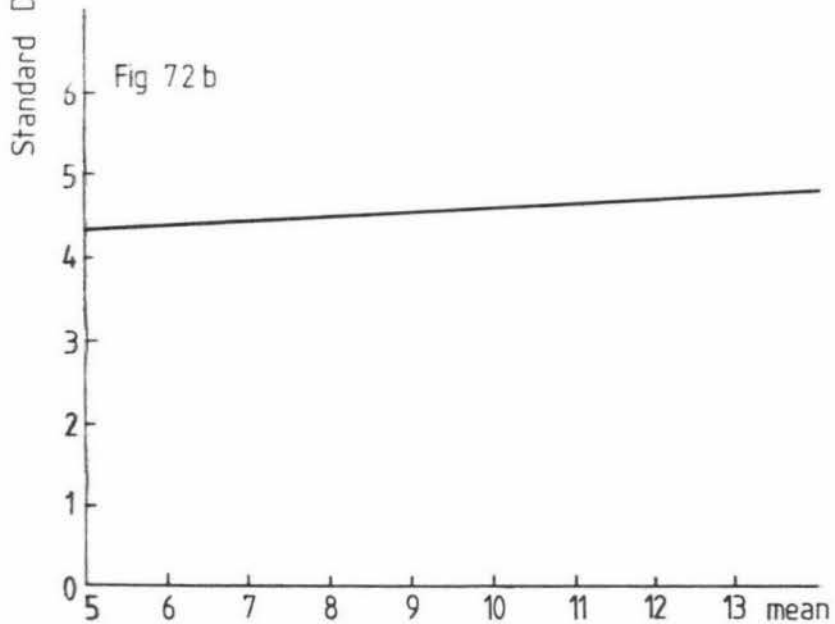


Fig 72 c Arithmetic & 3 Parameter Means v Standard Deviations for Average Height

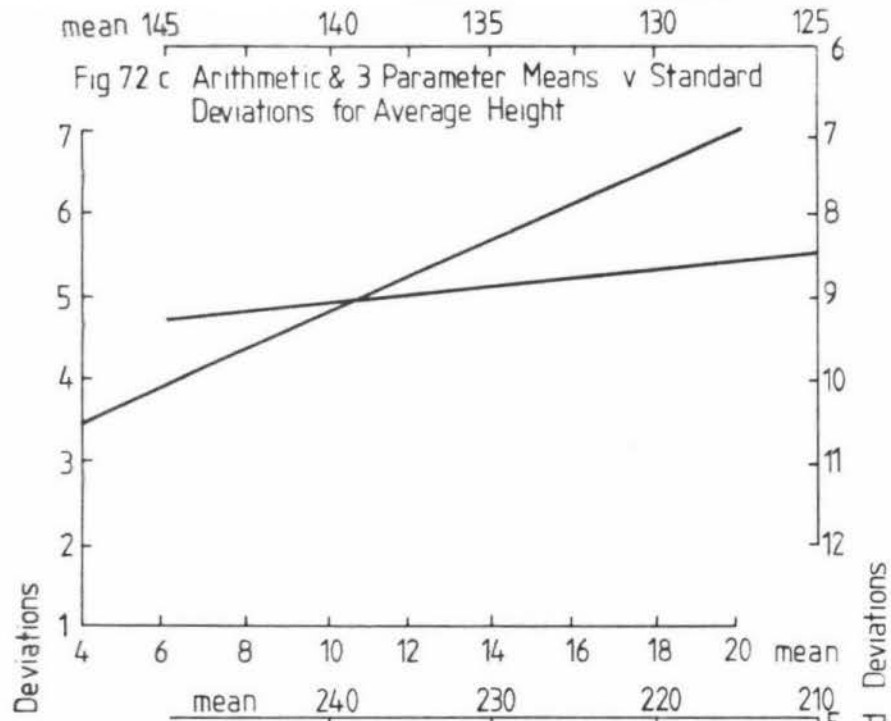
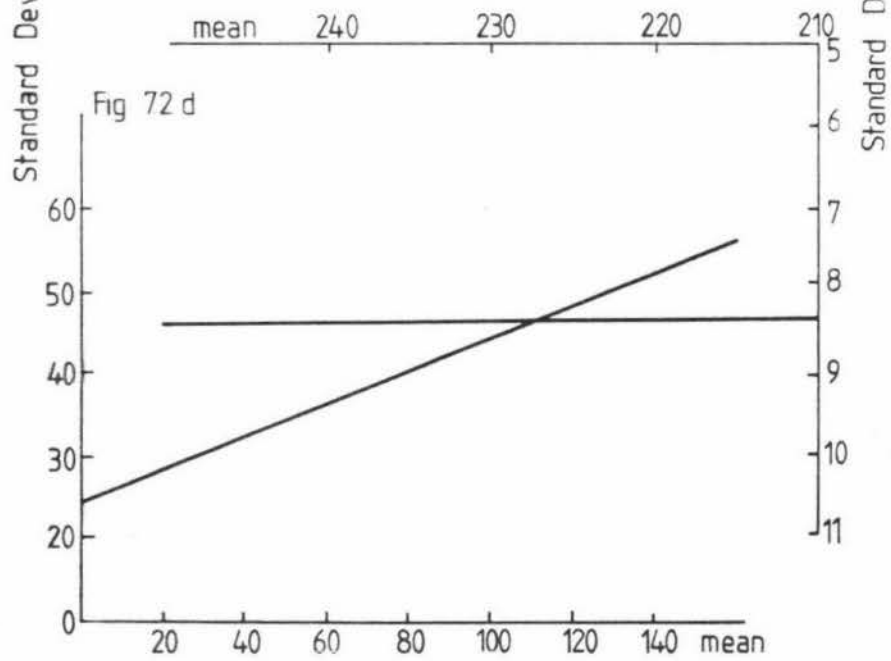


Fig 72 d



The trends exhibited in the graphed regression equations and the correlations were then considered, and particularly for those pairs of variables which had a significant between individual group regression F ratio. This meant that the variables did not vary concomitantly, or in other words, the regressions showed nonparallelism. Therefore an analysis of covariance could not be carried out for these data (Bliss 1970: 460).

The variable average height had a significant F ratio in the table of mean squares before adjustment by covariance. This indicated that there was a significant difference between the means of some or all of the individual group regressions. For these regressions, and those that showed nonparallelism, multiple t-tests were undertaken to test whether the significant F ratios were due to differences between adult males and adult females, adult females and juveniles, or both.

For the variables that showed parallelism an analysis of covariance was undertaken. This enabled me to identify the effect of each independent variable on the dependent variable it was paired with. Wind speed was always an independent variable. Each of the other three variables (average height, flaps and height changes) were paired alternately as independent and dependent variables.

The data were then sorted according to the second and third classifications: flying speed and wind direction relative to flying direction and habitats hunted. An analysis of covariance was carried out for those pairs of variables that showed parallelism. The original means and correlations were considered for those that did not show parallelism. A significant between groups F ratio from the analysis of variance of the adjusted means indicated that there were significant differences due to either between classification, within classification or interaction differences. Those differences considered biologically important were tested using multiple t-tests.

A multiple regression analysis of the data was not carried out because there was no programme available for the IBM 1620 computer to do so.

3.ii Season. There were insufficient data to make further subdivisions with respect to season. Because more of one age or sex class of

Australasian harrier was at Pukepuke Lagoon during some seasons it may be suggested that a seasonal bias exists in the data. For example, more juveniles were at Pukepuke Lagoon during autumn. If average wind speeds were higher when more data were collected for one age and sex class than another it may be suggested that this accounts for differences between the classes in other variables. Indeed the mean wind speed for data from adult females was higher than that from adult males which was in turn higher than that from juveniles.

If the range of wind velocities measured at Pukepuke Lagoon had had a pronounced biological effect on the hunting behaviour parameters, then statistically significant correlations would have been produced when wind speed was paired with some or all of the three dependent variables. The total estimates correlation coefficients for the dependent variables paired with wind speed range from -0.097 to 0.048 which are not statistically significant. Hence the measured range of wind speeds did not have a marked biological effect on the hunting behaviour parameters and the differences between the average wind speeds for the age and sex classes are negligible.

RESULTS

The results of the computer analysis are presented in detail in Tables A.16 - A.43 of the appendices. In the results the individual group regressions, adjusted means, correlations and results of the multiple t-tests are presented. I have included only those t-tests that are pertinent to the hypothesis that the three age and sex classes had different degrees of manoeuvrability, conspicuousness, energy use and experience.

A. WHEN AVERAGE HEIGHT IS THE DEPENDENT VARIABLE

A.1.i Overall age and sex comparison

For all nine individual group regressions (Figures 7.3.a-c), adult females flew significantly higher than juveniles which in turn flew significantly higher than adult males (Table 7.1.a-c (i-iv)). This occurred for all wind directions and flying speeds (Table 7.1.d (i-iii)) and over all habitats (Table 7.1.f (i-iii)).

FIGURE 7.3.a

Adult female: $Y = 0.085X + 140.48$
 $r = 0.0426; P = NS$
 Juvenile : $Y = -0.083X + 139.81$
 $r = -0.0734; P = NS$
 Adult male : $Y = -0.147X + 135.76$
 $r = -0.0954; P = NS$

FIGURE 7.3.b

Adult female: $Y = -0.161X + 143.25$
 $r = -0.0668; P = NS$
 Juvenile : $Y = 0.247X + 136.84$
 $r = 0.1243; P = NS$
 Adult male : $Y = 0.105X + 133.28$
 $r = 0.0616; P = NS$

FIGURE 7.3.c

Adult female: $Y = -0.369X + 222.88$
 $r = -0.2990; P < 0.01$
 Juvenile : $Y = -0.170X + 176.68$
 $r = -0.1931; P < 0.05$
 Adult Male : $Y = -0.218X + 182.40$
 $r = -0.2284; P < 0.05$

FIGURE 7.3.d

Adult female: $Y = -0.069X + 221.56$
 $r = -0.0431; P = NS$
 Juvenile : $Y = -0.359X + 224.33$
 $r = -0.2901; P < 0.01$
 Adult male : $Y = -0.072X + 221.57$
 $r = -0.0459; P = NS$

FIGURE 7.3.e

Adult female: $Y = 0.1862X + 218.64$
 $r = 0.0956; P = NS$
 Juvenile : $Y = -0.301X + 223.79$
 $r = -0.1336; P = NS$
 Adult male : $Y = -0.221X + 223.11$
 $r = -0.1267; P = NS$

FIGURE 7.3.f

Adult female: $Y = -0.242X + 255.10$
 $r = -0.2990; P < 0.01$
 Juvenile : $Y = -0.219X + 251.49$
 $r = -0.1931; P < 0.05$
 Adult male : $Y = -0.228X + 251.53$
 $r = -0.2228; P < 0.05$

FIGURE 7.3.g

Adult female: $Y = 0.021X + 6.67$
 $r = 0.0426; P = NS$
 Juvenile : $Y = -0.067X + 18.50$
 $r = -0.0734; P = NS$
 Adult male : $Y = -0.062X + 18.08$
 $r = -0.0954; P = NS$

FIGURE 7.3.h

Adult female: $Y = 0.051X + 9.07$
 $r = 0.0418; P = NS$
 Juvenile : $Y = 0.126X + 8.04$
 $r = 0.0693; P = NS$
 Adult male : $Y = 0.032X + 9.37$
 $r = 0.0293; P = NS$

FIGURE 7.3.i

Adult female: $Y = -0.027X + 15.55$
 $r = -0.0431; P = NS$
 Juvenile : $Y = -0.234X + 60.87$
 $r = -0.2901; P < 0.01$
 Adult male : $Y = -0.024X + 16.17$
 $r = -0.0459; P = NS$

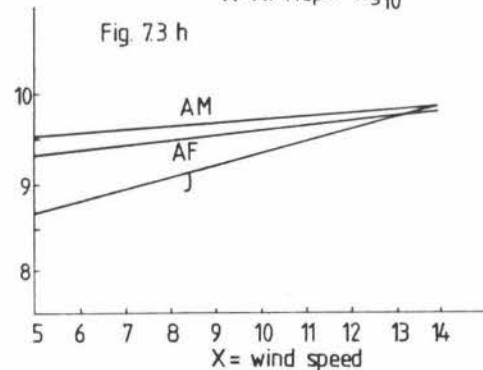
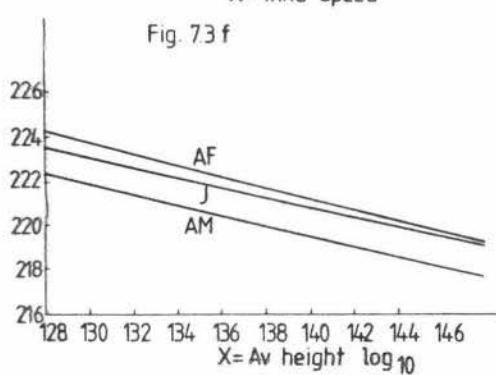
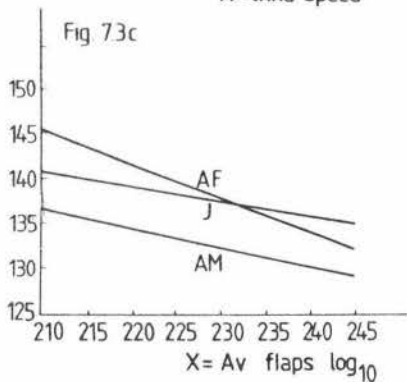
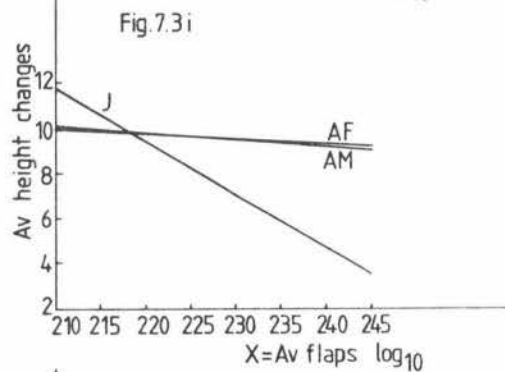
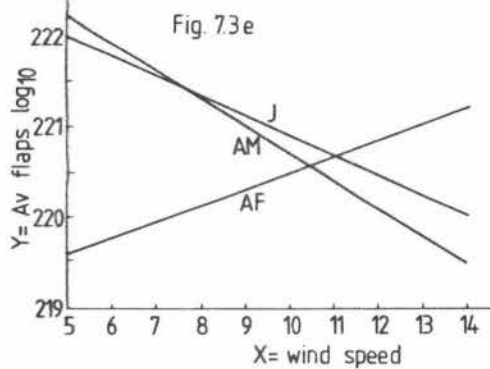
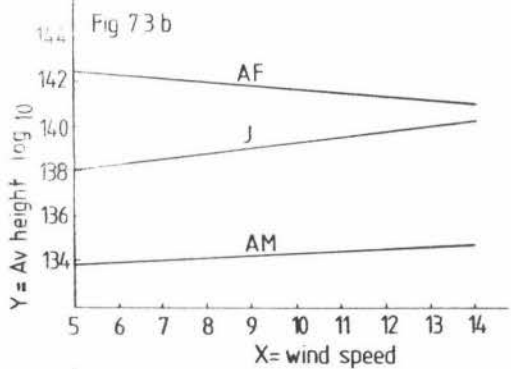
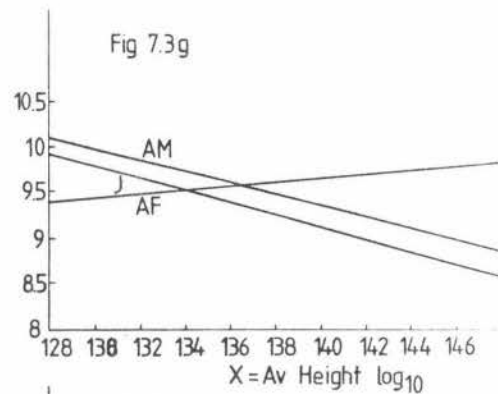
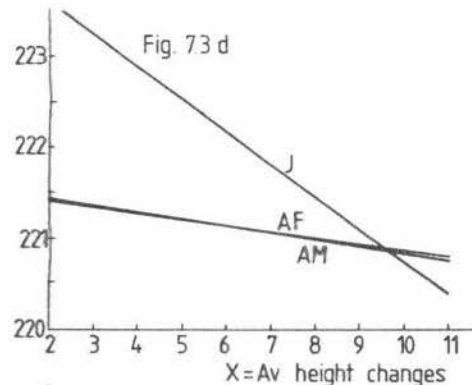
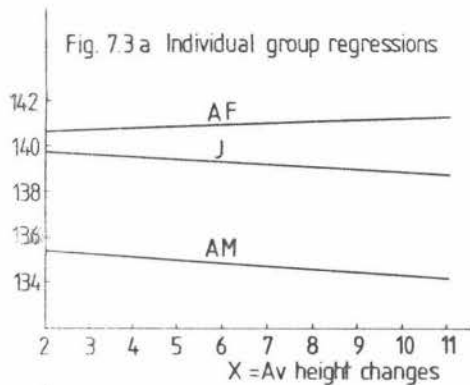


Table 7.1: When average height is the dependent variable
 Classifications: Overall sex and age

Table 7.1.a: Overall sex and age comparison: Y = Average height,
 X = Average flaps

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
Juveniles	221.04	139.08	.51	-.193	NS
Adult Males	220.87	134.33	.44	-.222	P<0.05
Adult Females	220.88	141.29	.57	-.298	P<0.01

Table 7.1.b: Overall sex and age comparison: Y = Average height,
 X = Winds

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
Juveniles	8.96	139.17	.53	.124	NS
Adult Males	10.14	134.35	.45	.061	NS
Adult Females	12.09	141.14	.59	-.066	NS

Table 7.1.c: Overall sex and age comparison: Y = Average height,
 X = Average height changes

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
Juveniles	9.17	139.02	.53	-.073	NS
Adult Males	9.69	134.35	.45	-.095	NS
Adult Females	9.67	141.31	.58	.042	NS

Table 7.1: When average height is the dependent variable: t-tests

Table	Comparison	Class	t	Significance level
7.1.a	(i) Means of individual group	AF v AM	16.572	P<0.001
	(ii) regressions	AF v J	5.622	P<0.001
	(iii) Slopes of individual group	AF v AM	1.292	NS
	(iv) regressions	AF v J	1.665	NS
7.1.b	(i) Means of individual group	AF v AM	18.848	P<0.001
	(ii) regressions	AF v J	4.988	P<0.001
	(iii) Adjusted means	AF v AM	9.142	P<0.001
	(iv)	AF v J	2.488	P<0.02
7.1.c	(i) Means of individual group	AF v AM	19.337	P<0.001
	(ii) regressions	AF v J	5.810	P<0.001
7.1.d	(i) Total average height	J v AM	6.802	P<0.001
	(ii) comparison	J v AF	3.078	P<0.001
	(iii)	AM v AF	9.298	P<0.001
	(iv) Average height into head wind	J	0.372	NS
	(v) v cross wind and tail wind	AM	3.856	P<0.001
	(vi)	AF	2.084	P<0.05
	(vii) Interactions between ages and	J v AM	4.829	P<0.001
	(viii) sexes	J v AF	2.658	P<0.01
	(ix)	AM v AF	1.782	NS
	(x) Average height at speed slow	J	1.870	NS
	(xi) v speed normal	AM	4.518	P<0.001
	(xii)	AF	0.555	NS
	(xiii) Interactions between ages and	J v AM	3.298	P<0.001
	(xiv) sexes	J v AF	1.845	NS
	(xv)	AM v AF	5.129	P<0.001
7.1.f	(i) Total average height comparison	J v AM	6.266	P<0.001
	(ii)	J v AF	3.048	P<0.01
	(iii)	AM v AF	9.125	P<0.001
	(iv) Average height over cabbage	J	0.744	NS
	(v) trees and flax v other habitats	AM	4.750	P<0.001
	(vi)	AF	3.545	P<0.001
	(vii) Interactions between ages	J v AM	9.980	P<0.001
	(viii) and sexes	J v AF	7.284	P<0.001
7.1.h	(i) Average height over farm drain	J	0.746	NS
	(ii) and pond vegetation v other	AM	3.346	P<0.001
	(iii) habitats	AF	1.409	NS
	(iv) Interactions between ages and	J v AM	4.485	P<0.001
	(v) sexes	J v AF	3.060	P<0.01
	(vi)	AM v AF	1.154	NS

Note: AM = adult male, AF = adult female, J = juveniles, NS = not significant.

From the correlations given for Figures 7.3.a-c, it may be seen that average flaps is the only independent variable that is significantly correlated with average height. The average number of flaps increased for all three age and sex classes as flying height decreased (Figure 7.3.c, Table 7.1.d). Because they flew highest, for a given decrease in flying height, adult females showed the least increase in average flaps. Juveniles made the greatest increase in average flaps although they did not flap significantly more than adult females (Table 7.1.a (iv)).

For all three age and sex classes neither wind speed nor the average number of height changes had a significant overall effect on average height flown.

A.2 Wind direction and flying speed

A.2.i Y = average height, X = average flaps. When the average heights flown into a head wind by all three classes were compared with the heights flown with a tail wind or a cross wind it was calculated that only juveniles did not fly significantly lower into a head wind (Table 7.1.d (iv-vi)). Unlike adult females and juveniles, adult males flew significantly lower when they flew slowly into a head wind than when they flew at normal speed (Table 7.1.d (x - xii)).

A.2.ii Y = average height, X = winds. While juveniles hovered at higher heights as wind speed increased, adults hovered at lower heights and adult females hovered significantly lower. By hovering at lower heights during strong winds adults may have been able to hold their position over quarry more successfully because they would have been buffeted by lower velocity winds. This is because wind speed increases linearly with the logarithm of height at heights below 20 m (Lockwood 1974).

A.2.iii Y = average height, X = average height changes. The correlations in Table 7.1.e demonstrate that when adult males and adult females flew lower they changed height more often or changed height at a similar rate. Changing height more often would have helped to prevent their flapping rate from increasing markedly as average flaps and average height changes are negatively correlated (Table 7.1.c). When juveniles flew slowly into a head wind and flew lower they changed height significantly fewer

Table 7.1: When average height is the dependent variable
 Classifications: Wind direction and flying speed

Table 7.1.d: Wind direction and flying speed: Y = Average height,
 X = Average flaps

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
<u>Juvenile</u>					
a	220.54	138.04	1.04	-.262	P<0.05
b	222.07	139.94	.86	-.033	NS
c	238.85	135.97	1.95	-.060	NS
d	217.52	139.02	1.18	-.159	NS
e	214.58	139.60	1.60	.004	NS
<u>Adult Male</u>					
a	221.58	131.52	.93	-.310	P<0.01
b	220.50	134.64	.72	-.008	NS
c	236.78	130.68	1.60	.079	NS
d	217.72	137.19	.94	-.068	NS
e	215.66	135.87	1.62	-.143	NS
<u>Adult Female</u>					
a	220.73	142.16	1.04	-.223	P<0.05
b	221.91	140.03	.98	-.341	P<0.01
c	239.77	130.46	2.99	.208	NS
d	218.64	142.23	1.03	-.045	NS
e	214.58	146.75	2.48	-.123	NS

Table 7.1.e: Wind direction and flying speed: Y = Average height,
 X = Average height changes

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
<u>Juvenile</u>					
a	9.75	138.12	1.05	.279	P<0.02
b	9.82	139.81	.86	-.190	NS
c	4.28	132.83	1.87	.054	NS
d	9.30	139.49	1.18	-.186	NS
e	10.16	140.59	1.59	-.318	NS
<u>Adult Male</u>					
a	10.64	131.54	.94	-.258	P<0.02
b	10.38	134.79	.72	-.058	NS
c	8.50	128.26	1.50	.138	NS
d	9.18	137.62	.93	.002	NS
e	8.83	136.57	1.61	-.183	NS
<u>Adult Female</u>					
a	10.27	142.27	1.04	.085	NS
b	9.25	139.86	.99	-.095	NS
c	3.58	127.11	2.95	.096	NS
d	10.92	142.70	1.04	-.092	NS
e	6.19	147.34	2.49	.239	NS

Group: a = head wind, speed slow d = cross wind, speed normal
 b = head wind, speed normal e = tail wind, speed normal
 c = head wind, hover

Table 7.1: When average height is the dependent variable
Classification: habitats hunted

Table 7.1.f: Habitats hunted: Y = Average height, X = Average flaps

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
<u>Juveniles</u>				
w	223.08	138.74	1.22	-.343 P<0.02
x	218.19	137.61	.86	-.110 NS
y	222.89	139.89	.73	-.179 NS
z	216.35	140.58	2.23	-.409 NS
<u>Adult Males</u>				
w	223.14	131.84	1.08	-.304 P<0.02
x	220.24	133.19	.78	-.399 P<0.01
y	222.42	138.37	.65	-.308 P<0.01
z	220.89	127.24	1.68	-.217 NS
<u>Adult Females</u>				
w	222.15	138.43	2.23	-.235 NS
x	219.69	139.21	1.13	-.263 NS
y	221.77	142.99	.68	-.387 P<0.01
z	216.42	134.79	1.91	-.286 NS

Table 7.1.h: Habitats hunted: Y = Average height,
X = Average height changes

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
<u>Juveniles</u>				
w	8.16	138.15	1.28	-.032 NS
x	8.28	138.40	.89	.034 NS
y	10.41	139.50	.76	-.129 NS
z	6.88	141.81	2.33	-.267 NS
<u>Adult Males</u>				
w	9.49	131.32	1.12	-.271 P<0.05
x	9.81	133.49	.81	-.082 NS
y	9.74	138.07	.68	.012 NS
z	10.18	127.39	1.75	-.081 NS
<u>Adult Females</u>				
w	8.53	138.13	2.32	.041 NS
x	10.56	139.71	1.18	.005 NS
y	9.44	142.85	.71	.051 NS
z	9.84	136.18	1.98	.359 NS

Group: w = farm drain and pond vegetation
x = dune grasses and lupins
y = raupo
z = cabbage trees and flax

times (Table 7.1.e) and therefore would have flapped at a significantly higher rate. The evidence for this conclusion is in the first correlation in Table 7.2.f which is significant and negative.

A.3 Habitats hunted

A.3.i Y = average height, X = average flaps. Adult males often flew below the cabbage tree canopy and above the flax subcanopy to surprise prey by suddenly appearing from behind tree trunks. Adult females employed this hunting technique less often. Juveniles generally flew above the cabbage trees (Table 7.1.f (iv-vi)).

A.3.ii Y = average height, X = average height changes. As well as flying low over and through cabbage trees and flax, adult males flew significantly lower over farm drain and pond vegetation than they flew over all other habitats combined (Table 7.1.h (i-iii)). The differences between the heights flown by adults over farm drain and pond vegetation and the other habitats were significantly greater than the differences between the heights flown by the juveniles (Table 7.1.h (iv-vi)). Thus juveniles tended to fly at a more intermediate height over both the highest and lowest vegetations rather than significantly lower as the adults indicated was possible.

B. WHEN AVERAGE FLAPS IS THE DEPENDENT VARIABLE

B.1 Overall age and sex comparison

From the significant correlations for Figure 7.3.f it may be reasoned that changes in average height resulted in significant changes in the average number of flaps for all three age and sex classes. This important result is the basis of many of the significant differences between the three classes established from the hunting behaviour comparisons for specified wind directions, flying speeds and habitats. For example, this is seen in Figures 7.3.b and 7.3.e and Table 7.2.a (i-ii): because adult females flew lower as wind speed increased their average number of flaps also increased, while adult males and juveniles flew higher and therefore flapped fewer times as wind speed increased.

The mean number of flaps made by the three classes did not differ significantly when average flaps was paired with the independent

Table 7.2: When average flaps is the dependent variable
 Classifications: Overall sex and age

Table 7.2.a: Overall sex and age comparison: Y = Average flaps,
 X = Winds

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
Juveniles	8.96	220.82	.53	-.133	NS
Adult Males	10.14	220.85	.45	-.126	NS
Adult Females	12.09	221.18	.59	.095	NS

Table 7.2.b: Overall sex and age comparison: Y = Average flaps,
 X = Average height

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
Juveniles	139.05	221.36	.51	-.193	NS
Adult Males	134.34	220.12	.45	-.222	P<0.05
Adult Females	141.30	221.73	.58	-.298	P<0.01

Table 7.2.c: Overall sex and age comparison: Y = Average flaps,
 X = Average height changes

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
Juveniles	9.17	220.96	.52	-.290	P<0.01
Adult Males	9.69	220.91	.45	-.045	NS
Adult Females	9.67	220.92	.57	-.043	NS

Table 7.2: When average flaps is the dependent variable: t-tests

Table	Comparison	Class	t	Significance level
7.2.a	(i) Slopes of individual group	AF v AM	2.033	P<0.05
	(ii) regressions	AF v J	2.015	P<0.05
7.2.b	(i) Adjusted means	AF v AM	2.236	P<0.05
	(ii)	AF v J	0.474	NS
7.2.c	(i) Slopes of individual group	AF v AM	0.011	NS
	(ii) regressions	AF v J	1.766	NS
7.2.e	(i) Total average flaps comparison	J v AM	1.096	NS
	(ii)	J v AF	0.236	NS
	(iii)	AM v AF	0.797	NS
	(iv) Average flaps into head wind	J	6.864	P<0.001
	(v) v cross wind and tail wind	AM	6.138	P<0.001
	(vi)	AF	3.881	P<0.001
	(vii) Interaction between ages and	J v AM	2.656	P<0.01
	(viii) sexes	J v AF	4.165	P<0.001
	(ix)	AM v AF	1.908	NS
	(x) Average flaps when hovering v	J	10.851	P<0.001
	(xi) average flaps for all other	AM	11.875	P<0.001
	(xii) flight	AF	6.884	P<0.001
	(xiii) Interaction between ages and	J v AM	3.291	P<0.001
	(xiv) sexes	J v AF	0.529	NS
	(xv)	AM v AF	2.629	P<0.01
7.2.g	(i) Total average flaps comparison	J v AM	1.516	NS
	(ii)	J v AF	0.677	NS
	(iii)	AM v AF	0.690	NS
	(iv) Average flaps over farm drains	J	4.635	P<0.001
	(v) and raupo v duneland and	AM	2.800	P<0.01
	(vi) cabbage trees	AF	2.707	P<0.01

Note: AM = adult male, AF = adult female, J = juveniles,
NS = not significant.

variables average number of height changes and wind speed (Figures 7.3.d, e). Further, there is only one significant correlation; for juveniles an increase in their average number of height changes brought about a significant decrease in their average number of flaps. This demonstrates that juveniles had a potential advantage over adults.

B.2 Wind speed and flying direction

B.2.i Y = average flaps, X = winds. Changes and differences in average height flown (Table 7.2e (iv-vi)) and not changes in wind speed (Table 7.2.d), caused the significant changes and differences in average number of flaps for: all three classes when they flew with a tail wind and a cross wind, adult males when they flew slowly into a head wind and adult females when they flew at normal speed into a head wind. This was because there was no overall significant correlation between average flaps and wind speed (Table 7.2.a) but there was one between average flaps and average height (Table 7.2.b).

However wind speed certainly influenced flying speed, for in all cases head wind speeds were on average stronger when the Australasian harriers flew slowly than when they flew at normal speed (Table 7.2.d).

B.2.ii Y = average flaps, X = average height. There was no significant overall difference in the average number of flaps made by the three classes for all wind directions and flying speeds (Table 7.2.e (i-iii)) and all habitats (Table 7.2.g (i-iii)).

When the interactions or differences between the number of flaps the three classes made were compared for firstly, when they flew into a head wind and secondly, with a tail wind and cross wind, it was calculated that adult males and adult females had similar differences in the number of flaps they made into the two classes of wind.

All birds flapped significantly more often when they hovered in a head wind than when they flew into or with other winds (Table 7.2.e (x-xii)). From the interactions there was a significant difference between the number of flaps adult males made when they hovered or flew into or with

Table 7.2 When average flaps is the dependent variable
 Classifications: wind direction and flying speed

Table 7.2.d: Wind direction and flying speed: Y = Average flaps,
 X = Winds

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
<u>Juvenile</u>				
a	10.89	220.67	.92	.228 P<0.05
b	8.50	221.69	.76	-.255 P<0.05
c	8.48	238.46	1.62	-.041 NS
d	8.56	217.15	1.03	-.329 P<0.01
e	7.02	213.88	1.40	-.401 P<0.05
<u>Adult Male</u>				
a	13.11	222.19	.83	.002 NS
b	9.57	220.34	.63	-.159 NS
c	8.89	236.48	1.32	.037 NS
d	9.78	217.61	.82	-.346 P<0.01
e	8.86	215.35	1.41	-.487 P<0.01
<u>Adult Female</u>				
a	12.63	221.24	.92	.363 P<0.01
b	12.16	222.32	.87	-.066 NS
c	13.70	240.51	2.57	.357 NS
d	11.47	218.90	.91	.019 NS
e	10.92	214.72	2.17	-.485 P<0.05

Table 7.2.e: Wind direction and flying speed: Y = Average flaps,
 X = Average height

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
<u>Juvenile</u>				
a	138.10	220.59	.92	-.262 P<0.05
b	139.78	222.31	.75	-.033 NS
c	133.36	238.37	1.62	-.060 NS
d	139.52	217.73	1.03	-.159 NS
e	140.53	214.91	1.39	.004 NS
<u>Adult Male</u>				
a	131.43	220.88	.84	-.310 P<0.01
b	134.70	220.17	.64	-.008 NS
c	128.37	235.74	1.34	.079 NS
d	137.66	217.72	.82	-.068 NS
e	136.64	215.55	1.41	-.143 NS
<u>Adult Female</u>				
a	142.19	221.25	.92	-.223 P<0.05
b	139.89	222.17	.86	-.341 P<0.01
c	127.71	238.66	2.58	.208 NS
d	142.56	219.20	.91	-.045 NS
e	147.68	215.71	2.18	-.123 NS

Group: a = head wind, speed slow
 b = head wind, speed normal
 c = head wind, hover

d = cross wind, speed normal
 e = tail wind, speed normal

Table 7.2: When average flaps is the dependent variable
 Classifications: (i) wind direction and flying speed
 (ii) habitats hunted

Table 7.2.f: Wind direction and flying speed: Y = Average flaps,
 X = Average height changes

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
<u>Juvenile</u>				
a	9.75	220.57	.92	-.256 P<0.05
b	9.82	222.12	.75	-.401 P<0.01
c	4.28	238.03	1.63	-.332 NS
d	9.30	217.48	1.03	-.202 NS
e	10.16	214.68	1.39	-.112 NS
<u>Adult Male</u>				
a	10.64	221.76	.82	.043 NS
b	10.38	220.63	.63	-.135 NS
c	8.50	236.62	1.31	.009 NS
d	9.18	217.66	.82	-.198 P<0.05
e	8.83	215.55	1.41	.135 NS
<u>Adult Female</u>				
a	10.27	220.85	.91	-.003 NS
b	9.25	221.87	.86	-.003 NS
c	3.58	238.83	2.57	.256 NS
d	10.92	218.86	.90	.125 NS
e	6.19	214.05	2.17	.073 NS

Table 7.2.g: Habitats hunted: Y = Average flaps, X = Winds

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
<u>Juvenile</u>				
w	9.68	222.94	1.29	-.160 NS
x	8.94	217.89	.90	-.300 P<0.01
y	8.62	222.52	.77	-.048 NS
z	9.87	216.25	2.34	-.051 NS
<u>Adult Male</u>				
w	11.02	223.28	1.13	-.069 NS
x	9.09	219.98	.82	-.229 P<0.05
y	10.75	222.51	.69	-.188 NS
z	10.92	221.02	1.77	-.135 NS
<u>Adult Female</u>				
w	14.90	223.12	2.36	.049 NS
x	9.55	219.53	1.19	.052 NS
y	12.59	222.25	.73	.112 NS
z	13.22	217.04	2.01	-.165 NS

Group: a = head wind, speed slow w = farm drain & pond vegetation
 b = head wind, speed normal x = dune grasses & lupins
 c = head wind, hover y = raupo
 d = cross wind, speed normal z = cabbage trees & flax
 e = tailwind, speed normal

other winds when compared with those made by adult females and juveniles (Table 7.2.e (xiii-xv)). This was because adult males flapped fewer times when they hovered than adult females and juveniles, but made a similar number of flaps on all other occasions.

B.2.iii Y = average flaps, X = average height changes. In Table 7.2.f it may be seen that only juveniles flapped significantly fewer times into a head wind if they changed height more frequently. However they did not exploit this advantage for they changed height slightly less often than adults did and they flapped at a similar rate.

B.3 Habitats

B.3.i Y = average flaps, X = winds. All birds flapped more often when they flew over farm drain and pond vegetation and raupo than when they flew over duneland and cabbage trees and flax (Table 7.2.g (iv-vi)). Duneland and cabbage trees and flax are considerably more contoured habitats than the others. Increased lift would have been obtained from winds passing over these contours and this would have enabled all birds to flap less often. This suggestion is supported by the correlations in Table 7.2.g where the only significant decreases in average number of flaps occurred as wind speed increased when juveniles and adult males flew over duneland.

From a study of the mean wind speeds in Table 7.2.g it may be seen that adults hunted over duneland most often when wind speeds were low. Juveniles did not exploit this habitat under these conditions. The increased lift from contoured duneland would have helped all birds to flap less when only light winds were blowing, for despite the overall negative correlation between wind speed and average flaps, Australasian harriers made comparatively few flaps over this habitat in light winds.

C WHEN AVERAGE HEIGHT CHANGES IS THE DEPENDENT VARIABLE

C.1 Overall age and sex comparison

All three age and sex classes changed height more frequently and at a similar rate as wind speed increased for there is no significant difference between the slopes of the individual group regressions in Figure 7.3.h. No significant correlations between wind speed and average

Table 7.3: When average height changes is the dependent variable
Classification: overall age and sex

Table 7.3.a: Overall age and sex comparison: Y = Average height changes,
X = Average flaps

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
Juveniles	221.04	9.18	.36	-.290 P<0.01
Adult Males	220.87	9.69	.31	-.045 NS
Adult Females	220.88	9.67	.40	-.043 NS

Table 7.3.b: Overall age and sex comparison: Y = Average height changes,
X = Winds

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
Juveniles	8.96	9.25	.37	.069 NS
Adult Males	10.14	9.70	.31	.029 NS
Adult Females	12.09	9.56	.41	.041 NS

Table 7.3.c: Overall age and sex comparison: Y = Average height changes,
X = Average height

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation
Juveniles	139.05	9.22	.37	-.073 NS
Adult Males	134.34	9.57	.32	-.095 NS
Adult Females	141.30	9.81	.41	.042 NS

Table 7.3: When average height changes is the dependent variable:
t-tests

Table	Comparison	Class	t	Significance level
7.3.a	(i) Slopes of individual group	AF v AM	0.040	NS
	(ii) regressions	AF v J	2.092	P<0.05
7.3.d	(i) Total average height changes	J v AM	1.069	NS
	(ii) comparison	J v AF	0.448	NS
	(iii)	AM v AF	0.546	NS
	(iv) Average height changes during	J	3.915	P<0.001
	(v) ^{head} wind hover v all other flight	AM	1.283	NS
	(vi)	AF	2.986	P<0.01
	(vii) Interactions between ages and	J v AM	8.054	P<0.001
	(viii) sexes	J v AF	1.760	NS
	(ix)	AM v AF	9.589	P<0.001
	(x) Average changes during head	J	0.180	NS
	(xi) wind slow and normal v cross	AM	1.665	NS
	(xii) wind and tail wind	AF	0.699	NS

Note: AM = adult male, AF = adult female, J = juveniles,
NS = not significant.

Table 7.3: When average height changes is the dependent variable
 Classifications: (i) wind direction and flying speed
 (ii) habitats hunted

Table 7.3.d: Wind direction and flying speed: Y = Average height changes,
 X = Winds

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
<u>Juvenile</u>					
a	10.89	9.73	.75	.043	NS
b	8.50	9.89	.62	.105	NS
c	8.48	4.35	1.33	-.052	NS
d	8.56	9.37	.84	.002	NS
e	7.02	10.29	1.14	.208	NS
<u>Adult Male</u>					
a	13.11	10.52	.68	.044	NS
b	9.57	10.41	.52	.069	NS
c	8.89	8.56	1.08	-.409	P<0.02
d	9.78	9.20	.67	.084	NS
e	8.86	8.89	1.16	-.119	NS
<u>Adult Female</u>					
a	12.63	10.17	.75	.095	NS
b	12.16	9.17	.71	-.064	NS
c	13.70	3.43	2.10	-.159	NS
d	11.47	10.87	.74	.177	NS
e	10.92	6.16	1.77	.130	NS

Table 7.3.e: Habitats hunted: Y = Average height changes, X = Winds

Group	X Mean	Adjusted Y Mean	Standard error Adjusted Y	Correlation	
<u>Juvenile</u>					
w	9.68	8.21	.93	.084	NS
x	8.94	8.38	.65	.202	P<0.05
y	8.62	10.54	.55	.034	NS
z	9.87	6.91	1.69	.089	NS
<u>Adult Male</u>					
w	11.02	9.44	.82	.027	NS
x	9.09	9.90	.59	-.097	NS
y	10.75	9.70	.49	.125	NS
z	10.92	10.13	1.27	-.036	NS
<u>Adult Female</u>					
w	14.90	8.19	1.70	.150	NS
x	9.55	10.62	.86	-.055	NS
y	12.59	9.27	.52	.132	NS
z	13.22	9.62	1.44	-.164	NS

Group: a = head wind, speed slow w = farm drain & pond vegetation
 b = head wind, speed normal x = dune grasses & lupins
 c = head wind, hover y = raupo
 d = cross wind, speed normal z = cabbage trees & flax
 e = tail wind, speed normal

number of height changes were recorded. However, juveniles changed height less frequently than adults did at low wind speeds and flapped fewer times. Juveniles also had the ability to flap significantly less often than adults if they changed height more often (Figure 7.3.i and Table 7.3.a (ii)).

C.2 Wind direction and flying speed

c.2.i Y = average height changes, X = winds. It was calculated that only juveniles and adult females changed height significantly fewer times when they hovered (Table 7.3.d (iv-vi)). Adult males changed height almost twice as often as the other classes. This is a significant difference (Table 7.3.d (vii-ix)). For all Australasian harriers the mean number of height changes did not differ significantly other than when they hovered (Table 7.3.d (x-xii)). Hovering was very energy demanding compared with other hunting flights and by changing height more often adult males flapped significantly fewer times than adult females and juveniles and therefore used less energy (Table 7.2.e (xiii-xv)).

C.3 Habitats

C.3.i Y = average height changes, X = winds. As wind speeds increased juveniles changed height more frequently over all habitats and significantly more over duneland. Conversely, both adult males and adult females changed height less often over the two strongly contoured habitats: duneland and cabbage trees and flax (Table 7.3.e). Like juveniles, adults changed height more frequently over farm drain and pond vegetation and raupo where less lift from wind passing over contours would have been obtained.

D. PROPORTION OF TIME ALLOCATED TO EACH FLYING SPEED AND WIND DIRECTION

All three age and sex classes spent similarly large proportions of their total hunting time flying into a head wind or with a cross wind. On average they flew into a head wind for 72.4% of the time and with a cross wind for a further 19.9% (Table 7.4). Flying with a tail wind and circling took up only 7.7% of hunting time.

Adult males (42.0%) spent a greater proportion of their time hunting into a head wind at normal speed than adult females (35.2%) and juveniles

Table 7.4: Time recorded for Australasian harrier flying speeds and wind direction relative to flying direction,

Harrier speed and flying direction	Adult Male		Adult Female		Juvenile		Total	
	Time (sec)	% Time	Time (sec)	% Time	Time (sec)	% Time	Time (sec)	% Time
Head wind/slow	1,329	26.3	1,254	35.1	1,348	32.2	3,931	30.7
Head wind/normal	2,124	42.0	1,258	35.2	1,456	34.8	4,838	37.8
Head wind/hover	215	4.3	123	3.4	168	4.0	506	3.9
Cross wind/normal	988	19.5	853	23.9	704	16.8	2,545	19.9
Tail wind/normal	187	3.7	56	1.6	276	6.6	519	4.0
Tail wind/fast	62	1.2	11	0.3	18	0.4	91	0.7
Circling/normal	152	3.0	19	0.5	215	5.2	386	3.0
TOTAL	5,058	100.0	3,574	100.0	4,185	100.0	12,817	100.0
Head wind	3,668	72.6	2,635	73.7	2,972	71.0	9,275	72.4
Cross wind	988	19.5	123	23.9	704	16.8	2,545	19.9
Tail wind	249	4.9	67	1.9	294	7.0	610	4.7
Circling	152	3.0	19	0.5	215	5.2	386	3.0
TOTAL	5,058	100.0	3,574	100.0	4,185	100.0	12,817	100.0

(34.8%). Adult females and juveniles flew slowly into a head wind more often. However this difference is not significant. Although the difference was small, adult males also flew fast with a tail wind more frequently than the other birds.

E.i DIFFERENTIAL HABITAT USE

Four hundred and thirty nine observations of individually marked Australasian harriers hunting over five habitats are recorded in Table 7.5, while the significance levels and relative distribution of the age and sex classes over these habitats are compared in Table 7.6.

Adult males hunted over duneland significantly more often and over raupo less often than did adult females. There is also a significant difference between the degree to which adult males and juvenile females hunted over the five habitats. This was mainly due to adult males hunting over and through cabbage trees and flax and pine plantations more frequently, and over raupo less frequently than juvenile females. It is pertinent that small agile passerines were much more abundant in duneland and pines, where adult males hunted more frequently, than in raupo (Table 5.7). Adult males and juvenile males hunted over the five habitats to similar degrees.

Adult females did not exhibit significant differences from either juvenile females or juvenile males in the extent to which they hunted over the habitats. Although not significantly different, their habitat preferences were more similar to those of juvenile females than juvenile males. Juvenile males and females were also not significantly different in their differential selection of hunting habitat.

Thus both age and sex had an influence on habitat preference during hunting. While the two adult sexes were most different, inexperience tended to draw the juvenile sexes closer together and towards the adult females in their choice of hunting habitat. Therefore adult males received the least intraspecific competition for hunting habitat while juvenile females received the most.

E.ii Time over habitats. Table 7.7 is a summary of the times the three classes spent hunting into a head wind at slow and normal speeds over the five habitats. These data provide information that eliminates

Table 7.5: Number and percentage of Australasian harriers observed hunting over five habitats.

	Adult Male		Juvenile Male		Adult Female		Juvenile Female		Total	
	Number harriers observed	% observed	Number harriers observed	% observed	Number harriers observed	% observed	Number harriers observed	% observed	Number harriers observed	% observed
Farm drain and pond vegetation	21	11.5	9	12.7	17	13.7	12	19.3	59	13.4
Duneland	77	42.3	28	40.8	34	27.5	19	30.6	158	36.0
Raupo	57	31.3	29	39.5	60	48.4	28	45.2	174	39.6
Cabbage trees and flax	10	5.5	4	5.6	7	5.6	3	4.8	24	5.5
Pines	17	9.4	1	1.4	6	4.8	0	0	24	5.5
TOTAL	182	100.0	71	100.0	124	100.0	62	100.0	439	100.0

Table 7.6: Chi-square test of relative distribution of Harrier age and sex classes over five habitats.

Compared Harrier classes	χ^2	Significance Level
adult male : adult female	11.49	P<0.01
adult male : juvenile male	3.16	NS
adult male : juvenile female	9.95	P<0.02
adult female: juvenile male	3.21	NS
adult female: juvenile female	2.54	NS
juvenile male:juvenile female	2.00	NS

Table 7.7: Time spent hunting over habitats into a head wind at slow and normal speeds.

	Adult Male		Juvenile		Adult Female		Total									
	Head wind Speed Slow		Head wind Speed Normal		Head wind Speed Slow		Head wind Speed Normal		Head wind Speed Slow		Head wind Speed Normal					
	Time (sec)	% Time	Time (sec)	% Time	Time (sec)	% Time	Time (sec)	% Time	Time (sec)	% Time	Time (sec)	% Time				
Farm drain and pond vegetation	335	25.2	201	9.5	294	21.8	208	14.3	129	10.3	39	3.1	758	19.3	448	9.3
Duneland	321	24.1	636	29.9	374	27.8	464	31.9	250	19.9	188	14.9	945	24.0	1288	26.6
Raupo	489	36.8	889	41.8	639	47.4	712	48.9	816	65.0	887	70.5	1944	49.4	2488	51.4
Cabbage trees and flax	162	12.2	196	9.2	41	3.0	72	4.9	59	4.8	144	11.5	262	6.7	412	8.5
Pines	22	1.7	202	9.6	0	0	0	0	0	0	0	0	22	0.6	202	4.2
TOTAL	1329	100.0	2124	100.0	1348	100.0	1456	100.0	1254	100.0	1258	100.0	3931	100.0	4838	100.0

one of the possible answers to the question: why did adult females fly lower at normal speed into a head wind than when they flew slowly? This result appears to contradict the first assumption made in the Hypothesis.

All Australasian harriers generally flew higher as habitat height increased (Table 7.1.f). It is therefore possible that adult females spent significantly more time over taller vegetation when they flew slowly into a head wind and that this accounted for their flying higher under these conditions. From Table 7.7 it may be seen that the reverse was true and that they flew over the shortest vegetation, found alongside farm drains and ponds, for proportionally longer when they flew slowly. This was true for all classes.

This provides a quantified example of how the type of prey hunted was able to influence hunting speed. Frogs were by far the most abundant prey in farm drain and pond vegetation. By flying slowly all Australasian harriers would have increased the probability of their sighting these less agile but well camouflaged prey. Had they generally flown faster they may easily have missed seeing these prey. Conversely, had the prey been agile adult passerines they may have readily escaped from a slow flying Australasian harrier.

DISCUSSION

Although there were no significant overall differences between the average number of flaps and average number of height changes made by the three age and sex classes, adult males would have been seen less readily by prey than the others because they flew significantly lower. On the basis of flying height, different degrees of aerial manoeuvrability would have been required by the classes when they attacked prey because adult females flew significantly higher than juveniles which flew significantly higher than adult males. Provided they also flew as fast as the other classes, adult males would therefore have needed to be the most manoeuvrable if they were to have halted their forward momentum on sighting prey and initiated a successful dive attack. On average adult males flew faster than adult females and juveniles and therefore should have caught more agile prey. This conclusion is supported by the diet data (Table 5.9).

Adult females, which were heavier than adult males and juveniles and had the highest wing loading (Table 2.2), would have struck prey with greater force when they dived from a greater height. This greater striking force, coupled with larger and stronger feet, would have enabled them to kill larger and stronger prey. Females took significantly more large (>200 g) prey than males (Table 5.9). Prey would have had more time to react and escape from adult females which flew higher and slower. Thus the hunting behaviour data indicate that they would have been less successful at catching agile prey. This is also supported by the diet data.

If wing loading is taken as a quantitative indicator of aerial buoyancy (Brown and Amadon 1968: 62) then juveniles, with slightly lower wing loadings than the adults of their respective sexes, should on average have flapped less often than adults. However they flapped as often or more often, particularly when they flew in strong winds and into head winds. The juveniles also flew higher than midway between the heights flown by the adult sexes. Therefore they were not exploiting their potential hunting ability as dictated by their morphology to its fullest, and the disadvantageous effects of their inexperience were greatest when they were flying under testing weather conditions.

Thus the general results I have obtained on the hunting behaviour of the three Australasian harrier age and sex classes agree with Nieboer's (1973) hypothesis that male harriers are more manoeuvrable than females. In a broad sense my results also support the contention of Schipper *et al.* (1975) who stated that intraspecific differences between adult males and adult females would be greater if juveniles were not also classed as "females". However juveniles have emerged from this study as a distinct class whose hunting behaviour characteristics did not always fit neatly between those of adult males and adult females. This I believe was largely due to their inexperience.

The broad trends discussed above do not, however, reveal the exact nature of many of the interactions that took place. For example, the result that showed that adult females flew higher when they flew slowly into a head wind than when they flew at normal speed questions the validity of a basic assumption I made in the Hypothesis. That is: all Australasian harriers flew as low and as fast as they could while still

being able to stop to take any prey sighted. If the behaviour of the adult females, when flying into a head wind, is compared with that of the adult males and juveniles then the reasons for the adult females' behaviour may be elucidated.

When they flew slowly into a head wind adult males and juveniles flew lower than they did at normal speed. Wind speeds were on average strongest when all birds flew slowly into a head wind. To fly at normal speed for long periods into these stronger head winds may have demanded too much energy. If the birds were unable to fly at normal speed then by flying lower adult males and juveniles would not have decreased their surprise effect for they would have been closer to the prey they met. This low flight would have required them to be more manoeuvrable. However, the increased braking obtained from stronger head winds, plus the fact that they were flying slowly, would have offset this.

All Australasian harriers flew slowly for proportionally longer periods over farm drain and pond vegetation where they were hunting for frogs. At first inspection it may be thought that adult females took advantage of these stronger head winds to fly slowly and scrutinise the farm drain and pond vegetation more thoroughly for these well camouflaged prey, but did not fly lower and so maintain optimum surprise effects during confrontations with frogs. However it was not over farm drain and pond vegetation that the adult females flew higher and slower. This was because, like adult males, adult females flew significantly lower over farm drain and pond vegetation than they did over all other habitats combined when compared with the heights flown by juveniles. Adult females also flew significantly lower over and through cabbage trees and flax than they did over all other habitats combined. Therefore the habitats that they flew slowly over at a higher height than when they flew at normal speed were raupo and/or duneland.

A possible solution to the question, why adult females flew higher when they flew slowly over these habitats, was that on these occasions they were hunting less agile but well camouflaged prey such as frogs or mice situated at the base of the tall vegetation. Greatest manoeuvrability is required when Australasian harriers are hunting over tall vegetation where prey is sighted at the last possible moment. In

this situation they would have to fly higher to still be able to see into the tall vegetation and have time to halt their forward momentum on sighting prey and dive to the ground. Thus it was seen that the most agile Australasian harriers, the adult males, flew higher as both vegetation height and flying speed increased. If the prey were less agile then the Australasian harriers' chances of success may not have been greatly reduced when it flew higher. When adult females flew lower and faster over habitats with taller vegetation they were possibly hunting agile prey such as adult passerines perched near the top of the vegetation.

This hypothesis is consistent with the idea that for optimum surprise Australasian harriers flew as low and as fast as they were able to and yet still be able to halt their forward momentum and dive and catch prey. What has been suggested is that Australasian harriers, and in this instance adult females, developed different search images (Tinbergen 1960, Croze 1970) when they hunted the habitats for different prey at different heights and speeds. Similarly, Schipper *et al.* (1975) noted for the hen harrier that fast hunting flights were generally aimed at surprising songbirds while during slow flights in search of voles, songbirds, though flying up to escape, were often ignored.

Juvenile inexperience. The degree of juveniles' inexperience is most readily gauged by comparing their hunting behaviour over the different habitats with that of the adults. All birds flapped significantly less often when they flew over the highly contoured duneland and cabbage tree and flax habitats. Unlike juveniles, adults made extra use of the updraughts generated by winds passing over the dune contours when only light winds were blowing. In this way the adults were able to flap less frequently. This was when the negative overall correlation between wind speed and average flaps indicated they should have flapped more frequently.

Unlike adults, juveniles did not regularly fly below the cabbage tree canopy but above the flax subcanopy. Because the juveniles flew higher they were less often in a favourable position from which to launch an attack. Also they would not have been able to use tree trunks to conceal their approach and so surprise prey.

Adult males and adult females flew significantly lower over farm drain and pond vegetation than they did over the other three habitats combined when compared with the heights flown by juveniles. Thus juveniles flew at a relatively intermediate height over all habitats and did not change their hunting height to suit the habitat as radically as the adults indicated was possible. The juveniles would therefore have been less likely to surprise prey than the adults.

As wind speeds increased adults changed height fewer times over the two contoured habitats. They used the extra lift provided by increasingly strong winds over the contours to help them to flap less often. Over the comparatively uniform raupo and farm drain and pond habitats they changed height more often and so flapped less frequently as wind speed increased. Juveniles were apparently unable to make this distinction and changed height more often over all habitats as wind speed increased. They changed height significantly more often over duneland as wind speed increased, possibly the habitat where an increase in height changes was least needed.

Because adult males and adult females flew significantly lower into a head wind than they did with cross and tail winds and the juveniles flew only slightly lower, it would be anticipated that the adults would have flapped more frequently than the juveniles. This is because the average number of flaps and average height are significantly and negatively correlated. Low flight did not allow long periods of gliding before the birds would have been too close to the vegetation and would have had to flap again to gain height. However, juveniles flapped more often than the adults when they flew into a head wind. This indicates that the juveniles were not as adept at using updraughts and other air currents as the adults were. That the juveniles flapped most often was probably due to their inexperience rather than their being morphologically less well adapted for gliding. This assumption is based on the knowledge that they had slightly lower wing loadings than the adults of their respective sexes and were therefore more buoyant. This suggestion is substantiated by the hunting behaviour results described below.

Although all birds flapped less often as their average number of height changes increased only juveniles had the potential to flap significantly less often. The correlations calculated demonstrate

that had the juveniles changed height more often over the two relatively uniform habitats, then they would have flapped significantly less often. They would also have flapped significantly less frequently if they had changed height more often when they flew slowly into a head wind. In the former situation they changed height at a similar rate to that of the adults and therefore flapped at approximately the same rate, while in the latter case they changed height significantly less often and consequently flapped significantly more often. Apparently the juveniles made little use of their morphological advantage.

The disadvantage of flapping most often into a head wind is highlighted when it is noted that on average Australasian harriers spent 72.4% of their total hunting time flying into a head wind. That all birds should have persisted with flying into a head wind which caused them to flap significantly more often, and therefore use more energy and rendered them more conspicuous, points to the importance of the increased braking effect of head winds and the fact that they enabled them to scrutinise the vegetation more thoroughly.

These quantitative examples of juvenile hunting inexperience, when coupled with the qualitative examples cited in Chapter 6, would have had a major bearing on juveniles being significantly less successful hunters than the adults (Table 6.2).

Intraspecific competition. The differential hunting behaviour of the adult male and adult female Australasian harrier can be seen as a means of reducing intersexual competition. Not only did the more manoeuvrable adult males hunt in a significantly different manner from the adult females, but they also hunted, to a significantly greater degree, those habitats where there were greater numbers of agile prey. Thus males took fewer large prey and greater numbers of agile prey than females did.

Similarly Schipper *et al.* (1975) found that adult male hen harriers were more agile than "females" (adult females and juveniles). They also took more small agile prey than females (Schipper 1973). Furthermore, Cade 1960, Storer 1966, Koplín 1973, De Vries 1975 and Snyder and Wiley 1976 have presented data which demonstrated that differential feeding or hunting behaviour reduced intersexual competition in other raptors.

Unlike other studies where juveniles have generally been classed with the adults of their respective sexes or with adult females, I classed juveniles separately. I found that juvenile Australasian harriers exerted a much stronger competitive force on the less agile adult females than the adult males. Despite this, juveniles were a distinct class that often exhibited different hunting behaviour from both adult sexes. This indicates that, for accurate results, in studies of intraspecific differential niche use, juveniles should be classed separately, particularly during their first six months of independence.

CHAPTER EIGHT

SEXUAL DIMORPHISM AND THE AUSTRALASIAN HARRIER

INTRODUCTION

In most Orders of birds males are larger than females. However a reversal of this pattern is seen in most species of the Falconiformes and Strigiformes. For several decades the adaptive significance of reversed sexual dimorphism exhibited by most hawks and owls has been debated, but to date no one hypothesis has gained universal acceptance.

In this chapter the degree of sexual dimorphism found in the Australasian harrier is calculated. This is then related, where pertinent, to the numerous hypotheses proposed to explain the degree of sexual dimorphism in raptors and why the females of most raptor species are larger than males. These hypotheses are critically reviewed.

A. THE DEGREE OF SEXUAL DIMORPHISM EXHIBITED BY THE AUSTRALASIAN HARRIER

In arriving at a mean dimorphism index for the Australasian harrier, data on weight, wing length and culmen length (Tables 2.2 and 2.3) were used as suggested by Snyder and Wiley (1976). The dimorphism index was calculated using the formula developed by Storer (1966):

$$\text{Dimorphism index} = \frac{\text{Female mean} - \text{Male mean}}{\frac{1}{2} (\text{Female mean} + \text{Male mean})} \times 100$$

The cube root of weights were calculated so that direct comparison with linear measurements could be made. The results of the calculations are presented in Table 8.1:

Table 8.1: Australasian harrier dimorphism index

	Female mean	Male mean	Female number	Dimorphism Index
			Male number	
Wing chord (mm)	423	404	107/95	4.6
Culmen (mm)	364	331	108/96	9.5
Weight (g)	835	625	179/165	9.6
Mean				7.9

Snyder and Wiley (1976) considered that raptors with a dimorphism index of about 4.5 or less were weakly dimorphic, about 7.0 moderately dimorphic and about 12.0 or greater strongly dimorphic. According to this scale the Australasian harrier is moderately to strongly dimorphic for weight and culmen length but weakly dimorphic for wing length. With an average dimorphism index of 7.9 the species is moderately dimorphic. Snyder and Wiley (1976) stated that the hen harrier (12.8) was strongly dimorphic.

B. SEXUAL DIMORPHISM HYPOTHESES

A point raised in most hypotheses on the adaptive significance of reversed sexual dimorphism is that the degree of sexual dimorphism exhibited by a raptor species is directly proportional to its degree of rapaciousness. Thus an increase in dimorphism is seen from vulturine species, through the intermediate mammalian and invertebrate-feeding raptors to the extreme found in those raptors that pursue birds. In the latter group the female may be almost twice as heavy as the male.

The hypotheses advanced in explanation of reversed sexual dimorphism fall into two broad categories. Those in the first category relate sexual dimorphism to aspects of reproductive behaviour. The second group relate it to ecological adaptations during the breeding season and many centre on the mutual advantages of a wider food niche. Some ecological hypotheses attempt to explain why there are different degrees of dimorphism in different raptor species, and others why most female raptors are larger than males. The following is a critical review of these hypotheses.

B.1. Behavioural explanations

It has been suggested (e.g. Amadon 1959, Earhart and Johnson 1970) that larger females were selected because they were able to protect the young from the filicidal tendencies of the male. Despite being accustomed to killing small animals the males of many raptors with pronounced sexual dimorphism incubate and feed their young so this argument is not tenable.

A hypothesis supported by Snyder and Wiley (1976) is that a larger female would be more successful at defending the nest from other predators.

Craighead and Craigheads' (1956) data indicate that many raptor species with varying degrees of dimorphism may inhabit a particular area, but it is unlikely that some species are more dimorphic than others because they have a greater need to protect their nests from predators. Amadon (1975) cited several examples of smaller males defending nests, while in other species with pronounced dimorphism neither sex may be vigorous in nest defence. My observations of the Australasian harrier show that neither sex will defend the nest against human intrusion while both sexes defend their young with equal vigour from potential predators such as bitterns (*Botaurus poiciloptilus*). Therefore differential nest defence of the sexes is an unlikely explanation of why most female raptors are larger than males.

Another possible behavioural explanation is that smaller males may be able to out-manoeuvre larger rivals in aerial territorial encounters. This hypothesis is not so attractive when used to explain reversed sexual dimorphism in owls where vocalisations play a major role in territorial establishment (Burton, 1973). Also Cade (1960) has shown that some species of large falcons make bodily contact during territorial encounters and that size and physical prowess are deciding factors for these species.

Earhart and Johnson (1970) and Amadon (1975) suggested that reversed sexual dimorphism may be explained with reference to the nature of the pair bond. Amadon (1975) believed that, "because male raptors are generally hostile to any approaching conspecific and seek to chase them away a male might appraise an approaching female of his own or smaller size as potential prey. Armed as he is with formidable beak and talons, he would pose a threat to the physical well-being of the female during pair formation. To offset this, selection would favour greater physical prowess in the female, and hence that sex has become the larger one, especially in the most aggressive species." I find this reasoning teleological. I also believe this conclusion is unfounded because Hinde (1966) has shown that greater size has nothing to do with preventing the male attacking the female during pair formation in those species of birds that have been closely studied. Avian courtship characteristically involves tendencies to attack, to flee from and to behave sexually towards a mate. A repertoire of behavioural fixed action patterns inhibits the male from attacking the female and ensures successful pairing in these species. What the male does depends on the stimuli

the female presents and on his own internal state and not on the relative sizes of the sexes.

Willoughby and Cade (1964) found that permutations of different sized male and female American kestrels of different races hindered neither pairing nor production of viable eggs. This is strong evidence that larger female size is not needed for successful breeding in raptors. Also, strong dimorphism does not necessarily increase agonistic behaviour. For example, Snyder and Wiley (1976) stated that relations between the sexes of strongly dimorphic Harris' hawks (*Parabuteo unicinctus*) appear to be unusually docile with one bird commonly perching on the back of another under circumstances that apparently have nothing to do with copulation. On the other hand, Cade (1955) recorded that smaller male American kestrels attacked larger females in the field.

In polyandrous birds many of the aspects of sex role reversal are accompanied by a larger size in the female sex (Jenni 1974). These include: the male performing all or most of the incubation and care of the young, the female being more aggressive than the male and the female initiating courtship and competing for mates. Although Amadon (1975) agreed that few aspects of sex role reversal occurred in raptor behaviour he stated, in support of his female dominance hypothesis that, "in higher vertebrates, sexual dimorphism in size is generally correlated with mating behaviour, not with foraging ecology; it is usually a result of competition by males for mates. When it is the females that compete for mates then that sex is the larger." However Ralls (1976) has shown that, for mammals at least, larger size of the female is not the result of sexual selection acting upon the female sex.

Therefore I do not believe that this or any of the other behavioural hypotheses can adequately explain reversed sexual dimorphism in raptors.

B.ii. Ecological explanations

Advantages and degree of sexual dimorphism. Rand (1952) and Storer (1966) viewed sexual dimorphism as an adaptation reducing intraspecific competition by enabling the raptor sexes to possess different feeding habits. Selander (1966) made a similar proposal for other birds. Differential niche use has been demonstrated for several raptor species including three North American accipiters (Storer 1966, Snyder and Wiley

1976). peregrine falcons (Cade 1960), Galapagos hawks (*Buteo galapagoensis*) (De Vries 1976), hen, marsh and Montagu's harriers (Schipper 1973) and American kestrels (Koplin 1973). My data on the Australasian harrier show that the sexes hunt in a significantly different manner and to different degrees over the available habitats from which they take different food items. Contrary to Balgooyen's (1976) assertions, I see no reason why similar differences may not be found for other raptors. That is, as Earhart and Johnson (1970) point out, provided the raptors are not food specialists faced with potential prey of relatively little size variation.

I agree with Snyder and Wileys' (1976) statement that differential niche use would be of greatest advantage during the breeding season when raptor movements are restricted to the home range around the nest site. During periods of autumn and winter food shortage raptors may travel greater distances to areas where food is more abundant. This phenomenon has been described for the Australasian harrier in Chapter 5.

Balgooyen (1976) stated that "perhaps the greatest influence on the degree of sexual dimorphism relates to the success of predation by the male of a species and that a high success of predation requires less energy output by the male for the energy gained, resulting in reduced sexual dimorphism." Surely energy gained is dependent on the biomass and calorific energy of the prey caught. While the males of the relatively monomorphic kestrels he observed made successful strikes 70% of the time, 96.5% of the number of prey caught were insects and reptiles. Balgooyen's (1976) hypothesis requires further supporting data demonstrating a positive correlation between success of predation by the male of a species and biomass captured before it can be accepted.

Schoener (1969) correlated the degree of dimorphism observed in raptors with their hunting habits. He predicted that raptors that actively pursue prey would be strongly dimorphic while those that spend more energy during the searching phase of the hunt would possess little sexual dimorphism. While this may be true for many raptors, for the Australasian harrier and hen harrier which possess moderate and strong dimorphism, respectively, the searching phase of hunting is the most energy demanding (Chapter 6, Schipper 1973). Snyder and Wiley (1976) presented evidence to show that at least seven species of African accipiters do not fit Schoener's (1969) model.

Reynolds (1972) suggested that the degree of dimorphism covaries with the agility of the prey taken. Thus agile prey demand agile predators and the size of those raptors feeding on very agile prey such as birds tends towards that of their prey. Snyder and Wiley (1976) stated that because the degree of dimorphism in North American owls also covaried with the amount of birds in their diets, this hypothesis was not tenable; presumably because owls should find sleeping birds less agile prey than nocturnal mammals. Snyder and Wileys' (1976) objection does of course rely on the owls concerned being strictly nocturnal and not hunting birds at dawn and dusk when they are active, but they did not mention this point.

Snyder and Wiley (1976) discuss at length their hypothesis which predicts that, "the extent of size dimorphism in a raptor species depends most critically on the regularity with which the species is stressed by food shortage during the latter part of the breeding season when both sexes are foraging. Such stress may regularly occur for species dependent on birds for food, at least in temperate regions where prey bird populations tend to peak rather sharply in spring and early summer. Raptors dependent on mammals or insects face more irregular prey populations, but populations that at least commonly are increasing during the latter part of the raptor breeding cycle. For these species food stress may be more characteristic of the early stages in the breeding cycle when only males are hunting and when dimorphism can do little to expand food supplies!" Snyder and Wiley (1976) admit that there are some raptors which do not conform well with the dimorphism versus bird-feeding correlation. Additional data are needed to test several aspects of their hypothesis but the answer to the question of whether or not food stress late in the breeding season correlates with strong dimorphism in tropical bird-hunting raptors as well as temperate species will prove critical.

Thus, in my opinion, all the major ecological hypotheses advanced to explain the degree of dimorphism in raptors have either serious deficiencies or require further evidence before they may be accepted without reservation.

Why are most female raptors larger than males? All the hypotheses that seek to answer this question centre their arguments on the well documented observation that for most accipiters and many falcons and buteos the male is the major provider of food throughout incubation and at least the first half of the nestling period (Brown and Amadon, 1968).

Storer (1966) and Reynolds (1972) considered that as it is the males which do most of the hunting during the nesting cycle there would be a selective advantage for them to be the smaller sex. A smaller male would encounter more accessible prey in its optimal prey size range because there are greater numbers of species and individuals of smaller prey (Eltonian pyramid of numbers). Reynolds (1972) argued that if a smaller male encounters more optimal, accessible prey, and has reduced total metabolic needs, then his efficiency at procuring excess food more frequently and at more regular intervals is enhanced.

There are two contentious points raised in this argument. The first is that while it is generally agreed that males may well take greater numbers of prey than females, whether they would also take a greater biomass of prey and therefore procure excess food more frequently is open to debate. Schoener (1968) has provided some indirect evidence (via territory size) that this may be the case. However Snyder and Wiley (1976) provided direct evidence that in all except one of the six habitats they sampled, female sharp-shinned hawks had a greater prey biomass available to them than males. They therefore questioned the validity of Reynold's (1972) hypothesis. I do not believe Snyder and Wiley's (1976) data questions Reynold's (1972) hypothesis because it is not so much the biomass of prey available but the biomass captured and delivered to the nest, or eaten, that is important.

The second contentious point concerns the male raptors' reduced metabolic needs. Mosher and Matray (1974) have demonstrated that male and female broad-winged hawks (*Buteo platypterus*) have similar resting metabolic rates on a per gram body weight basis. From this they calculated that by having only the smaller male hunting, the pair's energy needs are reduced by 17-23%. This is because males required less energy per day in direct proportion to their lesser weight at the same level of activity. However, comparative resting metabolic rates do not consider hunting efficiency, hunting success and prey available

to the sexes. In reference to this point, my data show that adult male and female Australasian harriers were equally efficient when hunting because they made similar numbers of flaps and height changes when they flew at their respective average heights, and had similar rates of successful prey capture.

The conclusion that smaller males need less energy for maintenance does not in itself predict that they would be superior to females or larger males in providing excess food. However, if smaller males also have available and capture a greater biomass of prey, then these two effects could be considered co-adaptive.

Mosher and Matray (1974) also provided several reasons why males do not continue to become smaller once an optimum size has been reached. These include the possibility of increased interspecific competition for some species, and physical incompatibility if the size differences between males and females became too great. They have not however provided any reasons why females should not also decrease in size because under the arguments presented the raptor family apparently would benefit most if both sexes were as small as possible.

One reason for females not decreasing in size is contained in an argument presented by Reynolds (1972) and elaborated by Balgooyen (1976). The argument is essentially that a bigger female with greater energy reserves is a better mother. It is interesting to note that this reason and the additional one that there may be more intense competition among females for some resources than among males, were the factors that Ralls (1976) concluded favoured larger size in female mammals. Reynolds (1972) stated that pair formation and subsequently egg formation begins for North American accipiters when energy reserves are relatively low. Studies of poultry and other birds show that egg formation makes high energy demands, and the number of eggs per clutch relates directly to the energy input of the female (Lack 1966, Perrins 1970). Of the several strategies Reynolds (1972) suggested females may adopt to conserve energy, the one with the most obvious advantages is for the female to rely on the male to supply her with the necessary energy while she remains near the nest site. Reynolds (1972) then incorporated this idea in his previously discussed hypothesis centred on the ability of the smaller male to provide more food for their mates and young.

Balgooyen (1976) on the other hand compared Verner and Wilsons' (1969) conclusions on mating systems, sexual dimorphism, and the role of the male North American passerine birds in the nesting cycle with those of male raptors. These show that passerine males of sexually dimorphic species (size and/or colour) participate less in nesting activities than males of sexually monomorphic species. In these cases, however, the male is the larger sex. Because of her important role in producing and rearing young the female passerine possesses a conservative combination of reproductive traits. Like smaller female passerines, male raptors have an important role in nesting activities and high parental investment. Balgooyen (1976) therefore concluded that because of this high parental investment, smaller body size has been selected in most male raptors.

This is an attractive hypothesis but it would be greatly strengthened if further evidence was provided showing that courtship feeding, or production feeding as Royama (1966) termed the behaviour, is common among raptors. According to Reynolds (1972), early courtship behaviour in raptors is one area of their biology about which little is known. I observed extensive courtship feeding by the Australasian harrier (Chapter 3). Similar observations have been made by Reynolds (1972) for the Cooper's hawk (*Accipiter cooperii*), by Brown and Amadon (1968) for the European sparrow hawk (*Accipiter nisus*) and by Balgooyen (1976) for the American kestrel.

Like the other hypotheses discussed it does not explain why raptors such as male burrowing owls (*Speotyto cunicularia*) and males of several species of owls of the *Ninox* genus should be larger than females when they show no obvious behavioural differences from other owls with reversed sexual dimorphism. Furthermore, Ralls (1976) found that for those species of mammals with males smaller than females, smaller male size was not correlated with greater parental investment. Perhaps detailed studies of closely related species that exhibit reversed and normal dimorphism will reveal important and hitherto little understood differences between them which may reveal why such anomalies exist. Probably the best opportunity for comparative studies of harriers lies in an extension of the work of Schipper (1973) and Schipper *et al.* (1975). They studied three sympatric species of harrier. Of these the hen harrier is strongly dimorphic (Snyder and Wiley 1976) while Montagu's harrier is relatively monomorphic (Schipper 1973).

I think that the advantages of reversed sexual dimorphism in raptors are to be found in differential niche use. This has been demonstrated to occur for the Australasian harrier in habitat use, hunting behaviour and diet. In my opinion, a combination of the ecological hypotheses of Reynolds (1972) and Balgooyen (1976) provides the strongest case that can be used to explain why female Australasian harriers are larger than males.

Although I believe the ecological explanations why most female raptors are larger than males hold sway over the behavioural explanations, I realise there is no one simple answer to this complex problem and no one hypothesis without its unanswered questions.

SUMMARIES OF CHAPTERS

1. NOMENCLATURE

It is brought to the attention of New Zealand ornithologists that the Australasian harrier and European marsh harrier are conspecific. Evidence is presented showing that there is no valid reason for considering *Circus aeruginosus* of the Pacific Islands to be a different subspecies from *C. aeruginosus* of Australia and New Zealand. The Australasian harrier is considered to be the most appropriate common name for the subspecies.

2. THE STUDY AREA AND METHODOLOGY

The soils, climate, physiography, vegetation and history of the study area are described. Some reasons for the postulated decline in the population density of the Australasian harrier are advanced. The field techniques used and the number of hours spent in the field are recorded. Three types of traps were used. They were cage traps, automatic bownets and bal-chatris. These traps are described and their advantages and disadvantages are listed. I trapped 212 Australasian harriers (19 adult males, 81 juvenile males, 34 adult females, 78 juvenile females), retrapped 76 of these birds a total of 220 times and made 319 sightings of individually marked birds. The methods of sexing, aging, measuring, and recording moult data and soft parts colours of these birds are described. The data thus collected are presented and discussed.

3. THE BREEDING BIOLOGY OF THE AUSTRALASIAN HARRIER

The ten territories in the 12 km² study area were defended by both males and females and averaged 31 ha. Nest sites were on average 910 m apart. Juveniles were not usually territorial. The 9 km² home ranges of pairs overlapped by about 70%. However pairs' 3 km² favourite hunting areas only overlapped by about 10%. It is suggested that the high population density (1 bird per 50 ha) may have decreased overall breeding success by increasing the number of territorial interactions and decreasing food availability. A fledging success rate of 1.8 young per successful pair and 1.1 young per nest site was recorded for two breeding seasons. Two cases of polygyny were observed. Territorial displays, evictions and border patrolling are described as are courtship

displays, courtship feeding, copulation and the aerial food pass. Data on nest building, nest parameters and conservatism and traditionalism in the siting of nests is presented and discussed. The time the female began regular hunting after the young hatched is correlated with the combined family's weight. Breeding season activities are summarised in a calendar of events.

4. THE NON-BREEDING BIOLOGY OF THE AUSTRALASIAN HARRIER

All sex and age classes dispersed from Pukepuke Lagoon during autumn and early winter. During this time previously untrapped birds passed through the area. Most (66.7%) of the adults that had been permanent residents returned after the dispersal phase and established home ranges in the sand country averaging 9 km². The home range of an adult female hunting open farmland was calculated to be 14 km² using radio-telemetry techniques. For several females the dispersal phase continued through winter and into spring. Juveniles were not usually permanent residents but those that established home ranges at Pukepuke Lagoon after the dispersal phase were likely to return after an absence of three or more months. The ringing returns and distant sightings of individually marked birds are recorded and incorporated in the discussion. There were about 15 birds in the 12 km² study area, or one bird per 80 ha, during the non-breeding season. Ninety-four evening and 16 morning observations were made of the communal roost. The roost was used by low numbers of birds throughout the year, although attendances fluctuated seasonally and from evening to evening. Data on roosting time, light intensity and weather conditions are presented. Their influences on the behaviour of birds arriving at and departing from the roost are considered. It is proposed that communal roosting by the Australasian harrier may have a primary social function and the roost may act as a centre providing information on the movements and density of a population and the resources of a region.

5. THE DIET OF THE AUSTRALASIAN HARRIER AT PUKEPUKE LAGOON

Four hundred and seventy food items were identified from 344 pellets (75 from the communal roost, 87 from nest sites, 182 from trapped birds), 120 prey remains (from 5 nest sites), five stomach contents and 64 observations of successful attacks or instances of Australasian harriers feeding from carrion. The results are presented as the frequency of

occurrence of each food type in the total number of food items identified. Mammals (46.4%) were numerically the most important food item with rabbits, hedgehogs, mice and sheep the major mammalian food species. Introduced passerines (29.0%) were the major bird food, particularly during summer. Game birds in the diet included ducks, pheasants and pukekos and they were taken in similar overall frequency (6.7%) to birds' eggs, aquatic prey and insects. Contrary to popular opinion, Australasian harriers ate significantly greater numbers of live prey than carrion annually. Seasonal trends in the diet data demonstrate a greater reliance on mammalian carrion during winter and early spring. The dietary emphasis changed in summer to live prey. Bird prey counts were made and their seasonal abundance and availability was significantly correlated with their occurrence in the diet. Seasonal trends in the diet are demonstrated to be correlated with food type availability and not palatability preferences. The inaccuracy of pellet data as a means of assessing the number of frogs, fish and bird pulli in the Australasian harriers' diet is demonstrated. It is suggested that the supply of greater numbers of large mammals may increase fledging success. No insects were found in nest site pellets or prey remains. Adult Australasian harriers took significantly greater numbers of agile food items than juveniles. Females ate significantly more large (>200 g) food items and significantly fewer agile food items than did males.

6. AUSTRALASIAN HARRIER HUNTING TECHNIQUES

Seven search techniques and five attack techniques are identified and described. They are: slow quartering, soaring and prospecting, listening, ground hunting, stooping to flush prey, fast contour hunting, still hunting, dive attacks, hover attacks, direct flying attacks, tail chasing and stooping and glide attacks. Ninety-five attacks on prey (24 by adult males, 14 by adult females and 57 by juveniles) are recorded and 15.8% of these were successful. Adult males (29.2%) and adult females (28.6%) were significantly more successful than juveniles (7.0%). Hunting success rates are compared with those given for other raptors. Observed qualitative hunting behaviour differences between adults and juveniles are discussed. Hunting in the daily cycle, feeding behaviour at carrion and prey escape tactics are described. Data on co-operative hunting, interspecific competition for carrion and interspecific

disruptions of hunting are presented and discussed. Hunting techniques are compared with those of other harriers and it is concluded that in the absence of strong competition from other raptors the Australasian harrier in New Zealand has evolved a wider range of hunting techniques than have been recorded for Eurasian and North American harriers. Prominent in this wide range is the use of buteonine hunting techniques by adult female Australasian harriers.

7. THE AUSTRALASIAN HARRIERS' HUNTING BEHAVIOUR: AN INTRASPECIFIC COMPARISON

Data were collected on height flown above vegetation, flying speed, wind direction relative to the Australasian harrier's flying direction, number of flaps and height changes and type of habitat hunted. The biometrical considerations in the analysis of these data are explained. The data were analysed to test for differences in manoeuvrability, conspicuousness, energy use and experience between adult males, adult females and juveniles. From the results it is concluded that adult males are more manoeuvrable and less conspicuous than juveniles and adult females because they flew significantly lower and faster. This conclusion concurs with the diet data. Adult males also hunted, to a significantly greater degree, those habitats where there were greater numbers of agile prey. These significant differences between the age and sex classes in hunting behaviour and habitat hunted are viewed as a means of reducing intraspecific competition. Juveniles are considered to be a distinct class for they exhibited a quantifiable degree of hunting inexperience that distinguished them from both adult sexes.

8. SEXUAL DIMORPHISM AND THE AUSTRALASIAN HARRIER

A mean dimorphism index of 7.9 was calculated for the Australasian harrier indicating that the species is moderately dimorphic. This is then related, where pertinent, to the numerous ecological and behavioural hypotheses proposed to explain the degree of sexual dimorphism in raptors and why the females of most raptor species are larger than males. These hypotheses are critically reviewed. It is considered that the advantages of reversed sexual dimorphism in raptors are to be found in differential niche use as was demonstrated for the Australasian harrier in diet, habitat hunted and hunting behaviour. It is concluded

that ecological explanations of why most female raptors are larger than males hold sway over behavioural explanations. The most likely hypotheses are centered on the ability of smaller male raptors, with a high parental investment, to provide more food for their mates and young and larger female raptors to have greater energy reserves for egg production.

Appendix Table A.1

Australasian harrier diet

Territory (1):B/9:D/4 No. pellets = 13 Dates = 5/12/76 26/ 1/77 1/ 2/77	Individuals in prey remains	No. pellets containing traces	Estimated number of individuals	% of total individuals
Rabbit	5	9	5	12.8
Hare	1	0	1	2.6
Hedgehog	3	2	3	7.7
Opossum	0	2	2	5.1
Mouse	0	3	3	7.7
Sheep	1	1	2	5.1
Total Mammals	10	17	16	41.0
Duck	1	1	2	5.1
Pheasant	2	0	2	5.1
Pukeko	1	0	1	2.6
Prion	2	0	2	5.1
Starling	1	0	1	2.6
Skylark	1	2	2	5.1
Yellowhammer	1	5	3	7.7
Goldfinch	1	0	1	2.6
Greenfinch	1	2	1	2.6
Hedge Sparrow	0	2	2	5.1
Chaffinch	1	2	1	2.6
Total Birds	12	14	18	46.2
Duck egg	0	1	1	2.6
Pheasant egg	1	0	1	2.6
Hedge Sparrow egg	0	1	2	5.1
Total eggs	1	2	4	10.3
Frog	0	1	1	2.6
Total	23	34	39	100.1

Appendix Table A.2

Australasian harrier diet

Territory (2):C/2:L17 No. pellets = 32 Dates = 23/12/76 6/ 1/77 26/ 1/77	Individuals in prey remains	No. pellets containing traces	Estimated No. of individuals	% of total individuals
Rabbit	5	10	6	12.0
Hare	0	1	1	2.0
Hedgehog	7	21	8	16.0
Mouse	0	2	2	4.0
Sheep	1	2	1	2.0
Total Mammals	13	36	18	36.0
Blackbird	3	0	3	6.0
Starling	1	1	1	2.0
Hedge Sparrow	4	4	5	10.0
Greywarbler	1	0	1	2.0
Chaffinch	1	1	2	4.0
Yellowhammer	1	6	4	8.0
Greenfinch	0	3	3	6.0
Goldfinch	0	1	1	2.0
House Sparrow	0	5	3	6.0
Prion	1	0	1	2.0
Unidentified Passerine	0	6	3	6.0
Total Birds	12	27	27	54.0
Duck egg	0	1	1	2.0
Blackbird egg	0	1	2	4.0
Total eggs	0	2	3	6.0
Frog	0	1	1	2.0
Eel	2	0	2	4.0
TOTAL	27	66	51	100.0

Appendix Table A.3

Australasian harrier diet

Territory (3):L/20:E/5 No. pellets = 8 Dates = 13/1/77 27/1/77	Individual in prey remains	No. pellets containing traces	Estimated number of individuals	% of total individuals
Rabbit	1	5	2	13.3
Mouse	0	1	1	6.7
Total Mammals	1	6	3	20.0
Duck	1	0	1	6.7
Pukeko	1	0	1	6.7
Magpie	1	0	1	6.7
Yellowhammer	1	2	2	13.3
Waxeye	1	0	1	6.7
Hedge Sparrow	1	0	1	6.7
Blackbird	0	1	1	6.7
Greenfinch	0	1	1	6.7
Unidentified Passerine	0	4	2	13.3
Total Birds	6	8	11	73.5
Unidentified egg	0	1	1	6.7
TOTAL	7	15	15	100.2

Appendix Table A.4

Australasian harrier diet

Territory (4):C/1:A/2 No. pellets = 10 Dates = 17/11/76 3/12/76 4/1/77 28/1/77	Individuals in prey remains	No. pellets containing traces	Estimated No. of individuals	% of total individuals
Rabbit	4	5	5	12.2
Hedgehog	2	2	2	4.9
Mouse	0	6	5	12.2
Sheep	1	0	1	2.4
Total Mammals	7	13	13	31.7
Duck	1	3	1	2.4
Pukeko	1	0	1	2.4
Skylark	1	1	2	4.9
Hedge Sparrow	7	1	7	17.1
House Sparrow	0	1	1	2.4
Unidentified Passerine	6	4	7	17.1
Total Birds	16	10	19	46.3
Duck egg	2	0	2	4.9
Unidentified egg	2	0	2	4.9
Total eggs	4	0	4	9.8
Frog	1	1	1	2.4
Eel	3	0	3	7.4
Carp	1	1	1	2.4
TOTAL	31	25	41	100.0

Appendix Table A.5

Australasian harrier diet

Territory (5):B/3:A/7 No. pellets = 26 Dates = 14/2/77	Individuals in prey remains	No. pellets containing traces	Estimated No. of individuals	% of total individuals
Rabbit	8	17	8	19.5
Hedgehog	2	16	4	9.8
Mouse	0	2	2	4.9
Total Mammals	10	35	14	34.2
Duck	1	0	1	2.4
Pheasant	2	2	2	4.9
Blackbird	2	1	2	4.9
Hedge Sparrow	1	2	2	4.9
Yellowhammer	1	7	5	12.2
Greenfinch	0	2	2	4.9
Chaffinch	0	1	1	2.4
Prion	0	2	1	2.4
Unidentified Passerine	3	9	9	22.0
Total Birds	10	26	25	61.0
Eel	1	0	1	2.4
Carp	0	2	1	2.4
TOTAL	21	63	41	100.0

Appendix Table A.6

Australasian harrier diet analysis : 70 pellets collected
from communal roost at Pukepuke Lagoon

Prey/Carrion Species	Autumn March-May		Winter June-Aug		Spring Sept-Nov		Totals	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Rabbit	5	20.8	11	20.8	2	7.1	18	17.1
Hedgehog	1	4.2	7	13.2	2	7.1	10	9.5
Opossum	1	4.2	2	3.8	1	3.7	4	3.8
Sheep	2	8.3	10	18.9	12	42.9	24	22.9
Mouse	2	8.3	8	15.1	2	7.1	12	11.4
Total Mammals	11	45.8	38	71.7	19	67.9	68	64.7
Duck	1	4.2	2	3.8	2	7.1	5	4.8
Pheasant	1	4.2	0	0	2	7.1	3	2.8
Blackbird	1	4.2	2	3.8	0	0	3	2.8
Yellowhammer	0	0	2	3.8	2	7.1	4	3.8
Greenfinch	0	0	0	0	1	3.7	1	1.0
House Sparrow	0	0	1	1.9	0	0	1	1.0
U.I.D. Passerine	0	0	4	7.5	0	0	4	2.8
Total Birds	3	12.6	11	20.8	7	25.0	21	20.0
Duck egg	0	0	1	1.9	0	0	1	1.0
U.I.D. egg	0	0	1	1.9	2	7.1	3	2.8
Total eggs	0	0	2	3.8	2	7.1	4	3.8
Orthoptera	10	41.6	1	1.9	0	0	11	10.5
Hemiptera	0	0	1	1.9	0	0	1	1.0
Total Insects	10	41.6	2	3.8	0	0	12	11.5
TOTAL	24	100.0	53	100.1	28	100.0	105	100.0

Number of prey items/pellet							
1 prey item		2 prey items		3 prey items		4 prey items	
No	%	No	%	No	%	No	%
42	60	21	30	5	7	2	3

Appendix Table A.7
 Adult Australasian harrier diet
 32 pellets + 2 stomach contents + 12 observations

Prey/Carrion Species	Summer Dec - Feb		Autumn March-May		Winter June-Aug		Spring Sept-Nov		Totals	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Rabbit	2	11.0	2	22.2	1	20.0	2	10.5	7	13.7
Hedgehog	1	5.6	3	33.3	0	0	1	5.3	5	9.8
Opossum	0	0	0	0	0	0	1	5.3	1	2.0
Sheep	0	0	0	0	0	0	4	21.0	4	7.8
Mouse	1	5.6	2	22.2	0	0	0	0	3	5.9
Total Mammals	4	22.2	7	77.7	1	20.0	8	42.1	20	39.2
Pheasant	1	5.6	0	0	0	0	1	5.3	2	3.9
Pukeko	2	11.0	0	0	0	0	1	5.3	3	5.9
Blackbird	1	5.6	0	0	0	0	0	0	1	2.0
Hedge Sparrow	1	5.6	0	0	1	20.0	1	5.3	3	5.9
Goldfinch	0	0	0	0	1	20.0	0	0	1	2.0
U.I.D. Passerine	5	27.8	2	22.2	1	20.0	2	10.5	10	19.5
Total Birds	10	55.6	2	22.2	3	60.0	5	26.4	20	39.2
Duck egg	0	0	0	0	0	0	1	5.3	1	2.0
Pheasant egg	0	0	0	0	0	0	1	5.3	1	2.0
U.I.D. egg	1	5.6	0	0	0	0	1	5.3	2	3.9
Total eggs	1	5.6	0	0	0	0	3	15.9	4	7.9
Frog	2	11.0	0	0	0	0	3	15.8	5	9.8
Carp	1	5.6	0	0	1	20.0	0	0	2	3.9
TOTAL	18	100.0	9	99.9	5	100.0	19	100.1	51	100.0

Number of prey items/pellet							
1 prey item		2 prey items		3 prey items		4 prey items	
No	%	No	%	No	%	No	%
14	44	14	44	4	12	0	0

Appendix Table A.8
 Juvenile Australasian harrier diet
 75 pellets + 3 stomach contents

Prey/Carrion Species	Summer Dec - Feb		Autumn March-May		Winter June-Aug		Spring Sept-Nov		Totals	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Rabbit	3	13.0	9	23.1	3	20.0	1	25.0	16	19.7
Hedgehog	2	8.7	4	10.2	1	6.7	0	0	7	8.7
Opossum	1	4.4	0	0	0	0	0	0	1	1.2
Sheep	0	0	1	2.6	3	20.0	1	25.0	5	6.2
Rat	0	0	2	5.1	2	13.3	0	0	4	4.9
Mouse	0	0	2	5.1	3	20.0	0	0	5	6.2
Total Mammals	6	26.1	18	46.1	12	80.0	2	50.0	38	46.9
Duck	0	0	3	7.7	0	0	0	0	3	3.7
Pheasant	0	0	1	2.6	0	0	0	0	1	1.2
Blackbird	1	4.4	0	0	0	0	0	0	1	1.2
Skylark	0	0	0	0	0	0	1	25.0	1	1.2
Hedge Sparrow	1	4.4	0	0	0	0	1	25.0	2	2.5
U.I.D. Passerine	2	8.7	4	10.2	1	6.7	0	0	7	8.7
Total Birds	4	17.5	8	20.5	1	6.7	2	50.0	15	18.5
U.I.D. eggs	3	13.0	0	0	0	0	0	0	3	3.7
Orthoptera	5	21.7	12	30.8	0	0	0	0	17	21.0
Hemiptera	4	17.4	1	2.6	0	0	0	0	5	6.2
Coleoptera	1	4.4	0	0	0	0	0	0	1	1.2
Total Insects	10	43.5	13	33.4	0	0	0	0	23	28.4
Eel	0	0	0	0	2	13.3	0	0	2	2.5
TOTAL	23	100.1	39	100.0	15	100.0	4	100.0	81	100.0

Number of prey items/pellet							
1 prey item		2 prey items		3 prey items		4 prey items	
No	%	No	%	No	%	No	%
38	51	28	37	7	9	2	3

Appendix Table A.9

Male Australasian harrier diet

54 pellets + 12 field observations + 5 stomachs

Prey/Carrion Species	Summer Dec - Feb		Autumn March-May		Winter June-Aug		Spring Sept-Nov		Totals	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Rabbit	4	12.9	4	25.0	3	23.0	2	13.3	13	17.3
Hedgehog	2	6.5	3	18.7	2	15.4	0	0	7	9.3
Opossum	2	6.5	0	0	0	0	0	0	2	2.7
Sheep	1	3.2	0	0	0	0	3	20.0	4	5.3
Rat	0	0	1	6.3	1	7.7	0	0	2	2.7
Mouse	1	3.2	1	6.3	2	15.4	0	0	4	5.3
Total Mammals	10	32.3	9	56.3	8	61.5	5	33.3	32	42.6
Pheasant	1	3.2	0	0	0	0	1	6.7	2	2.7
Pukeko	1	3.2	0	0	0	0	1	6.7	2	2.7
Blackbird	2	6.5	0	0	0	0	0	0	2	2.7
Hedge Sparrow	1	3.2	0	0	0	0	1	6.7	2	2.7
House Sparrow	0	0	1	6.3	0	0	0	0	1	1.3
Yellowhammer	0	0	0	0	2	15.4	0	0	2	2.7
Waxeye	0	0	0	0	1	7.7	0	0	1	1.3
Goldfinch	0	0	0	0	1	7.7	0	0	1	1.3
U.L.D. Passerine	7	22.6	3	18.7	1	7.7	1	6.7	12	16.0
Total Birds	12	38.7	4	25.0	5	38.5	4	26.8	25	33.4
Pheasant egg	0	0	0	0	0	0	2	13.3	2	2.7
U.I.D. egg	3	9.7	0	0	0	0	1	6.7	4	5.3
Total eggs	3	9.7	0	0	0	0	3	20.0	6	8.0
Coleoptera	1	3.2	0	0	0	0	0	0	1	1.3
Orthoptera	4	12.9	2	12.5	0	0	0	0	6	8.0
Hemiptera	0	0	1	6.3	0	0	0	0	1	1.3
Total Insects	5	16.1	3	18.8	0	0	0	0	8	10.6
Frog	1	3.2	0	0	0	0	3	20.0	4	5.3
TOTAL	31	100.0	16	100.1	13	100.0	15	100.1	75	99.9

Number of prey items/pellet							
1 prey item		2 prey items		3 prey items		4 prey items	
No	%	No	%	No	%	No	%
25	46.3	25	46.3	3	5.5	1	1.9

Appendix Table A.10
 Female Australasian harrier diet
 66 pellets + 3 field observations

Prey/Carrion Species	Summer Dec - Feb		Autumn March-May		Winter June-Aug		Spring Sept-Nov		Totals	
	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals	Estimated number of individuals	% of total individuals
Rabbit	2	11.8	6	26.0	2	20.0	2	13.2	12	18.5
Hedgehog	2	11.8	4	17.4	2	20.0	1	6.7	9	13.8
Opossum	0	0	0	0	0	0	1	6.7	1	1.5
Sheep	0	0	1	4.3	2	20.0	4	26.7	7	10.8
Rat	0	0	1	4.3	1	10.0	0	0	2	3.1
Mouse	0	0	2	8.8	1	10.0	0	0	3	4.6
Total Mammals	4	23.6	14	60.8	8	80.0	8	53.3	34	52.3
Duck	0	0	3	13.0	0	0	1	6.7	4	6.2
Pheasant	0	0	1	4.3	0	0	0	0	1	1.5
Pukeko	2	11.8	0	0	0	0	0	0	2	3.1
Skylark	0	0	0	0	0	0	1	6.7	1	1.5
Hedge Sparrow	1	5.9	0	0	1	10.0	1	6.7	3	4.6
UID Passerine	2	11.8	2	8.8	0	0	2	13.2	6	9.2
Total Birds	5	29.5	6	26.1	1	10.0	5	33.3	17	26.1
Duck egg	0	0	0	0	0	0	1	6.7	1	1.5
UID egg	1	5.9	0	0	0	0	0	0	1	1.5
Total eggs	1	5.9	0	0	0	0	1	6.7	2	3.0
Hemiptera	4	23.4	1	4.3	0	0	0	0	5	7.7
Orthoptera	2	11.8	2	8.8	0	0	0	0	4	6.2
Total Insects	6	35.2	3	13.1	0	0	0	0	9	13.9
Carp	0	0	0	0	1	10.0	1	6.7	2	3.1
Frog	1	5.9	0	0	0	0	0	0	1	1.5
TOTAL	17	100.1	23	100.0	10	100.0	15	100.0	65	99.9

Number of prey items/pellet							
1 prey item		2 prey items		3 prey items		4 prey items	
No	%	No	%	No	%	No	%
35	53	20	30	9	14	2	3

Appendix Table A.11

Australasian harrier stomach contents

Date	Age/Sex	Location	Cause of death	Stomach contents
12/1/77	adult male	Pukepuke Rd	Killed by car	Opposum Unidentified passeriformes
26/2/77	juvenile male	Lake Rd	Killed by car	Opossum
4/4/77	juvenile male	Pukepuke Lagoon	Unknown	Brown rat
21/4/77	adult male	Tangimoana Rd	Killed by car	Hedgehog
28/4/77	juvenile male	Pukepuke Lagoon	Unknown	House Sparrow

Appendix Table A.12
Pellets from trapped Australasian harriers

	Date	Bait	Pellet contents
Adult male	5.11.76	rabbit	pheasant unidentified egg
	8.12.76	rabbit	pheasant
	9.12.76	rabbit	pukeko unidentified egg
	14.1.77	rabbit	hedgehog hedge sparrow unidentified egg
	24.2.77	rabbit	unidentified passerine rabbit
	26.2.77	rabbit	mouse rabbit
	8.3.77	rabbit	sheep rabbit
	8.6.77	rabbit	goldfinch
5 more pellets contained rabbit only			
Juvenile male	19.8.76	rabbit	brown rat mouse rabbit
	26.8.76	rabbit	unidentified duck rabbit
	3.9.76	rabbit	wool rabbit
	23.11.76	rabbit	hedge sparrow rabbit
	16.12.76	rabbit	unidentified egg rabbit
	23.12.76	rabbit	blackbird 3 orthopterans
	24.3.77	rabbit	hedge sparrow rabbit
	27.3.77	rabbit	unidentified passerine rabbit
	6.4.77	rabbit	orthopteran rabbit
	6.4.77	rabbit	unidentified passerine orthopteran rabbit
	7 more pellets contained rabbit only		

Appendix Table A.12 (cont.)
Pellets from trapped Australasian harriers

	Date	Bait	Pellet contents
Adult female	8.9.76	rabbit	sheep rabbit
	14.9.76	hare	sheep hedgehog hare
	24.9.76	rabbit	hedge sparrow rabbit
	10.10.76	rabbit	sheep rabbit
	30.10.76	opossum	unidentified duck unidentified duck opossum
	4.5.77	rabbit	mouse hedgehog rabbit
8 more pellets contained rabbit only			
Juvenile female	12.8.76	hare	hedgehog hare
	12.8.76	hare	sheep hare
	31.8.76	rabbit	sheep hedgehog rabbit
	30.9.76	rabbit	skylark/N.Z. pipit rabbit
	8.12.76	rabbit	orthopteran 3 hemipterans hedge sparrow egg
	8.12.76	rabbit	orthopteran hedgehog rabbit
	24.2.77	rabbit	unidentified passerine hemipteran rabbit
	24.2.77	rabbit	hedge sparrow rabbit
	3.3.77	rabbit	2 hemipterans rabbit
	3.3.77	rabbit	brown rat rabbit
	3.5.77	rabbit	pheasant
	25.5.77	opossum	mallard duck sheep
	31.7.77	rabbit	brown rat
22 more pellets contained rabbit only			

Appendix Table A.13

Adult male Australasian harrier hunting techniques

	Search technique							Attack technique				Attack data																
	Slow quarter	Soaring	Listening	Ground hunting	Contour hunting	Flushing	Still hunting	Dive	Hover	Direct flying	Tail chase	Attack height (m)					Habitat				Direction			Success				
												1	3	5	7	9	drain	dune	raupo	other	back	forward	side	✓	x	?		
Frog	✓							✓	✓			✓				✓				✓			✓					
White faced heron	✓						✓	✓				✓				✓				✓			✓				x	
Blackbird	✓						✓	✓						✓				✓		✓			✓			x		
Duck	✓						✓		✓			✓						✓		✓			✓			x		
Duckling	✓						✓		✓			✓						✓		✓			✓			x		?
Small passerine	✓						✓		✓			✓						✓		✓			✓			x		
	✓						✓		✓			✓						✓		✓			✓			x		
Unknown					✓		✓		✓			✓						✓		✓			✓			x		
	✓						✓		✓			✓						✓		✓			✓			x		
	✓						✓		✓			✓						✓		✓			✓			x		
	✓						✓		✓			✓						✓		✓			✓			x		
	✓						✓		✓			✓						✓		✓			✓			x		
	✓						✓		✓			✓						✓		✓			✓			x		
	✓						✓		✓			✓						✓		✓			✓			x		
	✓						✓		✓			✓						✓		✓			✓			x		
Totals	21	0	0	0	2	0	1	16	8	0	0	6	13	3	1	1	6	9	8	1	14	9	1	7	15	2		

Appendix Table A.14

Adult female Australasian harrier hunting techniques

	Search technique							Attack technique				Attack data																
	Slow quarter	Soaring	Listening	Ground hunting	Contour hunting	Flushing	Still hunting	Dive	Hover	Direct flying	Tail chase	Attack height (m)					Habitat				Direction			Success				
												1	3	5	7	9	drain	dune	raupo	other	back	forward	side	✓	x	?		
Frog	✓							✓					✓						✓				✓					
Duckling		✓								✓			✓					✓									x	
	✓									✓								✓									x	
	✓									✓								✓									x	
	✓	✓								✓								✓									x	
Small passerine	✓	✓						✓									✓										x	
	✓							✓									✓								✓		x	
Carp	✓									✓							✓								✓		x	
Unknown	✓							✓					✓				✓								✓		x	
	✓	✓						✓									✓								✓		x	
				✓						✓						✓									✓			
				✓						✓						✓									✓			x
Total	10	4	0	2	0	0	1	6	6	2	0	3	6	5	0	0	3	4	7	0	5	9	0	4	10	0		

Appendix Table A.15 (continued)
 Juvenile Australasian harrier hunting techniques

	Search technique							Attack technique				Attack data																														
	Slow quarter	Soaring	Listening	Ground hunting	Contour hunting	Flushing	Still hunting	Dive	Hover	Direct flying	Tail chase	Attack height (m)					Habitat				Direction			Success																		
												1	3	5	7	9	drain	dune	raupo	other	back	forward	side	✓	x	?																
Unknown (cont)	✓							✓	✓				✓																				?									
	✓							✓					✓																						?							
	✓							✓					✓																							?						
	✓							✓					✓																								x					
	✓							✓					✓																								x					
	✓							✓					✓																										?			
				✓						✓				✓																									x			
				✓										✓																											?	
				✓										✓																												x
Total	49	4	1	3	0	2	0	29	24	2	2	10	29	16	1	1	3	23	28	3	21	32	4	4	47	6																

Appendix Table A.16

Number in group and mean for each variable
prior to transformation and adjustment

Number	Average Flaps/min	Winds (m.p.h)	Average Height (ft)	Average Height Changes/min
<u>Juveniles</u>				
78	43.36	10.89	11.48	9.75
115	49.72	8.50	12.67	9.82
25	129.87	8.48	8.85	4.28
62	33.28	8.56	12.43	9.30
34	23.05	7.02	12.94	10.16
<u>Adult Males</u>				
97	47.80	13.11	8.10	10.64
163	42.94	9.57	9.65	10.38
38	117.86	8.89	6.64	8.50
98	32.86	9.78	11.34	9.18
33	24.88	8.86	10.80	8.83
<u>Adult Females</u>				
79	42.91	12.63	14.28	10.27
88	47.90	12.16	12.78	9.25
10	134.24	13.70	6.20	3.58
80	36.54	11.47	14.24	10.92
14	22.71	10.92	17.37	6.19

Appendix Table A.17

Overall comparison: Y = Average Flaps X = Winds

Group	X Mean	Y Mean	Adjusted Y mean	Standard Error Adjusted Y	Correlation
Juveniles	8.96	221.04	220.82	.536	-.1335 NS
Adult Males	10.14	220.87	220.85	.454	-.1267 NS
Adult Females	12.09	220.88	221.18	.593	.0955 NS
Total estimates, ignoring groups correlation					-.0825
Within group estimates correlation					-.0835

Analyses of Variance

Source	D.F.	Average Flaps	Mean square for each variable		
			Winds	Average Height	Av. Height Changes
Total	1045	92.62	26.11	101.65	45.73
Between Groups	2	4.50	732.43	4578.50	30.09
Within Groups	1043	92.78	24.75	93.06	45.76
F Ratio		.04	29.58	49.19	.65
Std Deviation		9.63	4.97	9.64	6.76
General Mean		220.93	10.27	137.62	9.52

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	96779.00	92.78	
Due to average regression	1	675.16	675.16	7.320
Deviations from average regression	1042	96103.83	92.23	
Between individual group regression	2	808.23	404.11	4.410
Deviations from individual regression	1040	95295.59	91.63	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	92.07	
Between groups	2	12.58	.136
Within groups	1042	92.23	

Original mean square = 92.78 Percent reduction = .60

Appendix Table A.18

Overall comparison: Y = Average Flaps X = Average Height

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
Juveniles	139.05	221.04	221.36	.519	-.1930 NS
Adult Males	134.34	220.87	220.12	.454	-.2228 P<0.05
Adult Females	141.30	220.88	221.73	.580	-.2989 P<0.01
Total estimates, ignoring groups correlation					-.2190
Within group estimates correlation					-.2301

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	96779.00	92.78	
Due to average regression	1	5125.41	5125.41	58.270
Deviations from average regression	1042	91653.58	87.95	
Between individual group regressions	2	7.85	3.92	.044
Deviations from individual regressions	1040	91645.73	88.12	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	88.26	
Between groups	2	245.31	2.788
Within groups	1042	87.95	

Original mean square = 92.78 Percent reduction = 5.20

Appendix Table A.19

Overall comparison: Y = Average Flaps X = Average Height Changes

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
Juveniles	9.17	221.04	220.96	.526	-.2900 P<0.01
Adult Males	9.69	220.87	220.91	.450	-.0458 NS
Adult Females	9.67	220.88	220.92	.578	-.0431 NS
Total estimates, ignoring groups correlation					-.1503
Within group estimates correlation					-.1501

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	96779.00	92.78	
Due to average regression	1	2182.21	2182.21	24.037
Deviations from average regression	1042	94596.78	90.78	
Between individual group regressions	2	993.04	496.52	5.516
Deviations from individual regressions	1040	93603.74	90.00	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	90.61	
Between groups	2	1.83	.020
Within groups	1042	90.78	

Original mean square = 92.78 Percent reduction = 2.16

Appendix Table A.20

Overall comparison: Y = Average Height X = Average Flaps

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
Juveniles	221.04	139.05	139.08	.518	-.1930 NS
Adult Males	220.87	134.34	134.33	.444	-.2228 P<0.05
Adult Females	220.88	141.30	141.29	.570	-.2989 P<0.01
Total estimates, ignoring groups correlation					-.2190
Within group estimates correlation					-.2301

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	97070.40	93.06	
Due to average regression	1	5140.85	5140.85	58.270
Deviations from average regression	1042	91929.55	88.22	
Between individual group regressions	2	515.10	257.55	2.930
Deviations from individual regressions	1040	91414.45	87.89	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	96.86	
Between groups	2	4600.59	52.146
Within groups	1042	88.22	

Original mean square = 93.06 Percent reduction = 5.20

Appendix Table A.21

Overall comparison: Y = Average Height X = Winds

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
Juveniles	8.96	139.05	139.17	.538	.1243 NS
Adult Males	10.14	134.34	134.35	.456	.0615 NS
Adult Females	12.09	141.30	141.14	.595	-.0668 NS
Total estimates, ignoring groups correlation					.0694
Within group estimates correlation					.0469

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	97070.40	93.06	
Due to average regression	1	214.40	214.40	2.306
Deviations from average regression	1042	96855.99	92.95	
Between individual group regressions	2	503.01	251.50	2.714
Deviations from individual regressions	1040	96352.98	92.64	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	101.25	
Between groups	2	4429.54	47.654
Within groups	1042	92.95	

Original mean square = 93.06 Percent reduction = .12

Appendix Table A.22

Overall comparison: Y = Average Height X = Average Height Changes

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
Juveniles	9.17	139.05	139.02	.532	-.0734 NS
Adult Males	9.69	134.34	134.35	.455	-.0954 NS
Adult Females	9.67	141.30	141.31	.585	.0426 NS
Total estimates, ignoring groups correlation					-.0556
Within group estimates correlation					-.0543

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	97070.40	93.06	
Due to average regression	1	286.47	286.47	3.084
Deviations from average regression	1042	96783.92	92.88	
Between individual group regressions	2	275.31	137.65	1.483
Deviations from individual regressions	1040	96508.61	92.79	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	101.43	
Between groups	2	4557.53	49.067
Within groups	1042	92.88	

Original mean square = 93.06 Percent reduction = .19

Appendix Table A.23

Overall comparison: Y = Average Height Changes X = Average Flaps

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
Juveniles	221.04	9.17	9.18	.369	-.2900 P<0.01
Adult Males	220.87	9.69	9.69	.316	-.0458 NS
Adult Females	220.88	9.67	9.67	.406	-.0431 NS
Total estimates, ignoring groups correlation					-.1503
Within group estimates correlation					-.1501

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	47730.49	45.76	
Due to average regression	1	1076.24	1076.24	24.037
Deviations from average regression	1042	46654.25	44.77	
Between individual group regressions	2	957.33	478.66	10.893
Deviations from individual regressions	1040	45696.91	43.93	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	44.74	
Between groups	2	28.15	.628
Within groups	1042	44.77	

Original mean square = 45.76 Percent reduction = 2.16

Appendix Table A.24

Overall comparison: Y = Average Height Changes X = Winds

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
Juveniles	8.96	9.17	9.25	.377	.0693 NS
Adult Males	10.14	9.69	9.70	.319	.0292 NS
Adult Females	12.09	9.67	9.56	.417	.0418 NS
Total estimates, ignoring groups correlation					.0502
Within groups estimates correlation					.0455

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	47730.49	45.76	
Due to average regression	1	99.04	99.04	2.166
Deviations from average regression	1042	47631.45	45.71	
Between individual group regressions	2	41.75	20.87	.4561
Deviations from individual regressions	1040	47589.70	45.75	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	45.660	
Between groups	2	19.183	.419
Within groups	1042	45.711	

Original mean square = 45.76 Percent reduction = .11

Appendix Table A.25

Overall comparison: Y = Average Height Changes X = Average Height

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
Juveniles	139.05	9.17	9.22	.37	-.0734 NS
Adult Males	134.34	9.69	9.57	.32	-.0954 NS
Adult Females	141.30	9.67	9.81	.41	.0426 NS
Total estimates, ignoring groups correlation					-.0556
Within group estimates correlation					-.0543

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1043	47730.49	45.76	
Due to average regression	1	140.86	140.86	3.084
Deviations from average regression	1042	47589.63	45.67	
Between individual group regressions	2	151.97	75.98	1.665
Deviations from individual regressions	1040	47437.66	45.61	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	45.63	
Between groups	2	26.65	.583
Within groups	1042	45.67	

Original mean square = 45.76 Percent reduction = .19

Appendix Table A.26

Wind direction and harrier speed comparison:
Y = Average Flaps X = Winds

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
a	10.89	220.54	220.67	.920	.2287	P<0.05
b	8.50	222.07	221.69	.763	-.2554	P<0.05
c	8.48	238.85	238.46	1.627	-.0410	NS
d	8.56	217.52	217.15	1.035	-.3293	P<0.01
e	7.02	214.58	213.88	1.404	-.4016	P<0.05
<u>Adult Males</u>						
a	13.11	221.58	222.19	.838	.0025	NS
b	9.57	220.50	220.34	.637	-.1596	NS
c	8.89	236.78	236.48	1.320	.0372	NS
d	9.78	217.72	217.61	.821	-.3463	P<0.01
e	8.86	215.66	215.35	1.416	-.4872	P<0.01
<u>Adult Females</u>						
a	12.63	220.73	221.24	.922	.3634	P<0.01
b	12.16	221.91	222.32	.871	-.0663	NS
c	13.70	239.77	240.51	2.575	.3575	NS
d	11.47	218.64	218.90	.910	.0198	NS
e	10.92	214.58	214.72	2.172	-.4858	P<0.05
Total estimates, ignoring groups correlation						-.0824
Within group estimates correlation						-.1269

Where: a = speed slow/head wind
b = speed normal/head wind
c = hover/head wind
d = speed normal/cross wind
e = speed normal/tail wind

Analyses of variance

Source	D.F.	Mean square for each variable			
		Average Flaps	Winds	Average Height	Average Height Change
Total	1045	92.79	26.11	101.60	45.73
Between groups	16	1748.31	207.90	1047.81	138.76
Within groups	1029	67.05	23.28	86.89	44.28
F ratio		26.07	8.92	12.05	3.13
Std deviation		8.18	4.82	9.32	6.65
General mean		220.93	10.27	137.62	9.52

Appendix Table A.26 (cont.)

Wind direction and harrier speed comparison
 Y = Average Flaps X = Winds

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1029	68994.25	67.04	
Due to average regression	1	1111.55	1111.55	16.833
Deviations from average regression	1028	67882.69	66.03	
Between individual group regressions	16	3134.07	195.87	3.061
Deviations from individual regressions	1012	64748.62	63.98	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	92.25	
Between groups	16	1776.61	26.904
Within groups	1028	66.03	

Original mean square = 67.05 Percent reduction = 1.51

Appendix Table A.27

Wind direction and harrier speed comparison:
 Y = Average Flaps X = Average Height

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
a	138.10	220.54	220.59	.920	-.2625	P<0.05
b	139.78	222.07	222.31	.759	-.0332	NS
c	133.36	238.85	238.37	1.629	-.0601	NS
d	139.52	217.52	217.73	1.033	-.1595	NS
e	140.53	214.58	214.91	1.395	.0045	NS
<u>Adult Males</u>						
a	131.43	221.58	220.88	.841	-.3108	P<0.01
b	134.70	220.50	220.17	.641	-.0080	NS
c	128.37	236.78	235.74	1.341	.0790	NS
d	137.66	217.72	217.72	.820	-.0681	NS
e	136.64	215.66	215.55	1.414	-.1436	NS
<u>Adult Females</u>						
a	142.19	220.73	221.25	.922	-.2234	P<0.05
b	139.89	221.91	222.17	.868	-.3418	P<0.01
c	127.71	239.77	238.66	2.583	.2086	NS
d	142.56	218.64	219.20	.918	-.0450	NS
e	147.68	214.58	215.71	2.188	-.1232	NS
Total estimates, ignoring groups correlation						-.2190
Within group estimates correlation						-.1279

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1029	68994.25	67.04	
Due to average regression	1	1129.83	1129.83	17.114
Deviations from average regression	1028	67864.41	66.01	
Between individual group regressions	16	1092.65	68.29	1.035
Deviations from individual regressions	1012	66771.76	65.98	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	88.42	
Between groups	16	1528.19	23.148
Within groups	1028	66.01	

Original mean square = 67.05

Percent reduction = 1.54

Appendix Table A.28

Wind direction and harrier speed comparison:
 Y = Average Flaps X = Average Height Changes

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
a	9.75	220.54	220.57	.920	-.2564	P<0.05
b	9.82	222.07	222.12	.757	-.4015	P<0.01
c	4.28	238.85	238.03	1.637	-.3327	NS
d	9.30	217.52	217.48	1.031	-.2028	NS
e	10.16	214.58	214.68	1.393	-.1123	NS
<u>Adult Males</u>						
a	10.64	221.58	221.76	.826	.0434	NS
b	10.38	220.50	220.63	.637	-.1351	NS
c	8.50	236.78	236.62	1.318	.0094	NS
d	9.18	217.72	217.66	.820	-.1982	P<0.05
e	8.83	215.66	215.55	1.414	.1355	NS
<u>Adult Females</u>						
a	10.27	220.73	220.85	.914	-.0031	NS
b	9.25	221.91	221.87	.866	-.0036	NS
c	3.58	239.77	238.83	2.579	.2567	NS
d	10.92	218.64	218.86	.909	.1252	NS
e	6.19	214.58	214.05	2.175	.0737	NS
Total estimates, ignoring groups correlation						-.1501
Within group estimates correlation						-.1278
Analysis of within group variance of Y						
Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio		
Total within group	1029	68994.25	67.04			
Due to average regression	1	1128.03	1128.03	17.086		
Deviations from average regression	1028	67866.21	66.01			
Between individual group regressions	16	1846.58	115.41	1.769		
Deviations from individual regressions	1012	66019.63	65.23			
Analysis of variance of Y after fitting regression on X						
Source of variation	D.F.	Mean Square	F Ratio			
Total	1044	90.78				
Between groups	16	1682.10	25.479			
Within groups	1028	66.01				
Original mean square = 67.05		Percent reduction = 1.53				

Appendix Table A.29

Wind direction and harrier speed comparison:
 Y = Average Height X = Average Flaps

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation
<u>Juveniles</u>					
a	220.54	138.10	138.04	1.047	-.2625 P<0.05
b	222.07	139.78	139.94	.863	-.0332 NS
c	238.85	133.36	135.97	1.954	-.0601 NS
d	217.52	139.52	139.02	1.180	-.1595 NS
e	214.58	140.53	139.60	1.601	.0045 NS
<u>Adult Males</u>					
a	221.58	131.43	131.52	.939	-.3108 P<0.01
b	220.50	134.70	134.64	.724	-.0080 NS
c	236.78	128.37	130.68	1.600	.0790 NS
d	217.72	137.66	137.19	.941	-.0681 NS
e	215.66	136.64	135.87	1.620	-.1436 NS
<u>Adult Females</u>					
a	220.73	142.19	142.16	1.040	-.2234 P<0.05
b	221.91	139.89	140.03	.986	-.3418 P<0.01
c	239.77	127.71	130.46	2.999	.2086 NS
d	218.64	142.56	142.23	1.037	-.0450 NS
e	214.58	147.68	146.75	2.482	-.1232 NS
Total estimates, ignoring groups correlation					-.2190
Within group estimates correlation					-.1279

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1029	89410.98	86.89	
Due to average regression	1	1464.17	1464.17	17.114
Deviations from average regression	1028	87946.80	85.55	
Between individual group regressions	16	1771.47	110.71	1.300
Deviations from individual regressions	1012	86175.32	85.15	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	96.82	
Between groups	16	820.98	9.596
Within groups	1028	85.55	

Original mean square = 86.89

Percent reduction = 1.54

Appendix Table A.30

Wind direction and harrier speed comparison:
 Y = Average Height X = Winds

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
a	10.89	138.10	138.00	1.05	.1927	NS
b	8.50	139.78	140.06	.87	.0977	NS
c	8.48	133.36	133.65	1.86	.1332	NS
d	8.56	139.52	139.80	1.18	.1529	NS
e	7.02	140.53	141.06	1.60	.1595	NS
<u>Adult Males</u>						
a	13.11	131.43	130.97	.95	.0047	NS
b	9.57	134.70	134.82	.72	.0727	NS
c	8.89	128.37	128.59	1.50	-.1091	NS
d	9.78	137.66	137.74	.93	.3083	P<0.01
e	8.86	136.64	136.87	1.61	.2336	NS
<u>Adult Females</u>						
a	12.63	142.19	141.81	1.05	-.2576	P<0.05
b	12.16	139.89	139.58	.99	.1683	NS
c	13.70	127.71	127.16	2.94	-.6024	P<0.05
d	11.47	142.56	142.37	1.04	-.0891	NS
e	10.92	147.68	147.57	2.48	.2870	NS
Total estimates, ignoring groups correlation						.0694
Within group estimates correlation						.0843

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1029	89410.98	86.89	
Due to average regression	1	636.66	636.66	7.372
Deviations from average regression	1028	88774.31	86.35	
Between individual group regressions	16	2346.96	146.68	1.717
Deviations from individual regressions	1012	86427.34	85.40	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	101.21	
Between groups	16	1055.58	12.223
Within groups	1028	86.35	

Original mean square = 86.89

Percent reduction = .61

Appendix Table A.31

Wind direction and harrier speed comparison:
 Y = Average Height X = Average Height Changes

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
a	9.75	138.10	138.12	1.053	.2797	P<0.02
b	9.82	139.78	139.81	.867	-.1904	NS
c	4.28	133.36	132.83	1.874	.0543	NS
d	9.30	139.52	139.49	1.181	-.1860	NS
e	10.16	140.53	140.59	1.595	-.3180	NS
<u>Adult Males</u>						
a	10.64	131.43	131.54	.945	-.2581	P<0.02
b	10.38	134.70	134.79	.729	-.0583	NS
c	8.50	128.37	128.26	1.509	.1389	NS
d	9.18	137.66	137.62	.939	.0027	NS
e	8.83	136.64	136.57	1.619	-.1832	NS
<u>Adult Females</u>						
a	10.27	142.19	142.27	1.047	.0856	NS
b	9.25	139.89	139.86	.991	-.0959	NS
c	3.58	127.71	127.11	2.952	.0966	NS
d	10.92	142.56	142.70	1.041	-.0922	NS
e	6.19	147.68	147.34	2.490	.2390	NS
Total estimates, ignoring groups correlation						-.0556
Within group estimates correlation						-.0726

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1029	89410.98	86.89	
Due to average regression	1	471.80	471.80	5.453
Deviations from average regression	1028	88939.17	86.51	
Between individual group regressions	16	1870.90	116.93	1.359
Deviations from individual regressions	1012	87068.27	86.03	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	101.38	
Between groups	16	1056.77	12.214
Within groups	1028	86.51	

Original mean square = 86.89 Percent reduction = .43

Appendix Table A.32

Wind direction and harrier speed comparison:
 Y = Average Height Changes X = Average Flaps

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
a	220.54	9.75	9.71	.747	-.2564	P<0.05
b	222.07	9.82	9.94	.616	-.4015	P<0.01
c	238.85	4.28	6.14	1.395	-.3327	NS
d	217.52	9.30	8.94	.842	-.2028	NS
e	214.58	10.16	9.50	1.143	-.1123	NS
<u>Adult Males</u>						
a	221.58	10.64	10.71	.670	.0434	NS
b	220.50	10.38	10.34	.517	-.1351	NS
c	236.78	8.50	10.14	1.142	.0094	NS
d	217.72	9.18	8.84	.671	-.1982	P<0.05
e	215.66	8.83	8.29	1.157	.1355	NS
<u>Adult Females</u>						
a	220.73	10.27	10.25	.742	-.0031	NS
b	221.91	9.25	9.36	.704	-.0036	NS
c	239.77	3.58	5.53	2.141	.2567	NS
d	218.64	10.92	10.68	.740	.1252	NS
e	214.58	6.19	5.53	1.772	.0737	NS
Total estimates, ignoring groups correlation						-.1501
Within group estimates correlation						-.1278

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1029	45570.41	44.28	
Due to average regression	1	745.05	745.05	17.086
Deviations from average regression	1028	44825.35	43.60	
Between individual group regressions	16	1261.96	78.87	1.832
Deviations from individual regressions	1012	43563.38	43.04	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	44.74	
Between groups	16	117.95	2.705
Within groups	1028	43.60	

Original mean square = 44.28

Percent reduction = 1.53

Appendix Table A.33

Wind direction and harrier speed comparison:
 Y = Average Height Changes X = Winds

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
a	10.89	9.75	9.73	.753	.0432	NS
b	8.50	9.82	9.89	.625	.1059	NS
c	8.48	4.28	4.35	1.333	-.0527	NS
d	8.56	9.30	9.37	.848	.0020	NS
e	7.02	10.16	10.29	1.149	.2087	NS
<u>Adult Males</u>						
a	13.11	10.64	10.52	.686	.0448	NS
b	9.57	10.38	10.41	.522	.0693	NS
c	8.89	8.50	8.56	1.081	-.4091	P<0.02
d	9.78	9.18	9.20	.672	.0847	NS
e	8.86	8.83	8.89	1.160	-.1192	NS
<u>Adult Females</u>						
a	12.63	10.27	10.17	.755	.0952	NS
b	12.16	9.25	9.17	.714	-.0648	NS
c	13.70	3.58	3.43	2.109	-.1591	NS
d	11.47	10.92	10.87	.745	.1774	NS
e	10.92	6.19	6.16	1.778	.1305	NS
Total estimates, ignoring groups correlation					.0502	
Within group estimates correlation					.0306	

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1029	45570.41	44.28	
Due to average regression	1	42.71	42.71	.964
Deviations from average regression	1028	45527.70	44.28	
Between individual group regressions	16	1010.11	63.13	1.435
Deviations from individual regressions	1012	44517.58	43.98	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	45.66	
Between groups	16	133.88	3.023
Within groups	1028	44.28	

Original mean square = 44.28

Percent reduction = -.003

Appendix Table A.34

Wind direction and harrier speed comparison:
 Y = Average Height Changes X = Average Height

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
a	138.10	9.75	9.78	.751	.2797	P<0.02
b	139.78	9.82	9.93	.621	-.1904	NS
c	133.36	4.28	4.05	1.331	.0543	NS
d	139.52	9.30	9.40	.844	-.1860	NS
e	140.53	10.16	10.31	1.140	-.3180	NS
<u>Adult Males</u>						
a	131.43	10.64	10.32	.688	-.2581	P<0.02
b	134.70	10.38	10.23	.524	-.0583	NS
c	128.37	8.50	8.02	1.096	.1389	NS
d	137.66	9.18	9.18	.670	.0027	NS
e	136.64	8.83	8.78	1.156	-.1832	NS
<u>Adult Females</u>						
a	142.19	10.27	10.51	.753	.0856	NS
b	139.89	9.25	9.37	.709	-.0959	NS
c	127.71	3.58	3.06	2.111	.0966	NS
d	142.56	10.92	11.17	.750	-.0922	NS
e	147.68	6.19	6.71	1.788	.2390	NS
Total estimates, ignoring groups correlation					-.0556	
Within group estimates correlation					-.0726	

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	1029	45570.41	44.28	
Due to average regression	1	240.46	240.46	5.453
Deviations from average regression	1028	45329.94	44.09	
Between individual group regressions	16	1593.24	99.57	2.304
Deviations from individual regressions	1012	43736.70	43.21	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1044	45.63	
Between groups	16	144.55	3.278
Within groups	1028	44.09	

Original mean square = 44.28

Percent reduction = .43

Appendix Table A.35

Habitat comparison: Y = Average Flaps X = Winds

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	9.68	223.08	222.94	1.290	-.1609	NS
x	8.94	218.19	217.89	.903	-.3004	P<0.01
y	8.62	222.89	222.52	.773	-.0485	NS
z	9.87	216.35	216.25	2.348	-.0516	NS
<u>Adult Males</u>						
w	11.02	223.14	223.28	1.139	-.0691	NS
x	9.09	220.24	219.98	.827	-.2292	P<0.05
y	10.75	222.42	222.51	.692	-.1881	NS
z	10.92	220.89	221.02	1.775	-.1354	NS
<u>Adult Females</u>						
w	14.90	222.15	223.12	2.364	.0495	NS
x	9.55	219.69	219.53	1.193	.0522	NS
y	12.59	221.77	222.25	.730	.1124	NS
z	13.22	216.42	217.04	2.010	-.1657	NS
Total estimates, ignoring groups correlation						-.0974
Within group estimates correlation						-.1122

Where: w = farm drain and pond vegetation
 x = duneland
 y = raupo
 z = cabbage trees and flax

Analyses of variance

Source	D.F.	Mean square for each variable			
		Average Flaps	Wind Speed	Average Height	Average Height Change
Total	1008	91.62	26.80	99.42	46.00
Between groups	11	303.81	216.75	1248.18	55.89
Within groups	997	89.27	24.70	86.75	45.89
F ratio		3.403	8.772	14.388	1.217
Std deviation		9.44	4.97	9.31	6.77
General mean		221.28	10.34	137.91	9.54

Appendix Table A.35 (cont.)

Habitat comparison: Y = Average Flaps X = Winds

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	89008.62	89.27	
Due to average regression	1	1121.81	1121.81	12.713
Deviations from average regression	996	87886.80	88.23	
Between individual group regressions	11	1351.36	122.85	1.398
Deviations from individual regressions	985	86535.44	87.85	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F ratio
Total	1007	90.83	
Between groups	11	326.07	3.695
Within groups	996	88.24	

Original mean square = 89.27 Percent reduction = 1.16

Appendix Table A.36

Habitat comparison: Y = Average Flaps X = Average Height

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	138.24	223.08	223.17	1.244	-.3434	P<0.02
x	138.47	218.19	218.35	.868	-.1101	NS
y	139.44	222.89	223.33	.741	-.1799	NS
z	141.96	216.35	217.52	2.269	-.4099	NS
<u>Adult Males</u>						
w	131.32	223.14	221.24	1.117	-.3040	P<0.02
x	133.48	220.24	218.96	.806	-.3991	P<0.01
y	138.05	222.42	222.46	.668	-.3080	P<0.01
z	127.35	220.89	217.84	1.743	-.2175	NS
<u>Adult Females</u>						
w	138.19	222.15	222.23	2.265	-.2352	NS
x	139.65	219.69	220.20	1.152	-.2636	P<0.05
y	142.85	221.77	223.20	.709	-.3876	P<0.01
z	136.16	216.42	215.91	1.932	-.2866	NS
Total estimates, ignoring groups correlation						-.2569
Within group estimates correlation						-.2845

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	89008.62	89.27	
Due to average regression	1	7206.14	7206.14	87.739
Deviations from average regression	996	81802.47	82.13	
Between individual group regressions	11	966.46	87.86	1.070
Deviations from individual regressions	985	80836.00	82.06	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1007	85.65	
Between groups	11	404.47	4.924
Within groups	996	82.13	

Original mean square = 89.27

Percent reduction = 8.00

Appendix Table A.37

Habitat comparison: Y = Average Flaps X = Average Height Changes

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	8.16	223.08	222.74	1.280	-.4424	P<0.01
x	8.28	218.19	217.88	.893	-.1731	NS
y	10.41	222.89	223.10	.761	-.3650	P<0.01
z	6.88	216.35	215.71	2.330	.2300	NS
<u>Adult Males</u>						
w	9.49	223.14	223.13	1.129	-.2480	NS
x	9.81	220.24	220.31	.816	-.0374	NS
y	9.74	222.42	222.47	.686	.0032	NS
z	10.18	220.89	221.04	1.759	-.1838	NS
<u>Adult Females</u>						
w	8.53	222.15	221.90	2.328	.3848	NS
x	10.56	219.69	219.94	1.183	.1230	NS
y	9.44	221.77	221.75	.712	-.1286	NS
z	9.84	216.42	216.49	1.985	.1475	NS
Total estimates, ignoring groups correlation						-.1601
Within group estimates correlation						-.1728

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	89008.62	89.27	
Due to average regression	1	2659.39	2659.39	30.674
Deviations from average regression	996	86349.22	86.69	
Between individual group regressions	11	2457.52	223.41	2.623
Deviations from individual regressions	985	83891.69	85.16	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1007	89.35	
Between groups	11	330.22	3.809
Within groups	996	86.69	

Original mean square = 89.27

Percent reduction = 2.89

Appendix Table A.38

Habitat comparison: Y = Average Height X = Average Flaps

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	223.08	138.24	138.74	1.228	-.3434	P<0.02
x	218.19	138.47	137.61	.860	-.1101	NS
y	222.89	139.44	139.89	.730	-.1799	NS
z	216.35	141.96	140.58	2.238	-.4099	NS
<u>Adult Males</u>						
w	223.14	131.32	131.84	1.084	-.3040	P<0.02
x	220.24	133.48	133.19	.784	-.3991	P<0.01
y	222.42	138.05	138.37	.659	-.3080	P<0.01
z	220.89	127.35	127.24	1.688	-.2175	NS
<u>Adult Females</u>						
w	222.15	138.19	138.43	2.233	-.2352	NS
x	219.69	139.65	139.21	1.135	-.2636	NS
y	221.77	142.85	142.99	.683	-.3876	P<0.01
z	216.42	136.16	134.79	1.910	-.2866	NS
Total estimates, ignoring groups correlation						-.2569
Within group estimates correlation						-.2845

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	86491.36	86.75	
Due to average regression	1	7002.35	7002.35	87.739
Deviations from average regression	996	79489.00	79.80	
Between individual group regressions	11	1166.78	106.07	1.333
Deviations from individual regressions	985	78322.22	79.51	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1007	92.95	
Between groups	11	1283.05	16.076
Within groups	996	79.80	

Original mean square = 86.75

Percent reduction = 8.00

Appendix Table A.39

Habitat comparison: Y = Average Height X = Winds

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	9.68	138.24	138.28	1.279	.0794	NS
x	8.94	138.47	138.56	.895	.0362	NS
y	8.62	139.44	139.55	.767	.1582	NS
z	9.87	141.96	141.99	2.328	.4308	NS
<u>Adult Males</u>						
w	11.02	131.32	131.28	1.130	-.0329	NS
x	9.09	133.48	133.56	.820	.2169	P<0.05
y	10.75	138.05	138.03	.687	-.0041	NS
z	10.92	127.35	127.31	1.760	-.3846	P<0.05
<u>Adult Females</u>						
w	14.90	138.19	137.90	2.344	.4362	NS
x	9.55	139.65	139.70	1.183	-.1581	NS
y	12.59	142.85	142.71	.724	-.0978	NS
z	13.22	136.16	135.98	1.993	.0606	NS
Total estimates, ignoring groups correlation						.0579
Within group estimates correlation						.0337

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	86491.36	86.751	
Due to average regression	1	98.23	98.234	1.132
Deviations from average regression	996	86393.12	86.740	
Between individual group regressions	11	1960.04	178.185	2.078
Deviations from individual regressions	985	84433.08	85.718	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1007	99.19	
Between groups	11	1226.55	14.140
Within groups	996	86.73	

Original mean square = 86.75

Percent reduction = .0132

Appendix Table A.40

Habitat comparison: Y = Average Height X = Average Height Changes

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	8.16	138.24	138.15	1.280	-.0327	NS
x	8.28	138.47	138.40	.893	.0349	NS
y	10.41	139.44	139.50	.761	-.1297	NS
z	6.88	141.96	141.81	2.330	-.2672	NS
<u>Adult Males</u>						
w	9.49	131.32	131.32	1.129	-.2711	P<0.05
x	9.81	133.48	133.49	.816	-.0829	NS
y	9.74	138.05	138.07	.686	.0122	NS
z	10.18	127.35	127.39	1.759	-.0811	NS
<u>Adult Females</u>						
w	8.53	138.19	138.13	2.327	.0412	NS
x	10.56	139.65	139.71	1.183	.0056	NS
y	9.44	142.85	142.85	.711	.0511	NS
z	9.84	136.16	136.18	1.984	.3599	NS
Total estimates, ignoring groups correlation						-.0454
Within group estimates correlation						-.0431

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	86491.36	86.75	
Due to average regression	1	160.99	160.99	1.857
Deviations from average regression	996	86330.37	86.67	
Between individual group regressions	11	778.75	70.79	.815
Deviations from individual regressions	985	85551.61	86.85	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1007	99.31	
Between groups	11	1244.03	14.352
Within groups	996	86.67	

Original mean square = 86.75

Percent reduction = .08

Appendix Table A.41

Habitat comparison: Y = Average Height Changes X = Average Flaps

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	223.08	8.16	8.38	.917	-.4424	P<0.01
x	218.19	8.28	7.90	.643	-.1731	NS
y	222.89	10.41	10.61	.546	-.3650	P<0.01
z	216.35	6.88	6.26	1.672	.2300	NS
<u>Adult Males</u>						
w	223.14	9.49	9.72	.810	-.2480	NS
x	220.24	9.81	9.68	.585	-.0374	NS
y	222.42	9.74	9.88	.492	.0032	NS
z	220.89	10.18	10.13	1.261	-.1838	NS
<u>Adult Females</u>						
w	222.15	8.53	8.64	1.669	.3848	NS
x	219.69	10.56	10.37	.848	.1230	NS
y	221.77	9.44	9.50	.510	-.1286	NS
z	216.42	9.84	9.23	1.427	.1475	NS
Total estimates, ignoring groups correlation						-.1601
Within group estimates correlation						-.1728

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	45756.31	45.89	
Due to average regression	1	1367.10	1367.10	30.674
Deviations from average regression	996	44389.20	44.56	
Between individual group regressions	11	1907.46	173.40	4.020
Deviations from individual regressions	985	42481.74	43.12	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1007	44.85	
Between groups	11	72.04	1.616
Within groups	996	44.56	

Original mean square = 45.89

Percent reduction = 2.890

Appendix Table A.42

Habitat comparison: Y = Average Height Changes X = Winds

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	9.68	8.16	8.21	.930	.0848	NS
x	8.94	8.28	8.38	.651	.2021	P<0.05
y	8.62	10.41	10.54	.557	.0343	NS
z	9.87	6.88	6.91	1.692	.0895	NS
<u>Adult Males</u>						
w	11.02	9.49	9.44	.821	.0275	NS
x	9.09	9.81	9.90	.596	-.0973	NS
y	10.75	9.74	9.70	.499	.1259	NS
z	10.92	10.18	10.13	1.279	-.0364	NS
<u>Adult Females</u>						
w	14.90	8.53	8.19	1.702	.1500	NS
x	9.55	10.56	10.62	.860	-.0558	NS
y	12.59	9.44	9.27	.526	.1328	NS
z	13.22	9.84	9.62	1.448	-.1648	NS
Total estimates, ignoring groups correlation					.0482	
Within group estimates correlation					.0548	

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	45756.31	45.89	
Due to average regression	1	137.51	137.51	3.002
Deviations from average regression	996	45618.79	45.80	
Between individual group regressions	11	350.33	31.84	.692
Deviations from individual regressions	985	45268.45	45.95	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1007	45.94	
Between groups	11	58.56	1.278
Within groups	996	45.80	

Original mean square = 45.89

Percent reduction = .20

Appendix Table A.43

Habitat comparison: Y = Average Height Changes X = Average Height

Group	X Mean	Y Mean	Adjusted Y Mean	Standard Error Adjusted Y	Correlation	
<u>Juveniles</u>						
w	138.24	8.16	8.17	.930	-.0327	NS
x	138.47	8.28	8.30	.648	.0349	NS
y	139.44	10.41	10.46	.554	-.1297	NS
z	141.96	6.88	7.00	1.695	-.2672	NS
<u>Adult Males</u>						
w	131.32	9.49	9.28	.835	-.2711	P<0.01
x	133.48	9.81	9.67	.602	-.0829	NS
y	138.05	9.74	9.74	.499	.0122	NS
z	127.35	10.18	9.85	1.302	-.0811	NS
<u>Adult Females</u>						
w	138.19	8.53	8.54	1.692	.0412	NS
x	139.65	10.56	10.62	.860	.0056	NS
y	142.85	9.44	9.59	.530	.0511	NS
z	136.16	9.84	9.78	1.444	.3599	NS
Total estimates, ignoring groups correlation						-.0454
Within group estimates correlation						-.0431

Analysis of within group variance of Y

Source of variation	D.F.	Sums of Squares	Mean Square	F Ratio
Total within group	997	45756.31	45.89	
Due to average regression	1	85.16	85.16	1.857
Deviations from average regression	996	45671.14	45.85	
Between individual group regressions	11	501.85	45.62	.994
Deviations from individual regressions	985	45169.28	45.85	

Analysis of variance of Y after fitting regression on X

Source of variation	D.F.	Mean Square	F Ratio
Total	1007	45.95	
Between groups	11	54.95	1.198
Within groups	996	45.85	

Original mean square = 45.89

Percent reduction = .08

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