The behaviour and ecology of long-tailed bats (*Chalinolobus tuberculatus* Gray) in the central North Island.

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Abstract

The morphology, breeding season, juvenile development, activity and roosting behaviour of a North Island forest population of long-tailed bats (*Chalinolobus tuberculatus* Gray) was investigated intensively over spring and summer 1994 - 95. The diet of a cave dwelling population was studied by analysing guano collected regularly over a one year period.

Most body measurements taken were consistent with reported individuals caught at similar latitudes in other studies, while discrepancies in tail length, body length and wingspan may be the result in differences in measuring techniques. Females were significantly larger than males in forearm length, body length, left hind-limb length and wingspan. A higher proportion of adult females caught may reflect the higher activity and energy demands during pregnancy and lactation, but the higher proportion of juvenile males caught cannot be explained.

Most females gave birth in mid-November. Weight gain amongst females was more consistent up to than after parturition. Parturition was earlier than in closely related Australian species at similar latitudes in Australia. The onset of nipple enlargement coincided with parturition and did not reduce in size until volant juveniles were captured in early January. This suggests that lactation lasted approximately eight weeks, longer than in Australian *Chalinolobus* species. Most females captured during breeding (87.8%) showed signs of pregnancy or lactation. Cartilage bands and the lack of bulging in the metacarpal-pharangeal joint, body size and colour were all used to indicate bat age. Juvenile bats became volant from early January onwards. The age when juveniles are capable of sustained flight is probably greater than in closely related species in Australia.

Bat echolocation was recorded with an automatic bat detector and compared with weather, light intensity and potential insect prey abundance. Combinations of environmental variables best explained variation in bat activity. The number of passes during the night, the number of passes per hour and the number of passes in the first hour after sunset were all highest during pregnancy with reduced activity during lactation. The time of the first pass relative to sunset was earliest during September and February. Insect abundance was highest during lactation and when juveniles were volant. Diurnal bat activity generally followed a bimodal pattern with more activity in the first and last hour of darkness, however there were seasonal differences in this pattern.

Bats were tracked to roost sites using small transmitters (1.7 g) and directional receivers. Female bats used communal roosts only during lactation, but used combinations of communal and solitary roosts during pregnancy and when juveniles became independent. Communally roosting bats preferred mature trees or limbs of trees that were recently dead. These trees provided cavities with small entrances (6 - 7 cm) that were situated from 5 to 30 m above the ground. The number of bats observed emerging from communal roosts ranged from 5 to 208 (mean = 86). It is unlikely the same group of bats remained together every night. Individual bats changed roosts every one to three days therefore they probably transported juvenile bats with them.

Insect prey taxa were identified from long-tailed bat guano collected from a limestone cave roost over one year. It was concluded that bats feed mainly on Diptera, Lepidoptera and Coleoptera, while other orders are taken in smaller numbers. Quantitative data could not be used as an indication of seasonal changes in prey taken. There was no evidence of terrestrial insects in the faeces as reported for Australian *Chalinolobus* species. Estimated sizes of ingested prey items were smaller than the size range of available prey insects. Larger insects may be culled of identifiable body parts before ingestion.

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Chapter 1

General Introduction

There are nearly 1000 living species of bats, comprising almost one quarter of mammalian species. Apart from the cold regions of the Arctic, Antarctica, and some isolated islands, bats have successfully colonised every part of the world (Hill & Smith 1985). Bats are a unique group of animals that evolved flight, and in many species, the ability to echolocate has allowed them to successfully take advantage of the extensive temporal realm of night. Bats evolved at an astonishing rate and are remarkably diverse. They are however poorly represented as fossils (Hill & Smith 1985) and those that have been collected are usually highly fragmented. Even the oldest fossil bats are nearly as fully evolved as the modern bats we know today (Hill & Smith 1985). For these reasons, details of the evolution of bats are not well known.

The Order Chiroptera (meaning "hand wing") is divided into two suborders, the Megachiroptera (the old world fruit bats or flying foxes), and Microchiroptera, the diverse echolocating bats. Megachiroptera first occur in fossils from the Oligocene period but fossil bats with advanced microchiropteran characteristics are known from the Eocene period. It is suspected bats originated in the Paleocene or mid to late Cretaceous periods (70-100 mybp) (Hill & Smith 1985).

All Megachiroptera occur in one family, the Pteropodidae, and are distributed throughout tropical and sub-tropical areas of Asia, Africa and Indo-Australia. The Microchiroptera are more diverse and are divided into four superfamilies and 17 families, the smallest (Mystacinobidae) contains one surviving species, the New Zealand short-tailed bat *Mystacina tuberculata*. The largest and widest spread family (Vespertilionidae) contains the New Zealand long-tailed bat *Chalinolobus tuberculatus*. Megachiroptera include the largest living bats (weighing up to 1200 g and with wingspans of up to 2 m). These have not evolved echolocation (with a few minor exceptions) and use their large eyes to locate the fruit and flowers they eat. Microchiroptera on the other hand are small (as light as 2 g), most are insectivorous although some species are known to eat flesh (eg/fish, frogs and other bats), fruit, pollen, nectar, flowers and blood.

Bats are exceptionally vulnerable to extinction, in part because of their slow reproductive rate. Nearly 40% of American bat species are in severe decline or are already listed as endangered. The misconceptions about bats do not help their cause. New Zealand bats are relatively obscure and secretive. Most known large roosts that still remain occur in remote parts of the forest or on offshore islands. Bats in New Zealand therefore have largely escaped the hazards of human ignorance, but at the same time they have also escaped the attention of science. Consequently, relatively little is known about them. The first recorded observations of bats by Europeans was in Queen Charlotte Sound by Forster (1772 - 1774) on Captain James Cook's second voyage (Dwyer 1960). The first study (excluding the description of species) of New Zealand bats was conducted by Pam Lewis. She recorded observations on flight, emergence times and feeding behaviour of long-tailed bats in podocarp and beech forest, pasture and scrubland during the 1950's. Her observations were published in a collective work by Dwyer (1962).

The short-tailed bat evolved before introduced predators reached New Zealand and so, like many of our bird species, is especially vulnerable. Their low flying and ground foraging habits make them relatively easy prey for cats, rats and mustelids. The short-tailed bat is considered endangered and large roosts are mainly confined to offshore islands. Land clearance has probably been a major factor in the decline of both species.

New Zealand long-tailed bats are closely related to five other Australasian species (Daniel 1990) and so they probably evolved in the presence of Australian predators but then crossed the Tasman sea about one million years ago (Daniel 1979). They have a scattered distribution of low numbers throughout New Zealand, and are classed as threatened (vulnerable) (Bell 1986).

Increasing awareness of bats and their conservation problems both overseas and in New Zealand, together with the development of suitable micro radio transmitters and bat detectors has enabled more detailed studies to be made on bats. In order to preserve species that are in decline or in danger of decline, a basic understanding of the biology and ecology is needed.

Aims

The bulk of my research on long-tailed bats was conducted at Balls Clearing Scenic Reserve, Puketitiri, Hawkes Bay. This was done in cooperation with Landcare Research, Havelock North. The major aim of this study was to investigate the morphology and behaviour of long-tailed bats during the breeding season which included spring and summer. The five specific aims of the study were to: (1) monitor bat activity on a nightly basis so that diurnal and seasonal patterns in activity could be compared with changes in sunset, weather, moon phase and insect abundance; (2) describe the timing and duration of parturition, lactation and the onset of volant juveniles; (3) investigate the choice of roost trees and monitor emergence behaviour and the numbers of bats using roosts; (4) describe the morphology of adult male and female bats in the area and provide information about the development of juvenile bats; and (5) investigate what prey taxa are taken by long-tailed bats.

The above aims of this study were modified from the originally proposed study. My original aims were to conduct a comparative study of long-tailed bats that roosted in Grand Canyon Cave, Piopio and others that presumably roosted in native trees in the Tongariro National Park area. That study was intended to concentrate on the differences in roosting, foraging and breeding between the two populations. Much of it was to focus on how roost type and location may affect other facets of bat activity. Other aims were to determine prey insect taxa from faecal analysis, and add to information known about the distribution of both short and long-tailed bats in the Taupo/Tongariro Conservancy. After preliminary visits and surveys of the areas it appeared that bats were quite abundant. I spent three months surveying and attempting to catch bats in the area. However insufficient numbers of bats were caught to complete the proposed study. A change in geographical and to a lesser extent, ecological direction was decided upon. Reports on work conducted at Tongariro and Grand Canyon Cave are included in Appendix I and II.

The main chapters in this thesis are presented in strict paper format.

Study sites

Balls Clearing

Balls Clearing Scenic Reserve is situated 5 km from Puketitiri, Hawkes Bay (NZMS 260 V20 117088), Latitude 39° 17', Longitude 176° 33'. The topography consists of flat to gently rolling hills with a slope of 9-16°. Rainfall averages 2150 mm per year, the prevailing wind is northerly and there are snow falls two or three times a year with severe frosts (Lands and Survey 1982). The reserve is situated at the foot of the Kaweka Ranges at 640 m a.s.l. and consists of a 36 ha block of unmodified native forest together with areas of regenerating scrub and forest, an exotic conifer plantation, and a central clearing of farmed pasture (Figure 1). The native forest is dominated by a 35 m high canopy of rimu (*Dacrydium cupressinum* Lamb.), kahikatea (*Dacrycarpus dacrydioides* Laubenf.), miro (*Podocarpus ferrugineus* G. Benn. ex Don), matai (*Podocarpus spicatus* R.Br. ex Mirbel) and red beech (*Nothofagus fusca* Hook. f). Typical understorey species are listed in a full vegetation survey by Elder (1950).

Grand Canyon Cave

Grand Canyon Cave is situated on Puketiti Station, Piopio (NZMS R17 737030). The cave is essentially a 30m high natural limestone tunnel approximately 370m long. The northern end opens onto pasture through a small stand of scattered, mature, kahikatea trees (*D. dacrydioides*) while the south end opens into a ravine formed by collapse of the cave roof. The latter contains native sub canopy species. The cave floor is flat and mostly dry hard substrate with some areas of mud bog at the southern end.

Tongariro

Most surveying in the Tongariro area was conducted in the Rotoaira, Rotopounamu, Erua and Ohakune areas. The habitat type was mostly mature podocarp forest, although areas of scrub pasture and exotic forest were surveyed. Map references of sites surveyed are included in Appendix II.

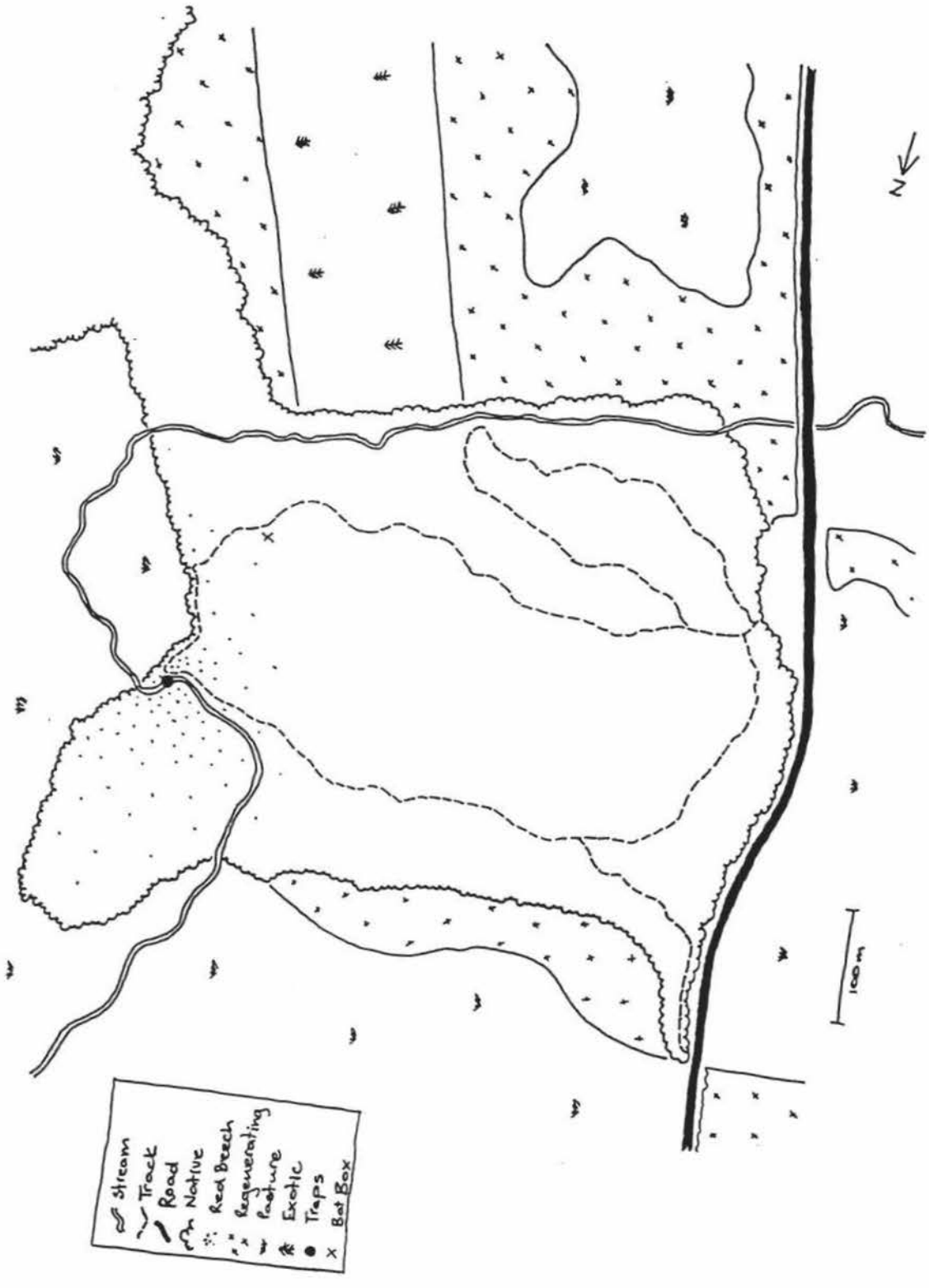

Figure 1. Balls Clearing Scenic Reserve.

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Chapter 2

The morphometrics and juvenile development of the New Zealand long-tailed bat *Chalinolobus tuberculatus* Gray (Vespertilionidae).

Abstract

The morphometrics and sexual dimorphism of adult and post-natal development of juvenile long-tailed bats (*Chalinolobus tuberculatus* Gray) is described using data collected from captured bats in a North Island forest during the breeding season. Most measures are consistent with measurements reported by other workers from long-tailed bats caught at similar latitudes, while discrepancies in tail length, body length and wingspan may reflect differences in measuring techniques. Some measures (eg. forearm length) are easier to take and provide more reliable information than others. A higher proportion of adult females than adult males caught may reflect the higher energy demands during pregnancy and lactation, but the higher proportion of juvenile males caught cannot be explained. Females were significantly larger than males in forearm length, body length, left hind-limb length and wingspan. The longest juvenile forearm was greater than the smallest recorded adult forearm. Adult or juvenile bats cannot therefore be distinguished on the basis of forearm length alone. Cartilage bands and the lack of bulging in the metacarpal-pharangeal joint, size and colour are all indicators of juvenility. The age when juveniles are capable of sustained flight is probably older than in closely related species in Australia.

Key words: Bats, Vespertilionidae, *Chalinolobus tuberculatus*, morphometrics, sex ratio, sexual dimorphism, juvenile development.

Introduction

Two bats survive in New Zealand, the lesser short-tailed bat *Mystacina tuberculata* Gray, (Mystacinobidae), and the long-tailed bat *Chalinolobus tuberculatus* Gray. The greater short-tailed bat *Mystacina robusta* Dwyer, is thought to have been extinct since 1965 (Daniel 1990). The long-tailed bat belongs to the largest and worldwide family Vespertilionidae. It has five

conspecifics in Australia, Tasmania, Norfolk Island, New Caledonia and New Guinea (Daniel 1990)

Little is published on the morphometrics of *C. tuberculatus*. The external and internal morphology was described by Forster (1772 - 1774), Gray (1843), Tomes (1857), Peters (1866), Hutton (1872), Knox (1872), Buller (1875), Dwyer (1960a, 1960b, 1962), Cody (1981) and Daniel (1990). These reports were based on small samples and the data do not include sufficient information about age, sex, or geographic location to attempt to explain any causes of variation amongst the specimens. Daniel (1990) extended the morphometric work on long-tailed bats by comparing the forearm lengths of *C. tuberculatus* from three geographical areas and found that this tended to increase with latitude, however the conclusions are tentative.

Juvenile development of long-tailed bats has not been studied. The external anatomy of one 12 mm foetus was described by Dwyer (1960b), and detailed studies of development in two closely related Australian species, *C. morio* Gray and *C. gouldii* Gray, were published by Kitchener & Coster (1981) and Kitchener (1975) respectively.

The main aim of this paper was to obtain morphometric information from a large sample of *C. tuberculatus* from a single population. These data are used to investigate sex ratio, sexual dimorphism of size, the reliability of different body measures and the post-natal development of juvenile bats. This information would also provide data for future studies on geographic variation.

Methods

All bats were captured at Balls Clearing Scenic Reserve, Puketitiri, Hawkes Bay (NZMS 260 V20 117088), Latitude 39° 17', Longitude 176° 33'. A review of the vegetation (Elder 1950), climate and geography is given in Chapter 1. All bats were caught with harp traps (1@ 2.4 x 1.8 = 4.2 m^2 and 1@ 2.4 x 1.4 = 3.3 m^2), (Tidemann & Woodside 1978) or mist nets (7 x 42 ft, with a mesh size of 1/4 inch). These were placed over or near the main stream where it exits to the north-eastern corner of the clearing through mature red beech forest (Figure 1 in Chapter 1). Even on nights of low activity there were usually some bats foraging under the canopy at this site. On nights when

captured bats were especially needed, a single mist net was set up across the stream with a harp trap below the bottom of the net, with the legs standing in the water . A third harp trap was used approximately 30 m down stream. Bats caught in mist nets were weighed and measured within ten minutes of capture whereas those bats caught in harp traps were usually left undisturbed until morning. The sex of captured bats was determined first, then bats were weighed using a 50 g spring scale attached to a small light cotton bag. Lengths of forearms, body (including head), tail and left hind tibia were measured with vernier callipers (Figure 1). Wingspan was measured from extended wingtip to wingtip against a small tape measure extended along a wooden rail. All captured bats were inspected for identifiable features such as scarring and these were recorded. Female nipples were inspected, and any enlargement was recorded. The metacarpal- pharangeal joints were checked for the presence of cartilage bands, which can be used as an estimate of sub-adult age (Parnaby 1982).

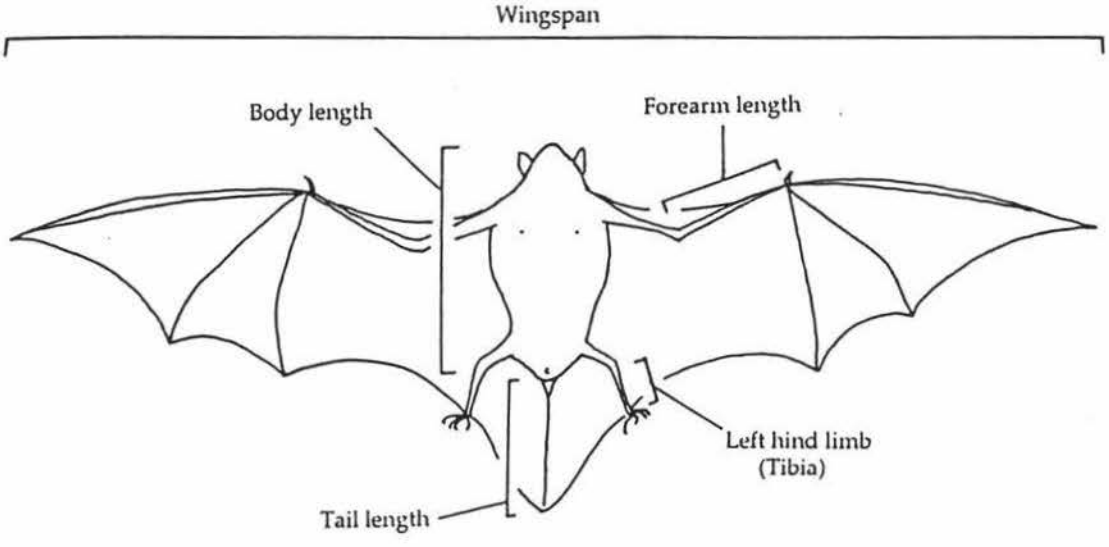

Figure 1. Measurements taken from C. *tuberculatus*. Ventral view, half actual size.

Sexual dimorphism was analysed using t-tests (MINITAB). Regression analysis and Spearman rank correlations were used to test relationships between juvenile morphometric variables (MINITAB). Sex ratios were tested using normal approximation (Tang Strait 1989).

Results

A total of 240 bats were caught during 99 nights of trapping over spring and summer (Sep 1994 - Feb 1995). Of all bats caught 82.5% were adults and the remaining 17.5% were juveniles (Table 1). Females comprised 73.2% of the adults ($P < 0.0001$) and 33.4% of the juveniles ($p < 0.0001$). Overall, 145 of the bats caught (60.4%) were females.

Table 1. Measurement data for adult and juvenile bats. Weight (g), right forearm, left forearm, tail, left hind limb (tibia), body length including head and wingspan (mm).

1(a) Adult females (n=145).

	Weight	R.Forearm	L.Forearm	Tail	L.H.Limb	Body.L	W.Span
Minimum	8.25	37.70	37.90	30.20	12.30	42.52	265.00
Maximum	16.00	41.95	41.90	45.90	19.820	63.20	298.00
Mean	11.90	40.30	40.31	36.90	17.75	54.57	282.65
Std Dev	1.18	0.87	0.85	2.64	0.76	3.49	7.03

1(b) Adult males (n=53).

	Weight	R.Forearm	L.Forearm	Tail	L.H.Limb	Body.L	W.Span
Minimum	7.00	38.2	37.44	30.60	16.0	41.80	261.00
Maximum	11.75	41.700	41.60	41.20	18.20	59.75	296.00
Mean	9.59	39.85	39.84	36.64	17.422	52.08	276.44
Std Dev	1.03	0.76	0.83	2.48	0.43	3.73	6.99

1(c) Juvenile females (n= 13).

	Weight	R.Forearm	L.Forearm	Tail	L.H.Limb	Body.L	W.Span
Minimum	6.75	36.15	36.00	31.15	15.55	46.25	243.00
Maximum	10.50	40.75	40.80	38.15	17.85	57.20	282.00
Mean	9.21	39.63	39.60	35.28	17.12	51.05	267.93
Std Dev	0.94	1.12	1.14	1.76	0.62	3.17	9.68

1(d) Juvenile males (n= 29).

	Weight	R.Forearm	L.Forearm	Tail	L.H.Limb	Body.L	W.Span
Minimum	6.25	37.5	37.80	24.80	14.75	42.60	234.00
Maximum	9.75	40.440	40.30	39.10	17.45	56.50	281.00
Mean	8.03	39.04	39.03	33.67	16.52	49.41	262.00
Std Dev	0.87	0.81	0.75	2.98	0.67	3.19	11.70

Bats showed considerable variation in individual body weight (Table 1). Other measurements that were variable were wingspan, body length and tail length. The mean values recorded for left and right forearms (in both adult and juveniles of both sexes) were very similar.

Adult female bats had significantly longer right and left forearms, left hind limbs, combined head and body lengths, and wingspan measurements than males ($p<0.01$). The differences however are small with mean female right and left forearm lengths being respectively, 0.45 mm (1.11%) and 0.47 mm (1.33%) longer than for males, and the mean wingspan was 6.21 mm (2.20%) greater in females than in males.

There was no significant difference between left and right forearms in juvenile or adult bats and the longest juvenile forearm was greater than the smallest recorded adult forearm. Therefore adult and juvenile bats cannot be distinguished on the basis of forearm length alone.

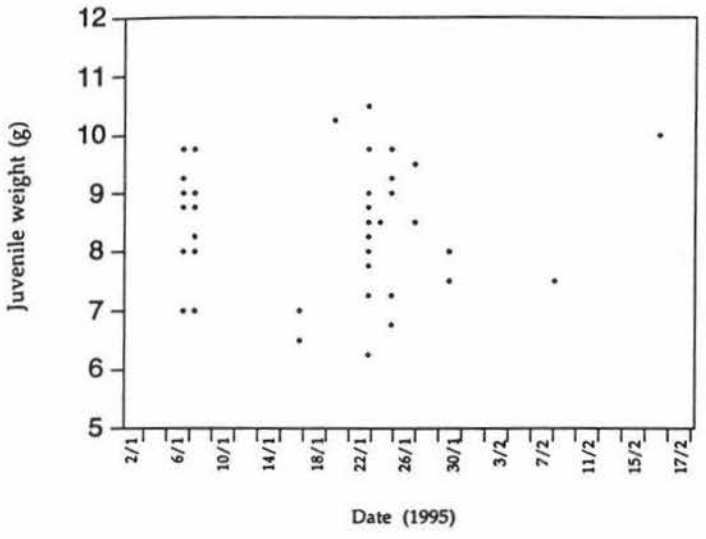

Figure 2. Weight of juvenile bats in relation to date of capture.

A total of 43 juveniles were caught during January and February 1995 (Figure 2). Variations of up to 4.25 g (range 6.25 - 10.50 g) occurred between juveniles caught on a single night (22/1/95). There was no significant relationship between juvenile weight and capture date (Spearman Rank Correlation) or between the number of cartilage bands in metacarpal-pharangeal joints and capture date. Initial indicators that bats may be sub-adult were light weight and dark colour. Juveniles were confirmed by the presence of (one or two) cartilage bands, or if no bands were evident, the absence of bulging in the metacarpal-pharangeal joint (Parnaby 1992). In some juveniles it was not possible to determine whether one or two bands were present, so these individuals were placed in the fourth category "one or two" bands.

As there was no significant difference between left and right forearm length in juveniles (R = 0.97), mean forearm length was used in this juvenile morphometric analysis instead of the individual left and right measures. As juvenile weight increased (Figure 3a and 3b) then so did forearm length and body length. Juvenile wingspan increased isometrically with body length (Figure 3c) as it does in adult males (Figure 4).

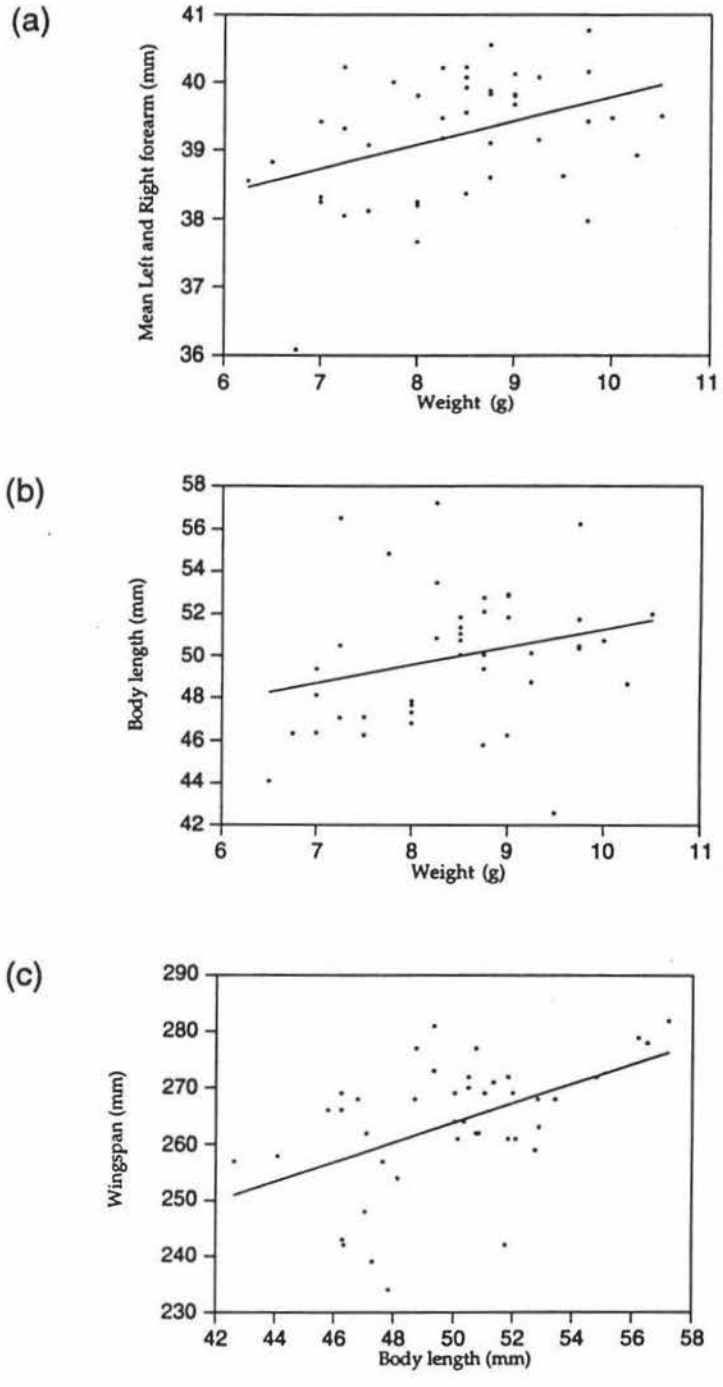

Figure 3. Relationship between (a) mean forearm length and weight of juvenile bats (R=0.397), (b) body length and weight of juvenile bats (R=0.265), (c) wingspan and body length in juvenile bats (R=0.488).

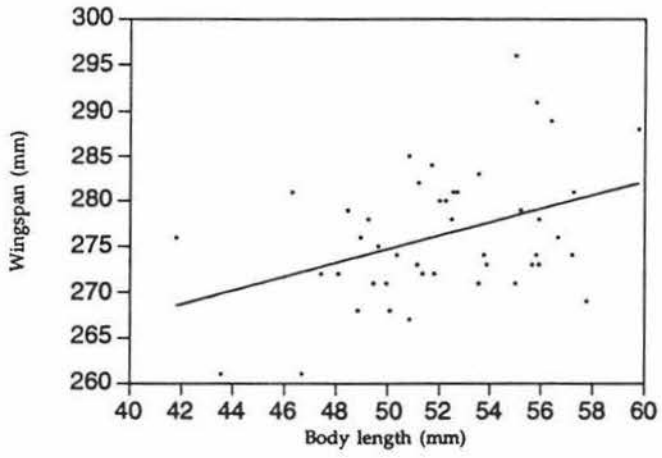

Figure 4. Relationship between wingspan and body length in adult male bats (R= 0.399).

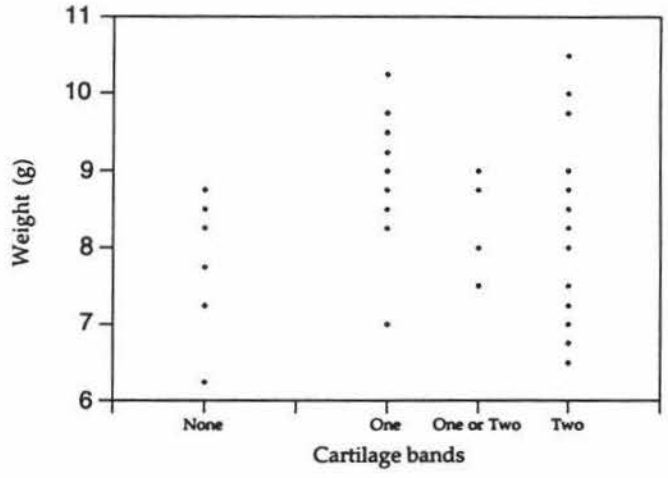

Figure 5. Relationship between weight and the number of cartilage bands in the metacarpal-pharangeal joints of juvenile bats.

There appears to be a negative relationship between the number of cartilage bands in the metacarpal-pharangeal joints and other body measurements of juvenile bats (Figure 6), but this was only significant ($P<0.02$) in the case of juvenile weight. There was also variation in body measurements between individuals with two distinct cartilage bands. For example, wingspan measurements ranging from 234-282 mm and weights ranging from 6.5 - 10.5 g were recorded in bats with two distinct cartilage bands (Figure 5). However, as the number of bands decreased to one or none, the body measurements generally increased. The best predictor of the number of

cartilage bands using regression analysis was tail length followed by wingspan and weight, although these were not significant at the 5% confidence level. The most common number of cartilage bands present in captured juvenile bats was two.

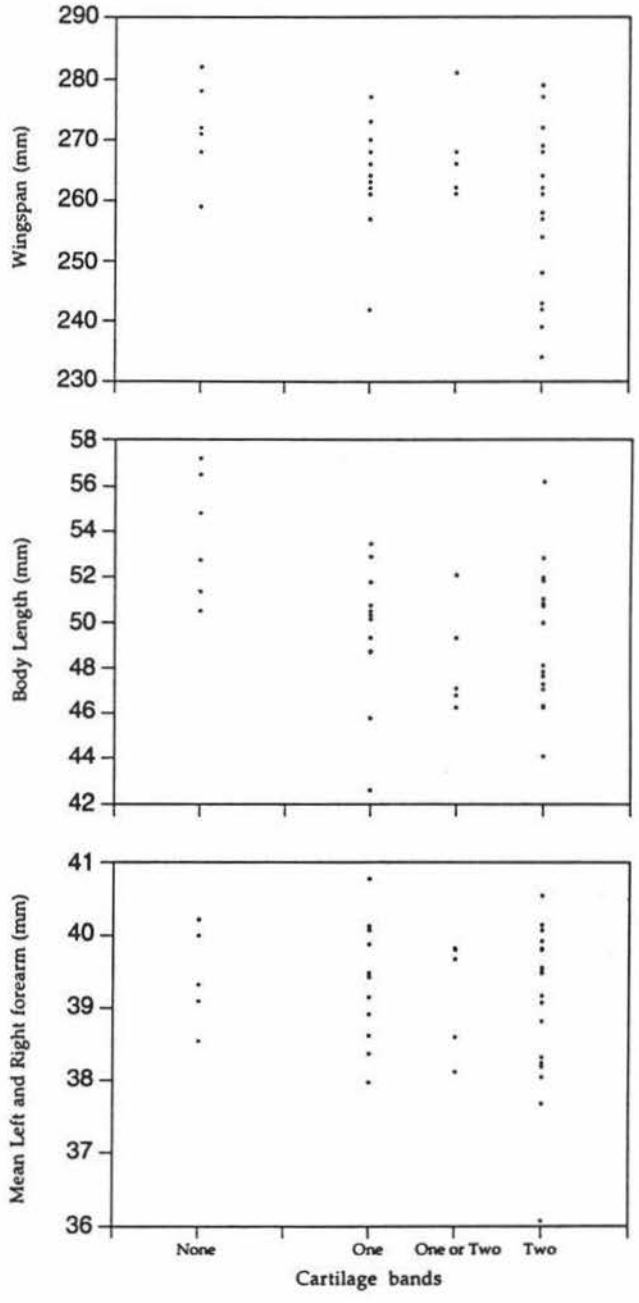

Figure 6. Relationships between wingspan, body length (including head), individual mean forearm length and the number of cartilage bands present in the metacarpal-pharangeal joints of juvenile bats.

Discussion

Measurements from long-tailed bats caught at Balls Clearing provided a significant data base to describe the morphometrics, sex ratio, sexual dimorphism, post-natal development, and an assessment of measurement reliability. In addition it should provide useful information for future comparative work.

Morphometrics

Morphometric data presented here is not entirely consistent with other reported measurements. Forearm data published by Daniel (1990) from 29 bats collected between Auckland and Oamaru have similar ranges and means to the Balls Clearing measurements. Body length and wingspan data have broader ranges than those reported by Daniel, while mean tail length measurements were considerably smaller than the minimum he reported. These discrepancies may be a consequence of different measuring techniques. A north-south cline in *C. tuberculatus* size is suggested by (Daniel 1990) and is evident in closely related Australian species such as *C. nigrogriseus* Peters, *C. morio*, and *C. gouldii* (Van Deusen & Koopman 1971; Hall 1970; Tidemann 1986). More morphological data collected from different populations of *C. tuberculatus* are needed to determine if a New Zealand north-south cline exists. More data will also help develop an understanding of how morphological differences vary with habitat type, climate type, geography and altitude.

Sex Ratio

No estimates could be made of the total number of long-tailed bats at Balls Clearing because few marked individuals were recaptured. Roost observations suggest that there are at least 208 bats in the reserve (Chapter 6).

The high ratio of adult female bats caught at Balls Clearing is not likely to reflect the true proportion of females in the population. Females have higher energy demands during pregnancy and lactation (Millar 1977; Kunz 1987; Rydell 1993; Kurta et al. 1989; Kurta et al. 1990) so are probably more

active, and are more likely to be captured, than males. It is also possible that females are easier to catch during pregnancy if their manoeuvrability is reduced because of their extra weight (Aldridge & Brigham 1988). The sex ratio bias for the juvenile bats caught was the reverse of that for adults, with more males being caught than females. The sample size of juvenile bats caught was relatively small so the sex ratio of juveniles caught may not be a good indication of the sex ratio in the population or even of juveniles born that season. There is no obvious reason why a large proportion of captured juveniles were male. If assuming male and female juveniles have the same energy demands (ie: storing sufficient fat reserves for winter) then they should have an equal chance of capture.

Measure Reliability

The reliability of morphometric data is likely to vary depending on which part of the body is measured because some body parts are more difficult to measure consistently than others. Bat forearms are basically a single fine bone, padded with skin at each end and so are relatively easy to measure. They are also readily accessible, and can be secured with the fore-finger and thumb while an accurate measure is taken. The ease with which accurate forearm measurements can be gained is reflected in the lack of variation in mean left and right forearm lengths. The tail on the other hand is harder to measure consistently as some bats extend their tail allowing easy measurement while the tails of other bats need to be extended with the fingers. The measurement of body length (which includes the head length) is also likely to be variable depending on the degree of stretching or compression of the neck and spine.

Sexual Dimorphism

Sexual dimorphism was exhibited in the size of long-tailed bats at Balls Clearing, with the tail being the only measurement that was not significantly larger in females than in males. Larger females, however, is not a characteristic shared by all *Chalinolobus* species. No sexual dimorphism was found in *C. gouldii* forearm measurements (Dixon & Huxley 1989), or in wing and skull dimensions (Tidemann 1986), while sexual dimorphism where males are larger than females, was found in the

closely related species *C. picatus* Peters (Richards 1979). Sexual dimorphism of size, therefore, appears to vary among *Chalinolobus* species. Most other Vespertilionidae tend to be sexually dimorphic (Williams & Findley 1979). Several theories attempt to explain this but are beyond the scope of this paper. Those concerning the occurrence of larger females than males are reviewed by Williams & Findley (1979).

Juvenile Development

There is much variation in morphometrics, weight and number of cartilage bands between juveniles at the same apparent stage of development. Juvenile *C. tuberculatus* with equally sized forearms and body lengths varied greatly in weight (Figures 3a and 3b) so weight is not a good predictor of juvenile age or stage of development. The relationship between juvenile wingspan and body length (Figure 3c) is also highly variable. Although the regression between juvenile wingspan and body length is strong, there is a lot of scatter. It is unlikely that the pattern is a result of the development of juvenile wings or bodies as there is just as much scatter with a weaker regression when adult male wingspan is plotted against body length (Figure 4). Males were compared as pregnancy may affect female body length. More reliable juvenile measures such as right forearm versus left hind limb (Appendix III 1) show it is unlikely that this scatter is caused by different juvenile parameters developing at different rates. It appears then that post flight juvenile bats develop isometrically.

Although young bats are relatively large, size was a good initial indicator of juvenility, with any bats with forearms less than 40 mm being checked for other juvenile characters. Fur colour can also be used as an indicator of age. Balls Clearing juvenile bats tended to have far darker, uniform colouring, approaching black, while the fur of adults was chocolate brown. The presence of cartilage bands in the fourth metacarpal-pharangeal joints of the finger was sufficient evidence to show that a bat was sub-adult. However some juveniles had lost all visible sign of cartilage bands and yet were still most likely to have been born in the current season because of their size, colour, and lack of thickening in the metacarpal pharangeal joints.

In this study, the most striking thing about the number of cartilage bands recorded in individuals was the amount of variation that existed in other

measurements within a cartilage band class. This suggests that the change in the number of bands present is slow relative to the morphometric change in body size.

The flying age of juvenile bats at Balls Clearing was estimated as approximately eight weeks (Chapter 3). This is approximately twice the age reported in Australian *Chalinolobus* species. *C. gouldii* juveniles were recorded flying soon after they reach one month of age (Lumsden & Andrews 1988; Dixon & Huxley 1989), and *C. dwyerii* Peters flew three or four weeks after birth (Hill & Smith 1984).

There was probably some variation in age between juvenile individuals caught on the same night because there was a wide range of juvenile weights recorded on the first night juveniles were observed. It is possible that *C. tuberculatus* juveniles were able to fly earlier than our estimate, but females may have been waiting for favourable conditions before taking juveniles on their first flights. The onset of juvenile capture was very sudden (Figure 2) and the weather patterns of the two proceeding nights offer no clue to this pattern (Chapter 4). On these nights minimum and maximum temperatures were slightly lower than average, 1 cm of rain fell, moonlight was low, and there was slightly below average prey abundance. The night when the first set of juveniles were caught was relatively warm (9.5 - 16.5°C), there was no rain, light wind, little sky cover and 32% of full moon. It was either a good night for juveniles to emerge, or a good night to catch juvenile bats.

It is not known whether juveniles were attached to females when they were caught as there were no actual observations of juvenile capture. Juveniles may have been in close pursuit of their mothers, or were captured completely independently of females. All but one captured juvenile (19/1/95) were present in the trap with adult females, and all juvenile bats captured were capable of sustained flight, and flew independently when released. Repeated efforts to match juvenile bats with females captured at the same time were made. Combinations of juveniles and adult females were left alone at release time, juveniles were held back or placed alone on tree perches, and on one occasion 18 females and 14 juveniles were released into a 2 m high shade cloth tent (approximately 3 x 2 m) and observed for any sign of mother/offspring matching, but no behaviour of this kind was observed.

Morphometric data such as that collected at Balls Clearing provides valuable information on the biology and development of long-tailed bats. Similar studies should be conducted in other parts of New Zealand to complement and extend this work.

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Chapter 3

The breeding season of long-tailed bats, *Chalinolobus tuberculatus* Gray (Vespertilionidae) in a North Island podocarp forest.

Abstract

The breeding season for long-tailed bats at Puketitiri, Hawkes Bay was determined by monitoring female weight, nipple size and the occurrence of juvenile bats. Most females gave birth in mid-November. Weight gain amongst females was more consistent up to parturition than weight loss after. Parturition was earlier than closely related species at similar latitudes in Australia. The onset of nipple enlargement coincided with parturition and nipples did not reduce in size until volant juveniles were captured in early January. This suggests that lactation lasted approximately eight weeks; up to four weeks longer than other *Chalinolobus* species in Australia. Almost all females (87.8%) captured during breeding showed signs of pregnancy or lactation.

Keywords: Bats, Vespertilionidae, *Chalinolobus tuberculatus*, breeding, parturition, lactation, juvenile.

Introduction

Two bats survive in New Zealand, the lesser short-tailed bat *Mystacina tuberculata* Gray, (Mystacinobidae), and the long-tailed bat *Chalinolobus tuberculatus* Gray (1843). The greater short-tailed bat *Mystacina robusta* Dwyer, is thought to have been extinct since 1965 (Daniel 1990). The long-tailed bat belongs to the largest and worldwide family, Vespertilionidae. It has five closely related species in Australia, Tasmania, Norfolk Island, New Caledonia and New Guinea (Daniel 1990).

The breeding biology of the long-tailed bat is virtually unknown. Daniel (1990) suggested that mating probably occurs in autumn, ovulation and fertilisation probably occur in spring and parturition, at least in the North Island, occurs in summer. Detailed studies of reproduction and development in two closely related Australian species, *C. morio* Gray and *C. gouldii* Gray, have been published (Kitchener 1975; Kitchener & Coster 1981, respectively). The timing of pregnancy, parturition and lactation have

been noted for *C. gouldii* and *C. morio* (Young 1979, 1980; Kitchener & Coster 1981; Lumsden & Andrews 1988; Dixon & Huxley 1989) and appear to vary with latitude as in many species (Racey 1982).

The main aim of this study was to determine the parturition times and the length of the lactation period in long-tailed bats. We predict that regular measurements of female weight in one population through spring and summer will help determine the period when most females are pregnant and give birth. From descriptions of nipple size and the presence of volant juveniles, the length of the lactation period should be able to be determined. Latitude and habitat types are likely to affect the timing of the breeding season and this was tested by comparing our data with closely related species in Australia. Bat and prey activity levels from concurrent studies will be used to discuss the energy demands of long-tailed bats during reproduction.

Study site

Data on the breeding season of the bats was collected at Balls Clearing Scenic Reserve, Puketitiri, Hawkes Bay. Vegetation types, climate and geography are described in Chapter 1.

Methods

Adult bats captured in harp traps (Tidemann & Woodside 1978) during spring and summer were weighed to the nearest 0.25 g using 50 g spring scales. Mean male and mean female weights were calculated for each week that bats were captured. The nipples of adult females were examined for signs of lactation as described in (Parnaby 1992) and classified as having either no obvious nipples, evident but not enlarged nipples, enlarged nipples, or very enlarged nipples. Bats were confirmed as juveniles by the presence of cartilage bands or the lack of bulging in the metacarpal-pharangeal joints (Kunz & Anthony 1982; Parnaby 1992), as well as the weight and colour of individuals (Chapter 2).

Results

A total of 240 long-tailed bats were captured from September 1994 to February 1995. Of these, 145 were adult females, 53 adult males, 13 juvenile females and 29 were juvenile males.

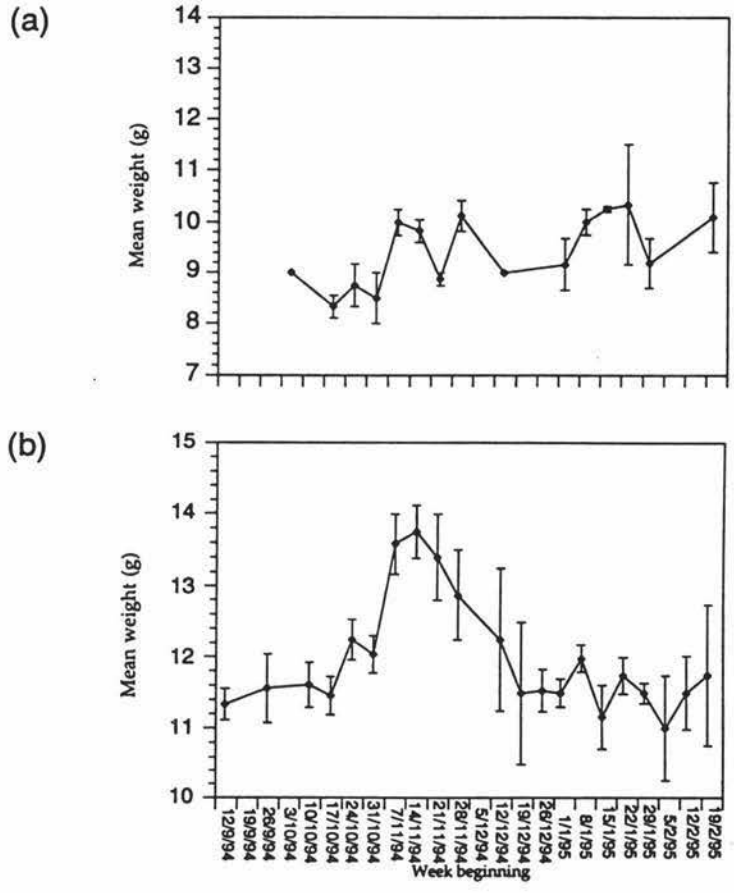

Figure 1. Relationship between mean weight and date of capture of (a) males, and (b) females. (Bars = mean $\pm$ 1 standard error).

Mean male weight per week fluctuated between 7 and 11.75 g (Figure 1a), and showed a slight overall increase from October to February, while a clear peak in female mean weight (Figure 1b) occurred in the week beginning 14 November. This increase in weight occurred from mid to late October and returned to normal (11-12 g) between mid and late December.

The first juvenile bats were captured on January 6, and juveniles continued to be caught through to late February (Figure 2) when trapping ceased.

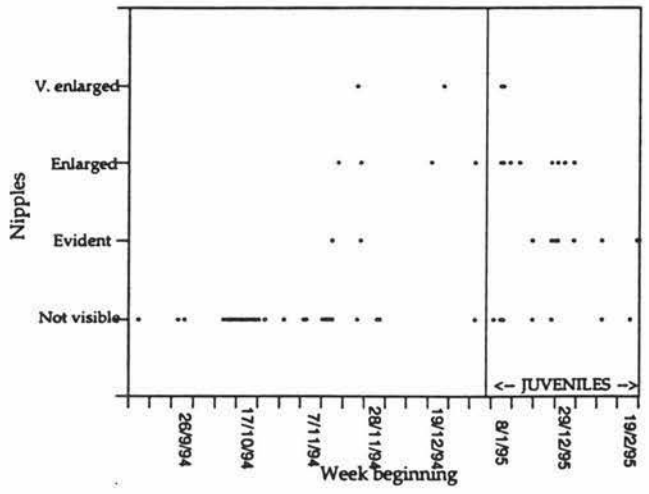

Figure 2. Change in adult female nipple size. Capture period of juvenile bats is indicated.

The peak in mean female weight coincided with the first occurrences of nipple enlargement (November 14). The first juvenile was captured approximately eight weeks later coincident with a marked decline in nipple size. Nipples remained clearly visible, although reduced in size, in some captured females until late February. The capture of juveniles was steady until late February, except for 22/1/95 when 14 juveniles were caught (Chapter 2, Figure 2).

Of the 82 adult females captured between 14 November when the first enlarged nipples were observed and 19 February when the last bat caught, easily found nipples were not evident in 10 individuals (12.2%).

```
                                                    VOLANT
<---------- PREGNANCY--------][------- LACTATION ------][----- JUVENILES ---->
-----------I-----------------I-----------------I-----------------I-----------------I------------
Sep          Oct               Nov               Dec               Jan          Feb
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Figure 3. Breeding season of long-tailed bats at Balls Clearing.

Discussion

Parturition dates and the length of the lactation period were identified for long-tailed bats at Balls Clearing, Hawkes Bay. Mean male weights generally increased from October through to February but were quite variable. This increase in male weight through the season was probably the result of increased fat reserves for winter. Female weights were more consistent, and showed a distinct increase during November prior to giving birth, peaking near the middle of the month. Weight varied less up to November than after parturition suggesting that weight gain in females was more consistent among individuals than the post natal weight loss. It also took longer for the mean weight to return to normal (approximately five weeks) than it did to reach its peak (approximately three weeks). It is possible that the onset of favourable environmental conditions resulted in this uniform weight increase while individual variability in foraging behaviour and physiology during the weeks following birth may contribute to the large variation in weight. Similar patterns have been observed in other Vespertilionidae species. In *Miniopterus schreibersii* Bonaparte, embryo implantation is thought to be synchronised in females and initiated by increasing day-length (Bernard 1994), foetal growth was synchronous during the first three months of post-implantation, then showed more variation in foetal weight and foetal age in the last month of pregnancy. The timing of breeding in many species reflects variations in food supply (Racey 1982). Parturition in *Eptesicus nilssonii* Rafinesque coincided with the shortest period of darkness around the summer solstice (Rydell 1993). This does not occur in *C. tuberculatus* as the summer solstice occurred approximately four weeks after the estimated parturition.

The timing of breeding of *C. tuberculatus* is different to closely related Australian species. Bats at Balls Clearing gave birth earlier than *Chalinolobus gouldii* at a similar latitude (Bass Straight) (Kitchener 1975), while the birth of *C. morio* in Queensland was observed as early as 20 October (Young 1979). Kitchener made detailed reproductive studies of several *Chalinolobus* species in Australia and concluded that the birth period varies with latitude; from late November to December in the south-west region, and earlier in northern areas. Latitude however must explain only part of the variation in parturition dates of different species. The birth of *C. gouldii* in Victoria however was observed on 10 November (Lumsden

& Andrews 1988) which is close to the parturition date at Balls Clearing. However, *C. gouldii* tend to give birth earlier in arid Western Australian areas, and the commencement of breeding is more variable (Kitchener 1975) than in the east (Dixon & Huxley 1989). Differences in parturition date between long-tailed bats and Australian *Chalinolobus* species is not surprising considering the variation shown between bats at different latitudes and in different climates in Australia. It appears that there are some environmental effects which may be (but are not always) a function of latitude, with some variation between species. Similar studies in other parts of New Zealand should help to determine whether this is a characteristic of the species or of the environment.

The onset of nipple enlargement in females at Balls Clearing coincided with the peak in mean female weight. This indicates that lactation for most females probably began in mid November. In late December the weights of females had returned to approximately normal while nipple size still showed much variation. Nipple size decreased in early January, but enlarged nipples were still recorded at the end of the study in late February. This coincided with the onset of volant juveniles and suggests that lactation for the population in general lasted approximately eight weeks. This is longer than reported in other species. Most insectivorous bats are weaned between four and eight weeks of age (Kleiman & Racey 1969; Bogan 1972; Kunz 1973; O'Farrel & Studier 1973; Burnett & Kunz 1982; Kunz et al. 1983). The lactation period in *C. tuberculatus* also appears to be longer than in closely related species. The length of lactation in long-tailed bats is not consistent with Australian *Chalinolobus* species that also gave birth during November. Most *C. gouldii* in a maternity colony in Melbourne had finished lactating by January, with a shrinking of nipples observed in lactating females between December and January (Dixon & Huxley 1989). In February, the *C. gouldii* females did not have obvious nipples and did not appear to be lactating, while in March no nipples were recorded but young were still present in the colony. The close study of three females by Dixon and Huxley showed that lactation lasted for a period in excess of one month. Young (1980) observed lactating *C. gouldii* females and non-volant young in February in Queensland.

Given that only 12.2% of adult females caught from mid November onwards had no nipple enlargement, then it is assumed that 87.8% of adult females captured must have been pregnant. The proportion of pregnant *C.*

tuberculatus females is high when compared to *C. gouldii* where only 40% (38 out of 95) of banded females were pregnant or lactating, with the majority of them breeding only once in two seasons (Dixon & Huxley 1989). However pregnant females are generally more active than non-pregnant females, and also may have reduced manoeuvrability (Aldridge & Brigham 1988; Young 1980) so the chance of their capture are increased. The mortality rate of juveniles is not known so this cannot be extrapolated to derive a measure of productivity. It could however be used as an indicator of changes in birth rate at this site as more data are obtained from future seasons.

Long-tailed bats at Balls Clearing were most active during pregnancy, and the peak in activity corresponds with the mean parturition date of females while there was a reduction in activity during lactation (Chapter 4). Assuming that there was no mass migration of females and their young out of the area (which is unknown), this suggests that pregnancy (and particularly the last stage of pregnancy) was the most energy demanding period. In general lactation is more energy demanding in insectivorous bats than pregnancy (Millar 1977; Kunz 1987; Rydell 1993; Kurta et al. 1989; Kurta et al. 1990). The reduction in activity during lactation in long-tailed bats may be a reflection of the time female bats require to suckle young.

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Chapter 4

The foraging activity of long-tailed bats *Chalinolobus tuberculatus* Gray (Vespertilionidae) over spring and summer.

Abstract

Bat activity in Balls Clearing was monitored using an automatic bat detector that records bat echolocation. The number of bat passes in the first hour after sunset, the number of passes per hour of darkness and the total number of passes during the night were analysed with respect to weather, light intensity and potential insect prey abundance. Combinations of month of the year, maximum temperature, sky cover, wind strength and moonlight intensity best explained variation in bat activity. All three measures of bat activity were highest during pregnancy with reduced activity during lactation. The time of the first pass relative to sunset was earliest during September and February. Lactation and juvenile volance occurred during the two highest peaks in insect abundance. Diurnal bat activity generally followed a bimodal pattern with peaks of activity in the first and last hour of darkness, however there were seasonal differences in this pattern.

Keywords: Bats, *Chalinolobus tuberculatus*, seasonal activity, diurnal activity, insect abundance, light intensity, weather.

Introduction

Most insectivorous bat species have evolved nightly activity patterns to minimise the time spent in flight (Kunz 1982). These can be affected by prevailing external conditions such as weather, light intensity, potential changes in prey availability and length of the night (Laufens 1972; Erkert 1974; Kunz 1974; Fenton et al. 1977; Swift 1980; Kunz 1982).

The annual activity of *Chalinolobus morio* was studied in Tasmania with respect to insect prey abundance (Taylor & O'Neill 1988; Taylor & Savva 1990), and some seasonal aspects of activity were described for *C. picatus* and *C. gouldii* (Richards 1979). Seasonal capture rates and emergence of *C. gouldii* are discussed by Dixon & Huxley (1989), but there are no published data describing the diurnal and seasonal changes in activity of New Zealand

bats, or the effects that environmental conditions have on their activity. Little is known of the long-tailed bat's (*C. tuberculatus* Gray) activity patterns other than the dates of long-tailed bat sightings (Daniel & Williams 1984). Most of these sightings were in January and February.

The major aim of this paper is to describe the activity of a forest population of long-tailed bats. Seasonal changes in the time of the first pass, the number of passes (over a fixed point) in the first hour after sunset, bat activity through the night and how the bats use the hours of darkness are described. Seasonal activity is analysed with respect to environmental condition including weather, light intensity and prey abundance.

Methods

Bat activity

All data was collected at Balls Clearing Scenic reserve between 9/9/94 and 22/2/95. A review of the location, geography, habitat type and climate is included in Chapter 1. Bat passes were automatically recorded using a sound-activated tape recorder (Sony TCM 38V) and a Mini-2 Bat detector (Ultra Sound, Birmingham). These were placed inside a three litre plastic container with the microphone of the detector pointed through a hole cut in the plastic, while the speaker was orientated toward the tape recorder. The tape recorder also recorded the time of each pass. The detector was powered by 2 AA Alkaline batteries which lasted for two nights. This set-up suited long periods in the field without the need to recharge batteries. The unit was tested in several sites during September until a suitable site was selected. This site was then used for the remainder of the study. The site (Chapter 1, Figure 1) was approximately 100 m into dense mature podocarp forest and was chosen for the following reasons. The number of passes per night usually ranged within the recording capabilities of a C90 audio tape so that the highest number of complete bat nights could be recorded. The site overlooked a slow moving tributary of the main Balls Clearing stream, and was central with easy access. The bat recorder was always set at full volume and the recording volume on the tape recorder was always set at 1/4 of full. The detector was placed on the forest floor, 1.5 m above water level with the microphone pointing towards the canopy at an approximate angle of 20° from level. This position and direction was kept as constant as possible

throughout the study. Tapes were analysed and the time to the nearest minute of each pass was noted on the day following each night's recording.

Seasonal changes in activity were investigated by analysing the total number of bat passes per night, the number of passes per hour of darkness, the time of the first pass and the number of passes in the first hour after sunset. Patterns of diurnal activity were investigated by splitting each night into 20 equal segments. This gave a nightly activity value for each segment relative to other periods during the night.

Insect abundance

Insects were sampled using a malaise trap. This provided an indication of possible bat prey species abundance (Barclay 1985). The malaise trap site was chosen so that it was adjacent to four habitat types used by the bats at the reserve: mature podocarp forest; mature red beech forest; stream; and pasture. The malaise trap was emptied during the last hour of sunlight every three days, and the insects stored in 70% ethanol.

Insect taxa that were either known prey items (Daniel & Williams 1983; Dwyer 1962; Colenso 1890; Roach & Turbott 1953; Lewis, pers. comm.[1] 1995; Chapter 5) or known to be nocturnal or crepuscular, and likely prey species, were identified and removed from the samples and sorted into three size classes: small (< 4 mm in body length), large (> 20 mm body length), and medium (4 mm - 19 mm). Insects in the small class were mostly Sciaridae, Mycetophilidae and micro- Lepidoptera. Large insects included huhu beetles and lemon tree borer (Cerambycidae), large green chafers and large grass grub beetles (Scarabaeidae), large moths, and Tipulidae, while medium sized insects included all remaining moths, Tipulidae, Tanyderidae, Chironomidae, Culicidae, Plecoptera, Tricoptera and Neuroptera.

Alcohol was then evaporated from analysed samples by placing the individual vials under 60 w light bulbs for two days. When only small quantities of ethanol and water remained, the vials were placed in a drying oven at 60°C for five days. The dry weight of each sample was measured

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[1] c/o David Lewis, RD 4 Puketitiri, Hawkes Bay.

using electronic scales. Preliminary trials indicated that 7.78 % to 34.11% of the weight of insects were dissolved in the ethanol and remained on the surface of the vials as a fatty layer. Each sample was dried and weighed in its original vial and the mean weight (n=30) of new vials was subtracted so this residue was included. The effect that potential prey abundance factors have on insect activity were tested separately from other environmental variables.

Weather

Five meteorological characteristics were measured during this study. Maximum and minimum temperatures were taken from a thermometer placed 1 m above the bat detector. The thermometer was reset at dusk and the temperature was recorded every morning when the tape was collected. Rainfall was measured using a rain gauge placed in pasture adjacent to the native forest. Wind strength was estimated as either still, light, moderate, strong or very strong. Numerical values (0 - 4) were later assigned to these estimates. Several measures of light intensity were calculated: the percentage of the full moon; the time in minutes that the moon was out; and the percentage cloud cover of the sky (which took cloud thickness into consideration). The length of twilight, sunset and sunrise time, moon phase and the amount of time the moon was out per night were calculated from local data obtained from the Carter Observatory, Wellington. Originally the percentage of full moon and the time when the moon was out were combined to get a figure of moonlight intensity. The two variables are closely related such that when there is half moon, the moon is visible for half of the maximum in its cycle, and likewise with all intermediate phases from no moon to full). Moon minutes were used because more detailed data were available for intermediate phases.

Statistical analyses

The effects of individual environmental variables on the measures of bat activity were tested using single regression analysis in MINITAB.

Multivariate analysis using a standard stepwise procedure was run using SAS (SAS 1985) on the seven environmental variables: month, minimum temperature, maximum temperature, rain, % moon, moon duration, sky cover and wind. This stepwise procedure isolated extrinsic factors affecting

each measure of activity and allowed a model to be constructed that best explains the variation in bat activity using combinations of relevant individual variables.

Stepwise regression analysis was also used to test the effects of potential prey species abundance on bat activity. Bat activity data was converted to three day mean activity values when testing prey abundance effects because malaise trap samples were emptied every three days. Variables used in these models were: the total number of insects trapped every three days; the total number of potential prey insects trapped; total potential Diptera prey; total potential Lepidoptera prey; total potential Coleoptera prey; and the total weight of potential prey individuals.

Results

Passes recorded from 78 full nights were used in the analysis. A further 67 nights of bat passes were not used for the following two reasons. First, there was so much activity that the tape ended during the night. The inclusion of this data would result in under-representation of the later part of the night. Second, on some nights with heavy rain it was difficult to confirm which recorded sounds were bat echolocation and which were rain drops falling onto leaf litter. The tape would usually run out before sunrise during nights of heavy rain. The effect that rainfall has on bat activity is therefore under-represented.

Bats were least active between December and February, with sharp declines from December in the number of passes in the first hour after sunset, the number of passes per hour of darkness and the total number of passes during the night (Figure 1). Mean passes in the first hour of darkness were highest in September. Mean total passes per night were highest in October while mean passes per hour of darkness were highest in November.

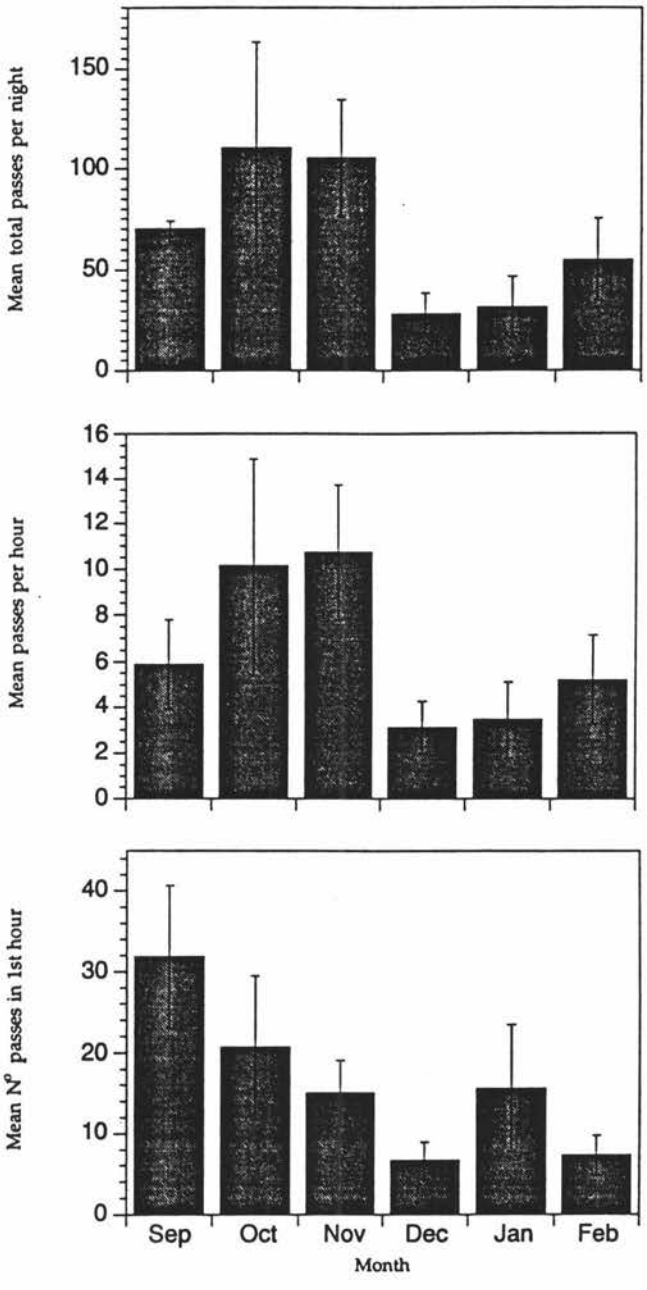


Figure 1. Seasonal changes in (a) mean total passes for the whole night, (b) mean number of passes per hour of darkness, and (c) mean passes during the first hour after sunset. Bars = mean ± 1 standard error.

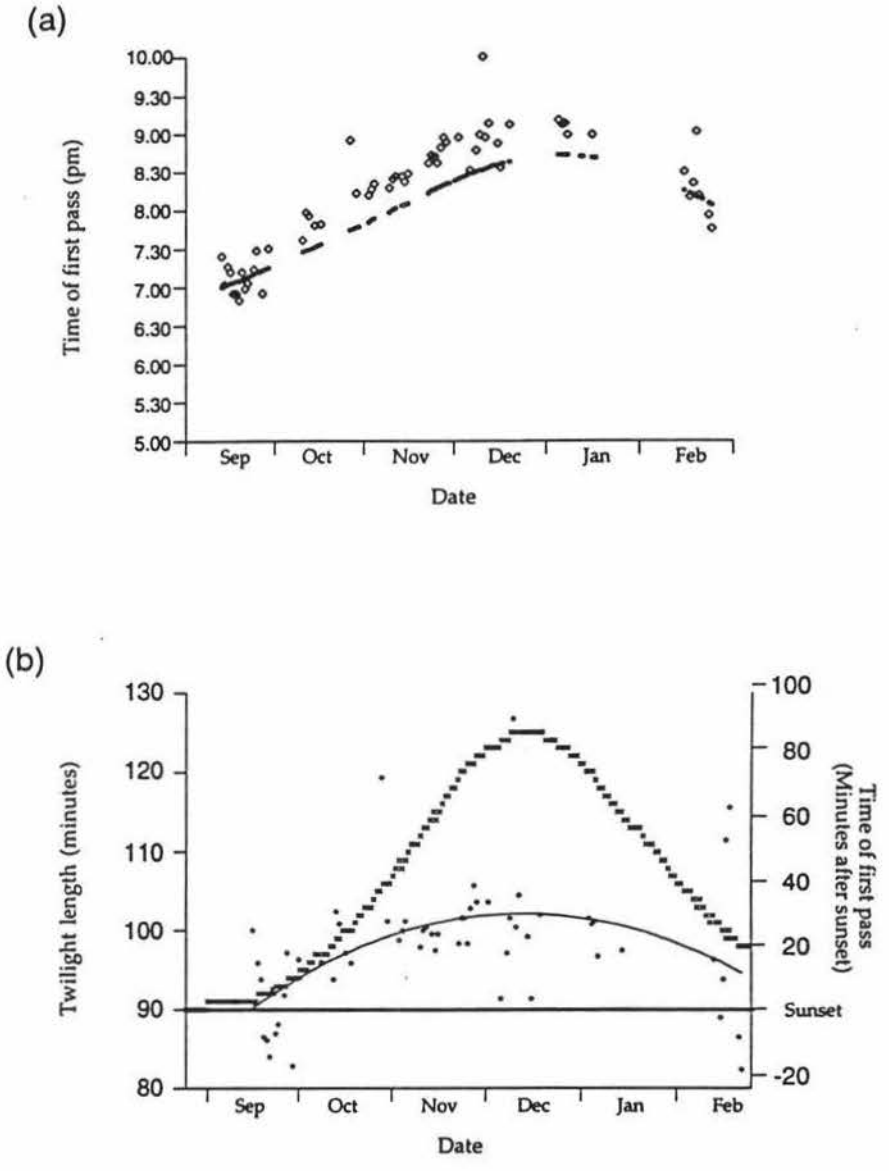


Figure 2. Seasonal change in (a) time of first pass (◊) and time of sunset (•), and (b) time after sunset that first pass was recorded (◊) and astronomical twilight length (x). Regression line of time of first pass also shown (R = 0.508). Data is corrected for day-light saving.

The mean time of the first recorded pass was 19.10 min after sunset. When the time of sunset is standardized, the time period between sunset and the

first recorded pass was at a maximum during early December, while astronomical twilight length was at a maximum from 16 - 26 December (Figure 2b). There was some variability in the time of the first recorded pass. During September and February the first pass was recorded up to 20 minutes before sunset , while no passes were recorded before sunset during October, November, December or January.

Using single regression analysis no individual environmental variable significantly explained the variation in the three measures of bat activity. Some combinations of variables do explain significant components of this variation using multivariate stepwise regressions (Table 1).

Table 1. Summary of stepwise regression procedure for time of first pass.

Variable	Partial R^2	Model R^2	C(p)	F	Prob>F
Month	0.284	0.284	15.951	11.084	0.002
Max T	0.232	0.516	4.358	12.942	0.001
Sky	0.085	0.601	1.355	5.570	0.026

The model that best describes the time of the first pass consists of the following three significant variables. Month of the year alone explained 28.36% of the variance in time of first pass (Prob>F = 0.003), whereas maximum temperature together with month explained 51.57% of the variance (Prob>F = 0.002). When sky cover was added to the model in the third step, the R^2 value is increased to explain 60.12% of the variation in time of first pass (Prob>F = 0.03). The best three-variable predictor model to fit a linear function to the time of first pass data is the equation:

$$T = -49.878 + \underset{\text{(Month)}}{3.201} + \underset{\text{(Max Temperature)}}{3.605} + \underset{\text{(Sky cover)}}{0.080}$$

Table 2. Summary of stepwise regression procedure for number of passes in the first hour after sunset.

Variable	Partial R^2	Model R^2	C(p)	F	Prob>F
Wind	0.3115	0.3115	10.3845	15.3845	0.0004
Moon min	0.1245	0.4360	4.6229	7.2860	0.0109
Month	0.0548	0.4908	3.2599	3.4426	0.0728

The model that best describes the number of bat passes in the first hour after sunset also consists of three significant variables. Month alone explained 31.15% of the variance in recorded passes (Prob>F = 0.0005). When the time that the moon was out (which reflects both moon light intensity and duration) is added to the model, the two variables together explain 43.60% of the variance (Prob>F = 0.02). Wind strength was added to the model and increased the R^2 value so the complete three variable model explained 49.08% of the variation. The best predictor model to fit a linear function to the number of passes recorded in the first hour after sunset is the equation:

$$P = -28.845 + 2.241\,(\text{Month}) + 0.070\,(\text{Moon minutes}) + 0.241\,(\text{Wind strength})$$

No model of environmental variables using the stepwise procedure significantly explained the variation in the total number of passes recorded during the night (Appendix III).

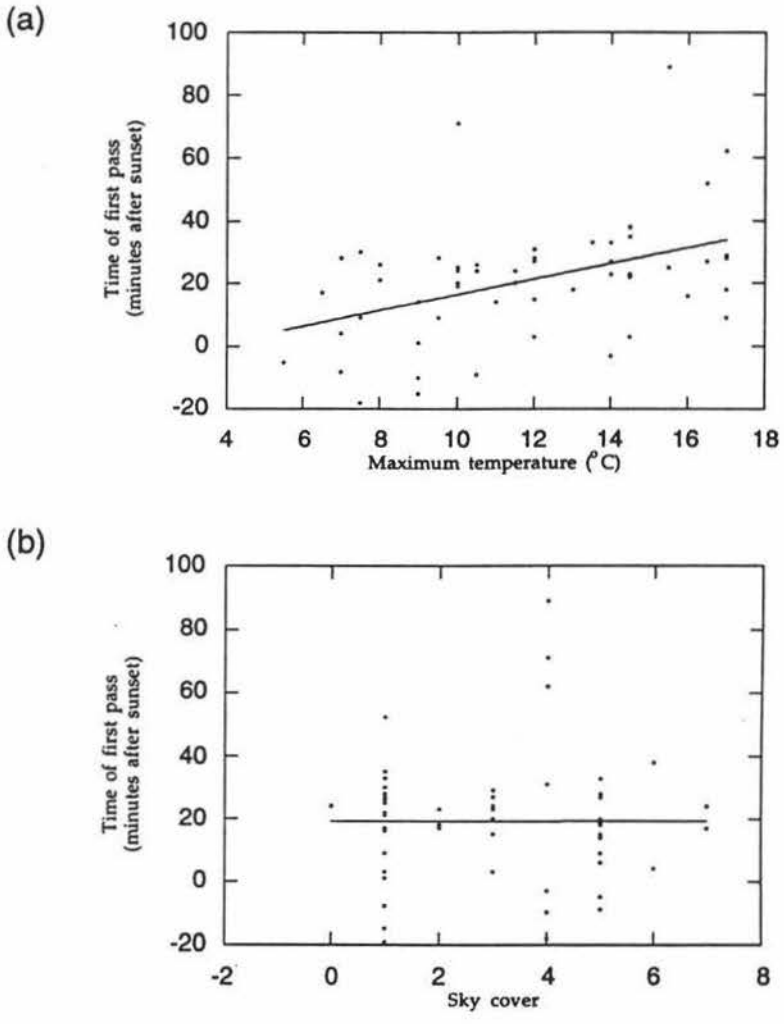
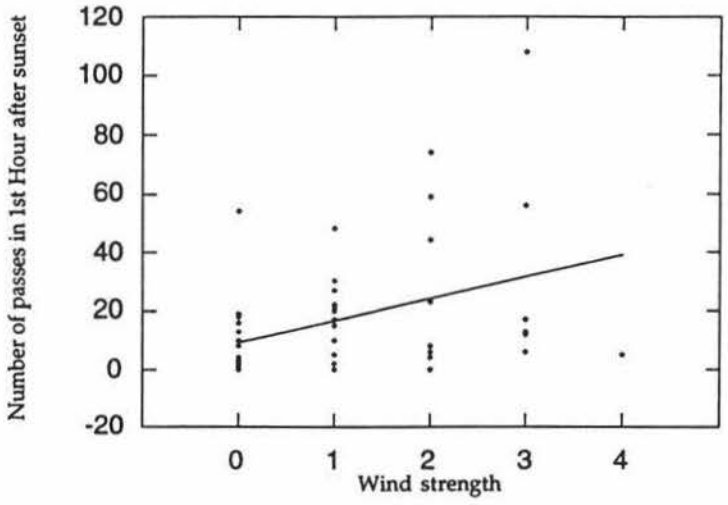


Figure 3. The relationship between the time of the first recorded pass and individual variables (a) maximum temperature at dusk, R = 0.4235 (-8.648 + 2.504 * x), and (b) amount of sky cover, R = 0.003284. Two points over 200 minutes on each graph not shown but were included in the regression analysis.

(a)



(b)

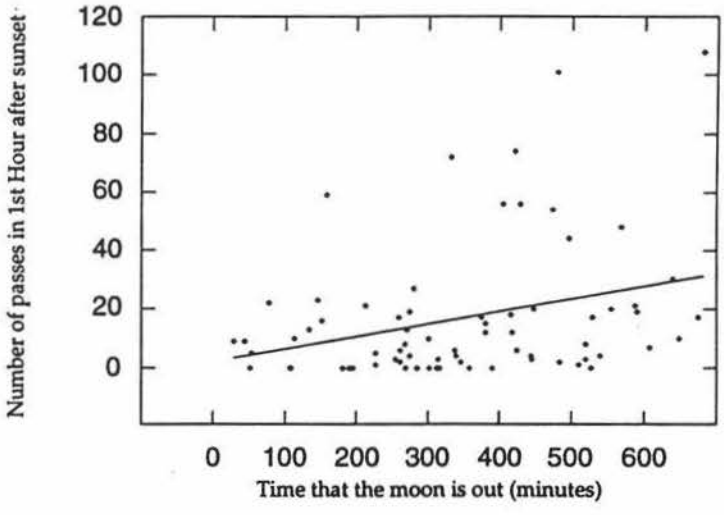


Figure 4. The relationship between the number of passes in the first hour after sunset and (a) wind strength, $R^2 = 0.3836$ (9.0981 + 7.4793 * x), and (b) the time that the moon is visible, $R^2 = 0.3049$ (2.1824 + 0.042233 * x).

The relationships between bat activity and the environmental variables that were significant in the multivariate models are shown in Figures 3 and 4. These environmental factors do not significantly explain variation in bat activity by themselves. However they do show that the first pass was recorded later as temperature increased and that there was much variation in sky cover and how it may affect the time of the first pass. In addition, the

number of passes recorded in the first hour also increased as wind strength increased and the moon intensity and duration increased.

The five nights that the most passes per hour of darkness were recorded provide no real pattern except that there was very little rain, usually some sky cover and little or no wind. Moonlight was variable with one night near the minimum, another at the maximum, and the other three nights at intermediate levels.

The least passes recorded per hour of darkness occurred during nights when there was usually some rain and temperature was not especially low. Wind strength, sky cover and moon light were not especially high.

The nine earliest recorded passes relative to time of sunset all occurred on nights when moonlight intensity was lower than 15% of maximum.

On the nights when the first recorded pass occurred the latest, temperatures and moonlight intensity were higher than the mean. There was usually some sky cover (mean = 38%).

On nights when the most passes in the first hour after sunset were recorded, maximum temperature, moon light, sky cover, wind strength and rainfall all showed considerable variation.

The 14 nights when no passes were recorded in the first hour after sunset were usually wet, however bat activity was observed during rain on other nights. Only 4 out of 14 nights had no rain, with up to 29 mm of rain falling over the preceding 24 hours. Moonlight was variable with approximately 37% mean moonlight. Minimum temperature, sky cover and wind strength were not high.

Insect prey abundance

The Malaise trapping provided samples of terrestrial and aquatic flying insects from the modified and native habitats in which the bats forage.

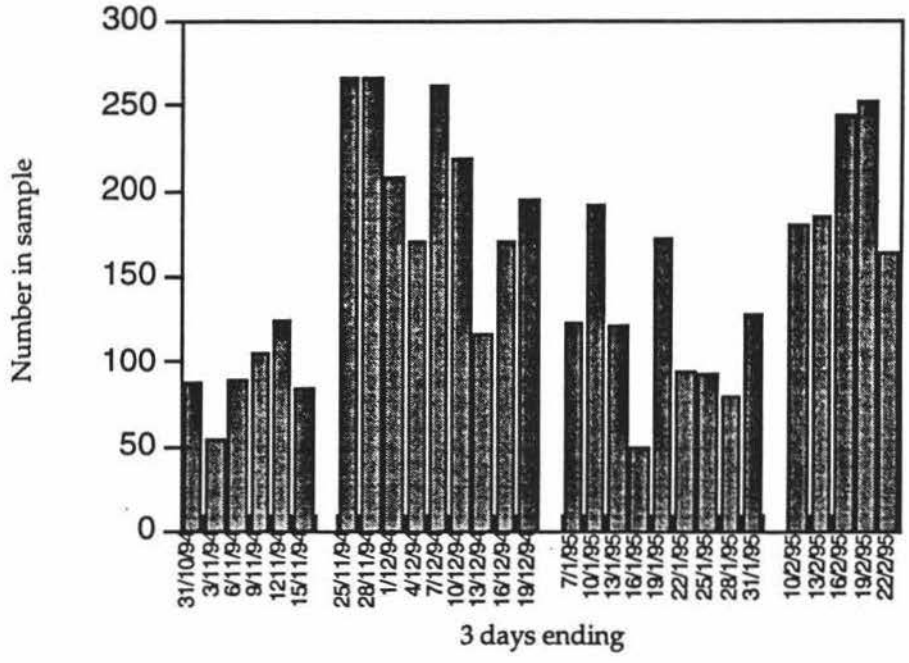


Figure 5. The total number of potential insect prey numbers caught in each three day malaise trap sample.

Prey weight and the total number of potential prey insects trapped showed some correlation with bat activity in the first hour after sunset (Appendix III 2c). The combination of these two variables explain 23% of the variation in the number of passes during the first hour after sunset. However, the model was significant only at Prob> F = 0.2, and potential prey abundance did not significantly affect the total number of bat passes and the time of the first pass. Maximum potential prey abundance occurred between late November to early December and in mid-February (Figure 5). The abundance of Diptera (Appendix III, 2b) follows peaks in the total potential prey, both being greatest during February. Lepidoptera were most abundant from late November to mid-December, while Coleoptera were most abundant between mid-December and mid-January (Appendix III 2b).

Diurnal activity

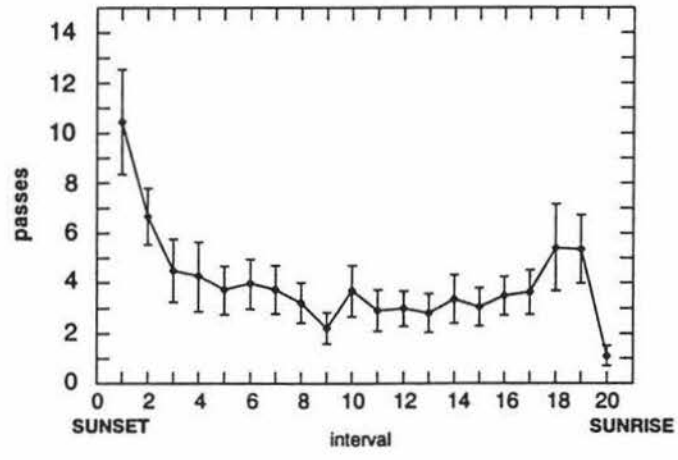


Figure 6. The mean number of passes in each equal segment of the night (all months included). Bars = mean ± 1 standard error.

A bimodal pattern of flight activity is clearly evident when data for every full night of activity are grouped. The first peak (mean = 10.46 passes per segment) and the second peak (mean = 5.35 passes per segment) are separated by a lull in activity. The bimodal pattern was most clear during December and January. There was considerable variation around this bimodal pattern when data for individual months are considered (Appendix III, 2a).

Discussion

Activity patterns in long-tailed bats are hard to predict. They change seasonally and appear to be mainly affected by combinations of environmental conditions. Combinations of variables are probably more important as no single variable significantly explained variation in the three measures of bat activity. In contrast, other species of bats may be affected by

the extremes of some individual variables like minimum temperature, heavy rain and wind (Stebbings 1968; O'Farrell & Bradley 1970; Erkert 1982), although extreme conditions have not prevented bat activity in heavily pregnant and lactating *Myotis lucifugus* Kaup that were observed foraging through severe thunderstorms (Stebbings 1968). Long-tailed bat activity was both recorded and observed during periods of heavy rainfall at Balls Clearing. It appears that rain may prevent foraging during the first hour of activity on some nights but could not really be tested because of the bias discussed above. Under normal circumstances a night that is favourable for bat foraging probably requires several variables to be favourable.

Time of first pass

The significant effect that month had on the time of the first pass is probably due to the related sunset time and twilight length (Figure 2b) that have set patterns through time. The timing of flight is correlated with sunset in several insectivorous bats (Erkert 1978).

The maximum night-time temperature in this study was generally at dusk (when the maximum and minimum thermometer was reset), and temperature rarely increased above this level during the night. Minimum temperature data was excluded from this multiple regression because it usually occurred in early morning and thus was considered irrelevant to bat activity at dusk. The delaying of the first pass with increased temperature is not consistent with other studies (Laufens 1973; O'Shea & Vaughan 1977; Funakoshi & Uchida 1978), as prey abundance also generally increases with temperature (Wellington 1945).

Sky cover could contribute to the time of first pass in two ways. Firstly by reducing heat loss from the earth's surface so that the beginning of the night is warmer. Secondly, increased sky cover also reduces light intensity during twilight which is an important factor in the timing of emergence in other species (Laufens 1972; Gould 1961; Voute et al. 1974; Erkert 1978). The earliest *C. tuberculatus* passes were on nights with little moonlight and the latest recorded first passes were on nights with above average moonlight.

The mean time of the first pass was latest during December (Figure 2) but due to the scatter, was not apparently different to adjacent months and would not explain the large drop in activity for December (Figure 1b and 1c).

Activity in the first hour after sunset

There were far more passes recorded during the first hour after sunset in September than there were in other months. Apart from the possible effects that the breeding season has on this activity (Chapter 3), date may have been an important variable because of its relationship with sunset, moon phase and twilight length that follow set patterns through time.

Bat activity in the first hour after sunset increased as moonlight intensity and duration increased. Moonlight generally reduces activity in insectivorous species (Erkert 1974) and this is thought to be a response to reduce predation by nocturnal avian predators (Erkert 1982, 1969; Morrison 1978). Kunz (1982) and Morrison (1978) report that when the moon is full, activity is often concentrated in the first and last part of the night, hence a bimodal pattern is accentuated. It appears that long-tailed bats may restrict their foraging periods to times when other variables are most favourable.

Total activity through the night

The results from the stepwise regression analysis show that it is difficult to predict the environmental factors that affect the variation in the total number of passes recorded in a night. Temperature, which is an important factor to some species, did not significantly explain variation in bat activity at Balls Clearing. Taylor & Savva (1990) found that *C. morio* are more active during winter than other Tasmanian bats suggesting that temperature is less important in this species, while temperature does not seem to affect activity in some studies of *Eptesicus nilssonii* Rafinesque (Rydell 1993) and *Myotis lucifugus* (Fenton 1970). The reduction in long-tailed bat activity during December is similar to a large reduction in capture rates of *C. morio* recorded in Tasmania during January (Taylor & Savva 1990). High rainfall was the suggested cause in Tasmania, but rainfall was not especially high during this time at Balls Clearing.

The mean total activity (Figure 1a) follows the pattern of mean total passes per hour of darkness (Figure 1b). This suggests that the total number of passes is relatively independent of hours of darkness. Essential activity periods for *C. tuberculatus* may be completed regardless of length of night. Total bat activity is more likely to be governed by the need to gain essential energy, and limited by stomach size (Diamond et al. 1986; Flemming 1988)

and extreme environmental conditions. I suggest that the number of passes in the first hour after sunset is the most accurate measure of bat activity relative to the environment and a more efficient way to gain a seasonal index of activity.

Effects of Breeding

The highest number of passes per hour of darkness (mid-November) is coincident with the peak in mean female weight so *C. tuberculatus* were most active during pregnancy. The bats were less active during lactation with the mean number of passes per hour and the number of passes in the first hour after sunset decreasing in December. The reduction in activity during lactation in long-tailed bats could be a reflection of (1) the time female bats require to suckle young, or (2) a result of increased prey availability during this period (Figure 5) allowing more profitable foraging. Regardless of prey abundance, reproduction probably places certain limitations on activity (Aldridge & Brigham 1988; Morrison 1978).

Seasonal prey abundance vs bat activity

Seasonal prey abundance does not significantly explain variation in bat activity. However there was more activity during periods of low insect abundance. The first peak in insect abundance (late November to early December) occurred at approximately the same time as the reduction in bat activity, while the second occurred in February. The seasonal lull in prey abundance corresponds with the peak in bat activity in November, while the second low was during January.

There is evidence that closely related species *C. picatus* and *C. gouldii* (Richards 1979) and other insectivorous species (Racey & Swift 1985; Rydell 1989) will not forage in unproductive areas. It appears that long-tailed bats may increase activity in response to low insect numbers rather than migrate to other foraging areas.

Use of night

In long-tailed bats, the considerable variation around a bimodal activity pattern in different months indicates a seasonal change in how bats used the night. Just what seasonal factors contribute to this variation is unclear. Studying the seasonal changes in how bats use the night is difficult because comparisons are needed between nights of different lengths. For this reason each night of activity was divided into 20 equal segments from sunset to sunrise. As night length changes, then so do the length of the segments. This method was used to describe the diurnal abundance of insects (Williams 1935).

The main activity peak is at the beginning of the activity phase and the second activity peak is usually towards the end, for almost all insectivorous bats studied in the field (Erkert 1982). This was interpreted as a response to the time of maximum food availability (Erkert 1982; Swift 1980; Funakoshi & Uchida 1978) and the overall pattern observed in this study is consistent with this.

The initial maximum activity peak in Figure 6 was largely a reflection of the activity during the first hour of the night during September. The second was probably due to an increase in activity recorded at the end of the night during November. The first three months (September, October and November) had more activity than the later three months. This is also shown in Figure 1. The only individual months that showed bimodal activity patterns were November, December and January, however these were not particularly pronounced.

Insectivorous bat species are more unlikely to exhibit a clear-cut bimodal activity pattern when prey density is low (Erkert 1982). Individual variation from a bimodal pattern was demonstrated in Noctilionid bats (Fenton et al. 1993), while variation in bimodal patterns according to sex, age and reproduction were reported in other insectivorous bats (Herreid & Davis 1966; Fenton 1970; Swift 1980; Anthony et al. 1981). Herreid & Davis (1966) found that *Myotis californicus* Kaup and *Pipistrellus hesperus* Kaup show a bimodal pattern only if temperatures are above 15^{o}C. Insect prey sampling offered no clues to the variation in bimodal patterns for long-tailed bats. This was also reported in seven Tasmanian bats, including *C. morio* where bat activity was not significantly correlated with insect activity (Taylor &

O'Neill 1988). I suggest that the bimodal pattern in long-tailed bats changes through the season to suit foraging restrictions such as night roosting, pregnancy and lactation.

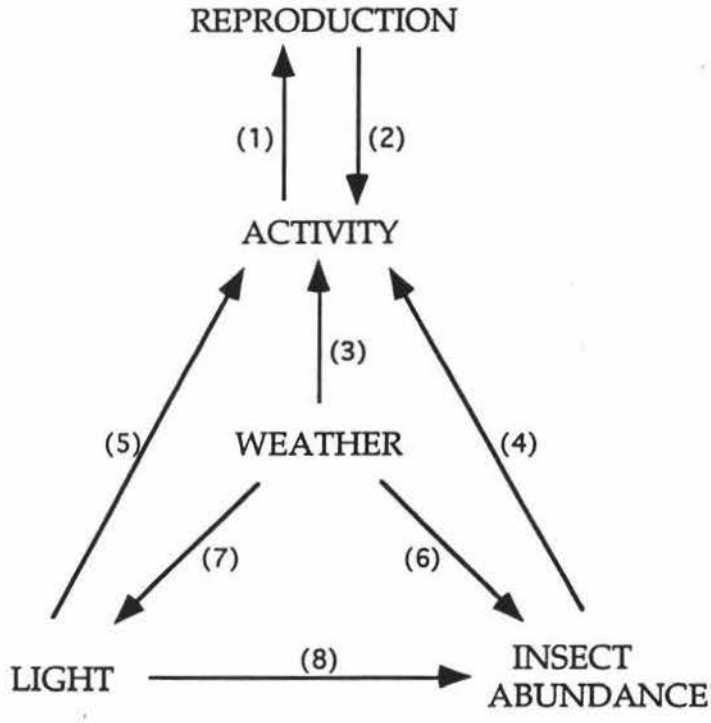


Figure 7. Physiological and environmental variables that are likely to affect the activity of insectivorous bats.

Many variables affect bat activity patterns. It appears that the effect of some variables on bat activity may vary depending on how other variables affect activity. Certain combinations of conditions may override normal, expected patterns. The probable interactions of these variables are shown diagrammatically in Figure 7. Other bat studies have shown that: (1) The amount and quality of foraging probably affects the speed of foetal and juvenile development (Racey 1969, 1973). (2) The reproductive condition of females may affect activity by limiting available suckling time (Morrison 1978) and possibly reduced foraging efficiency due to extra weight reducing flight manoeuvrability (Aldridge & Brigham 1988). (3) Extreme conditions may prevent activity altogether (O'Farrell & Bradley 1970) while high winds,

cool temperatures and rain probably adversely affect activity to varying degrees (Stebbings 1968; Erkert 1982). (4) The abundance of potential insect prey is likely to influence the foraging efficiency of bats (Rydell 1989). (5) Light intensity governs emergence time. It also directly influences bat activity by increasing predation pressure (Morrison 1978) and (8) indirectly by affecting the abundance of insects (Anthony et al. 1981; Fenton et al. 1977). (6) Weather is known to affect prey abundance (Wellington 1945) and this will also change light intensity (7) through cloud cover, mist, fog and rain.

The interactions between the physiological and environmental variables discussed above suggest that explaining microchiropteran patterns of activity is extremely complex. The continued collection of accurate environmental data with recorded bat echolocation will help explain these interactions.

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Chapter 5

The diet of long-tailed bats, *Chalinolobus tuberculatus* Gray (Vespertilionidae) roosting in a limestone cave, Piopio.

Abstract

Insect taxa were identified from long-tailed bat guano collected from a limestone cave roost near Piopio, King Country, over one year. Of identified fragments Diptera made up the largest proportion of the diet with 29.11%, Coleoptera made up 25.04%, while Lepidoptera fragments accounted for 17.46%. One fragment was identified as Ephemeroptera, one as Tricoptera and three as Acarina. Of the 1065 fragments mounted on slides for identification, 276 (25.9%) could not be identified. Quantitative data could not be used as an indication of seasonal changes in prey taken because of bias resulting from some types of insects being more easily identified than others. Estimates of the size of ingested prey items were smaller than the available prey insects. Larger insects may be culled of identifiable body parts before ingestion. There was no evidence of terrestrial insects in the faeces as reported for Australian *Chalinolobus* species.

Keywords: Bats, *Chalinolobus tuberculatus*, faecal-analysis, prey, diet.

Introduction

Long-tailed bats belong to the worldwide family of insectivorous bats Vespertilionidae. They are thought to be solely insectivorous like their Australian conspecifics. Like most insectivorous bats (Barclay 1985) long-tailed bats are aerial feeders (Dwyer 1962; Daniel 1976; Daniel 1979; Daniel & Williams 1983). There is no published evidence that *C. tuberculatus* glean or forage terrestrially or that they feed on nectar, pollen or fruit as reported for short-tailed bats (McCartney 1994; Arkins, pers. comm.[1]).

Previous reports give a general indication of the orders of insects most frequently taken by long-tailed bats. Large numbers of small Lepidoptera

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[1] Alina Arkins, Department of Biological Sciences, Auckland University.

and Diptera were identified from guano samples analysed by B. May, M.J Meads and M.J. Daniel (Daniel & Williams 1983), and moths, mosquitoes, and midges are all recorded as food items by bat observers (Dwyer 1962).

Acceptance of small flies (Colenso 1890), meal worms (Tenebrionidae), praying mantis (Roach & Turbott 1953), and grass grub beetles *Costelytra zealandica* (Lewis, pers. comm.[2]) by captive and partially tame long-tailed bats has been reported. Liver fragments and milk were also accepted by a captive long-tailed bat (Roach & Turbott 1953).

This paper reports on the abundance and size of prey fragments identified from *C. tuberculatus* faeces collected at Grand Canyon Cave, Piopio and compare the diet of resident long-tailed bats with those of closely related Australian species.

Study area

Grand Canyon Cave is situated on Puketiti Station, Piopio (NZMS R17 737030). The cave is essentially a 30 m high, 370 m long, natural limestone tunnel approximately 370m long. The northern end opens onto pasture through a small stand of scattered mature kahikatea (*Dacrycarpus dacrydioides*) while the south end opens into a ravine formed by collapse of the cave roof. The latter contains native subcanopy species. The cave floor is flat and generally dry hard substrate with some areas of mud bog at the southern end.

Methods

Fresh faecal pellets were collected from recent concentrations of guano on the floor of Grand Canyon Cave, Piopio, during eight visits to the cave between June 1993 and August 1994. Five individual pellets were randomly selected from each sample, and stored in vials containing water and dish-washing detergent for up to 11 months until they had broken up into their components.

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[2] c/o David Lewis, RD 4, Puketitiri, Hawkes Bay.

Each of the eight samples was spread over a large petrie dish with a grid marked on the bottom. Potentially identifiable insect fragments were located systematically using a dissecting microscope. All fragments that appeared distinct enough or large enough to be identified were transferred to a vial of 70% ethanol. Such fragments commonly included large pieces of exoskeleton, heavy sclerotin such as joints and claws, parts of eyes, tarsi, antenna, pieces of wing, parts of legs, eggs and halteres. These were subsequently mounted on cavity slides with DPX for identification with dissecting and compound microscopes. They were then compared with insects in a large insect reference collection as well as with insects sampled from the site using a light trap. Identification usually entailed matching specific pieces, systematically eliminating likely taxa. This process often resulted in fragments (such as fly wings) being identified to a small group of families or to a single superfamily. Some fragments were only identified to order, while others were identified to genus level. Proportions of pieces assigned to different orders and those unidentified were expressed as a percentage frequency of those mounted for identification (Kunz 1974; Belwood & Fenton 1976; Anthony & Kunz 1977; McAney et al. 1991).

Fragments were measured using a calibrated eyepiece in a dissecting microscope. Leg fragment diameter was recorded from all fragments that appeared to originate from different insects. All complete tarsi and haltere length, eggs width and length, and micro insect body length, wing length and legs were measured.

Results

The separated contents of long-tailed bat guano comprises a soup of tiny exoskeleton fragments and moth scales together with less frequent larger pieces of exoskeleton, insect eggs, eyes and wing fragments. Most fragments were flat and non-descriptive, or sections of insect appendages that were too small to identify.

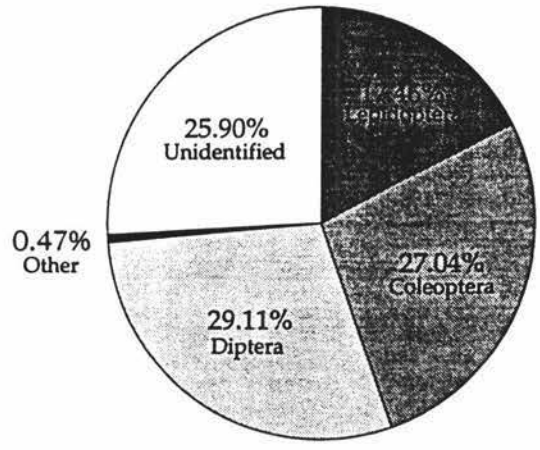

Figure 1. Proportions of insect fragments identified to different orders. Other = Ephemeroptera, Tricoptera and Acarina.

In all, 1065 insect fragments were mounted on slides and 789 were identifiable, representing an average of 27 identifiable insect fragments per faecal pellet. Diptera, Lepidoptera and Coleoptera comprised 784 of the 789 identifiable fragments. Dipteran fragments made up the largest proportion (29.11%). These were mainly eggs, halteres, wing fragments, tarsi, feet and legs. Beetles (25.04%) were identified by the heavy scleritization and colour of tarsi, claws, antennal segments, whole legs and elytra. Lepidopteran fragments (17.46%) were generally identified by the presence of scales still attached to body parts or the pattern left on the soft body parts where scales were removed during digestion. The fragments were usually thin-walled and often transparent. Tarsi, claws and antennal segments were also used to identify moths. One fragment was identified as Ephemeroptera, one as Tricoptera and three as Acarina. The mayfly and caddisfly were identified from antennae. 276 fragments (25.9%) remained unidentified, and of the successfully identified fragments, 63.84% were identified to order, 33.84% to family, 0.68% to a superfamily (or a small group of families) and 1.64% to genus level of classification.

Table 1. Fragments identified to family or better, with sample occurrences. * = Most likely taxa.

Fragment	Taxon	Notes	Sample occurrence
Black eggs	Tipulidae	abundant	1,2,3,4,5,6,8
Halteres	Tipulidae		1,2,3,4,6,8
Wing Pieces	Tipulidae	7 pieces, 1 whole	1
	Mycetophilidae	5 nearly whole	1,8
	Muscoidea	1 piece	4
	Culicidae	2/3 of wing	7
	Psychodidae	whole wing + pieces	7,8
Head capsule	Mycetophilidae	whole	7
Whole insect	Psychodidae	1	2
	Acarina	1	1
Cuticle	Calliphoridae*	probably abdomen	4
	Hemiptera*		4
Antennae	Tricoptera		1
	Coleoptera	Staphylinidae or Tenebrionidae*	1,3,4,7,8
	Lepidoptera	Noctuidae or Geometridae*	1,7,8
	Ephemeroptera		7
Tarsi and claws	Coleoptera	whole + bits	1,3,4,5,7,8
	Diptera	whole + bits	1,2,4,8
	Lepidoptera	whole + bits	1,2,3,4,5,6,7,8
Leg fragments	Coleoptera	some Anthricidae*	1,2,3,4,5,6,7,8
	Diptera		1,2,3,4,5,6,7,8
	Lepidoptera		1,2,3,4,5,6,7,8
	Acarina	+ tarsi and claws	1,2
Elytra	Scarabaeidae	*C. zealandica*	3,5
Heavy scleritin	Coleoptera	brown and black	1,2,3,4,5,6,7,8
Eggs	Tipulidae	black, some whole	1,2,3,4,5,6,7,8
	Lepidoptera	white	4,5,7
	other		1,2,3,4,6
Eye fragments	Diptera*		1,2,3,4,5,6,7
	other		7
Tree fern	Cyathea*	scales and spores	8

More dipteran fragments were identifiable to family than for Coleoptera and Lepidoptera. Beetle antennal segments (probably from Tenebrionidae or Staphylinidae) occurred in half of the samples, while only one type of fragment was identified to a single lepidopteran family.

Tipulidae fragments occurred in more samples than any other identified Family, seven out of eight samples contained tipulid halteres and five out of eight contained tipulid eggs (McAney et al. 1991). These eggs were sometimes whole, but usually torn open. The tipulid wing fragment was probably from a small individual.

The metallic green fragments closely matched calliphorids of the genus *Lucilia* and were probably from the thorax or abdomen as they were large, uniform and flat. The undersides were pale black and had several bristle holes. Calliphorids are crepuscular and have been collected in light traps (Colless & McAlpine 1991) so are potential prey for long-tailed bats, especially in pasture habitats as exist at Grand Canyon Cave. Another unidentified set of green fragments which was more pale and far less scleritized was found in the same sample. The colour and texture of the pieces (probably abdominal) were most like that of pale green stonefly adults or some soft bodied green Hemiptera but they could not be identified.

The distinct colour and pattern of grass grub beetle (*Costelytra zealandica*) elytra allowed relatively easy identification. Nearly all fragments of this type could be assigned to the genus, and all were definitely Coleoptera.

It is not known what species the mites belong to, or whether they are parasites of the bats or parasites of the bat prey. Either way it is most likely they were consumed accidentally.

Two wings presumably culled from a larger tipulid were found 78 m into the cave amongst guano collected on 29/1/94. A single wing measured 18 mm, so the estimated wingspan including a 3 mm wide body was 35 mm. A pair of culled Lepidoptera hind wings were also found at the same location. One wing measured 12 mm in length and was identified (Dugdale, pers. comm.[3]) as Noctuidae (Trifinae), *Graphania ustistriga* Walker .

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[3] John Dugdale, Landcare Research, Mt Albert, Auckland.

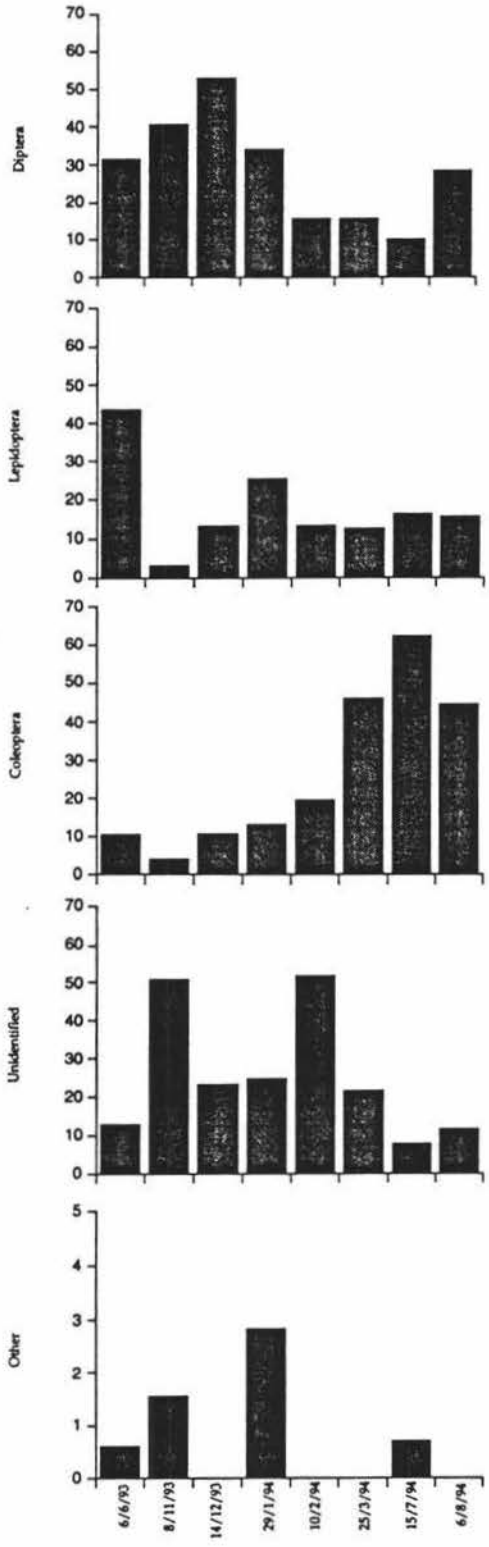

Figure 2. Change in percentage of invertebrate fragments identified from long-tailed bat guano collected from Grand Canyon Cave on different sample dates.

Spores and scales of tree ferns were identified as probably *Cyathea* species (Large, pers. comm. [4]). The percentage frequency of Diptera (Figure 2) was at a maximum (52.98%) in December (summer) and at a minimum (9.93%) in July (winter). Coleoptera show the opposite pattern with larger proportions occurring in winter (62.25 % of the July 1994 sample) and the lowest proportion in November (3.91%). No clear pattern was evident in the proportion of Lepidoptera in samples. The highest proportion of Lepidoptera occurred in the June 1994 sample (43.56%). The proportion of samples that could not be identified showed no seasonal pattern. Approximately 50% of the November 1993 and February 1994 samples could not be identified. The lowest frequencies of unidentified fragments occurred in June 1993, July 1994 and August 1994.

Table 2. The size of measured fragments (mm) and estimations (*) of body size based on reference specimens.

Fragment	Range (mm)	*Insect	*Probable wingspan	*Probable Body length
Leg width (Fly)	0.05 - 0.40	Culicidae	< 9.6	< 6.2
		Chironomidae	< 11	< 6
		Mycetophilidae	< 5.4	< 2.6
		Tipulidae	16 - 47	4.5 - 14
Leg width (Beetle)	0.11 - 0.50	Grass grub		< 14
		Huhu		< 40
Leg width (Moth)	0.10 - 0.45	Noctuidae	< 35	< 14
Leg width (Other)		Tricoptera	< 23	< 12.5
		Ephemeroptera	< 24	< 8
Tipulidae eggs	0.40 - 0.93			
White eggs	0.23 - 0.43			

[4] Mark Large, Department of Plant Biology, Massey University.

The width of insect legs was the only measure where a reasonable number of data could be collected. They are not large samples but rather are selected specimens with which to compare fragment size.

Discussion

Faecal content

Long-tailed bats (*Chalinolobus tuberculatus*) at Grand Canyon Cave feed mainly on flies, moths and beetles, while other orders are taken in small numbers. The proportions of these orders of insects give an overall indication of which prey taxa are taken, but this cannot be used as a quantitative measure of diet due to bias resulting from some types of insects being more easily identified than others. Almost all fragments that originated from beetles could be assigned to order, while fewer fly and moth fragments could confidently be identified. Flies and moths therefore are probably under-represented in these results.

Although beetle fragments were readily identifiable to order, the similarity of certain fragments (antenna and tarsi) between distantly related families meant assigning fragments to superfamily or even suborder was difficult. While fly fragments overall were difficult to identify, some were easily recognisable to family or superfamily so more detailed and reliable information could be gathered. The presence of Lepidoptera in the sample was easy to determine from scales, but isolating families and estimating the proportion of Lepidoptera in the sample was difficult.

In two congeneric species of Australian bats (*C. gouldii* and *C. nigrogriseus*) studied by Vestjens & Hall (1977), stomach contents analysis showed Lepidoptera to be the most abundant order present in both species with Diptera clearly the next abundant order in *C. gouldii*. This is not consistent with the results in this study, although faecal analysis generally underestimates lepidopteran fragments because of the difficulty with identification. Cockroaches (Blattodea), crickets (Gryllidae), a number of Hemiptera (Cicadidae, Pentatomidae and Notonectidae), and six coleopteran families were also evident in the Australian study. The analysis also showed the remains of one spider, one praying mantis, an earwig and numerous ants. There was no evidence of terrestrial insects in the faecal

samples from Grand Canyon Cave. A tree-fern spore and scale identified in this study were most likely attached to insect prey items.

Seasonal

The seasonal variation in percentage frequency in this study (Figure 2) is not likely to be a reliable indicator of changes in the bat diet through the year. There are two obvious reasons to question the quantitative results. There are large differences in the proportion of flies and moths in samples 1 (6/6/93) and 7 (15/7/94). If the sample size of five pellets collected per sample was large enough, some similarity would be expected between samples collected in the same season over different years. Secondly, grass grub beetles which were a large proportion of identified beetle fragments are predominantly a summer species, yet beetles were poorly represented in summer samples while the apparent (and clear) peak in coleopteran fragments occurred in winter.

Size

Only limited information could be obtained from the measurements of insect fragments. It is difficult to measure a leg and estimate potential wingspan or body length because variation in accuracy of a leg width measurement can mean a huge difference in estimated body length. There is also vast variation in size of insects in the same family and even subfamily. Table 2 gives some indication of the thickness of insect legs and their corresponding wingspan and body size. Those appendages that remained whole during digestion were usually from Psychodidae or Acarina. There is some question as to whether they are targeted prey species, because only the exoskeleton remained. They had probably been digested so it is unlikely that they were collected incidentally during sampling. It is most likely that bats consumed them while grooming or in pursuit of other prey. From comparing digested fragments with measurements taken from insects in the reference collection, there is no evidence that long-tailed bats eat insects in the size range of huhu beetles (*Prionoplus reticularis*). The largest leg width measured in the samples was more than three times smaller than the huhu beetle measured. Likewise, there was no evidence that the bats eat large hepialid moths. Even the

measured Noctuidae from the reference collection had thicker legs than any recorded in the faecal samples. Grass grub beetle tibia in the museum specimens were approaching the maximum beetle leg width found in the guano. All measured Tipulidae legs were of similar diameter to dipteran legs in the sample. Measured Culicidae, Mycetophilidae and Chironomidae museum specimens fell within the leg width range found for Diptera legs in the guano. Tricoptera and Ephemeroptera specimens also seemed a suitable prey size for the bats. Large insects cannot be excluded as possible prey items because legs from such prey items may be culled from the body (as are some wings) before consumption (Poulton 1929; Phillips 1966; Coutts et al. 1973). Tipulid wing fragments were found in guano samples, as well as culled on the cave floor, so there must be a size limit below which the bats do not cull wings. From night observations it would appear that insects the size of the culled moth or tipulid were not flying inside the cave. This suggests on occasions the bats carry prey to be consumed at feeding perches or to roosting juveniles inside the cave.

Similar sized bats (eg *Pipistrellus pipistrellus* Kaup) are capable of taking large tipulids (up to 35 mm) and Scarabaeidae up to 25 mm (Swift et al. 1985) so it may be possible that long-tailed bats can take beetles like New Zealand's green mumu chafers (Scarabaeidae) which are similar in size. I would expect huhu beetles are too large to fit into a long-tailed bat's mouth or tail membrane, and handling the aggressive beetles may also risk injury. The mean leg widths for Diptera, Coleoptera and Lepidoptera were similar, suggesting that the bats target similar sized insects from different orders. In no sample was there a large proportion of a single type of prey. Tipulids are obviously taken regularly but are not over-represented in any sample. It is unlikely therefore that the bats exclusively targeted specific prey items in this study. However, given the opportunity to target a single abundant taxa, for example hatching caddisflies, it would be surprising if they never do so.

The methods described in this paper are useful tools for investigating the prey taxa consumed by long-tailed bats, but they are very limited in their ability to detect seasonal changes in the quantities of taxa consumed. Large guano samples collected accurately and regularly may improve the reliability of results but the time needed to analyse such samples would be considerable.

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Chapter 6

The roosting behaviour of long-tailed bats, *Chalinolobus tuberculatus* Gray (Vespertilionidae), in a North Island podocarp forest.

Abstract

The roosting behaviour of long-tailed bats in a North Island podocarp forest at Balls Clearing, Hawkes Bay, was studied during the breeding season. Most communal roosts were located in holes with small (6-7 cm) entrances into recently dead trunks or limbs while solitary bats roosted in dead trees, as well as in healthy trees with no obvious cavities. This differs from previous roosting reports in New Zealand where most long-tailed bats were found in hollow trunks or under the bark of trees. There are however some similarities in cavity height (5 - 10 m for most located cavities) and the roost tree age (mature) with the Australian *Chalinolobus* species. The number of bats in communal roost (mean = 86) was larger than in other studies within Australasia (10 - 37). Most communal roosting coincided with lactation during November and December. No communal roosts were found during February when juveniles became independent. Lactating females changed roosts every one to three days. Most bats changed roosts from 3 to 5 am, juvenile bats were probably transported to new roost sites at this time.

Keywords: Bats, Vespertilionidae, *Chalinolobus tuberculatus*, roosting, communal, solitary, cavity, emergence, nursery.

Introduction

Little has been published on the roosting behaviour of long-tailed bats (*Chalinolobus tuberculatus* Gray). They are known to roost inside the hollows of trunks and branches (Dwyer 1960), amongst the epiphytes of large trees (Dwyer 1962), or under the bark of nine native tree species; kauri (*Agathis australis* Salisb.), rimu (*Dacrydium cupressinum* Quinn.), totara (*Podocarpus totara* Laubenf.), kahikatea (*Dacrycarpus dacrydioides* Laubenf.), rata (*Metrosideros* sp Gaertner.), taraire (*Belschmiedia tarairi* Nees.), puriri (*Vitex lucens*), kanuka (*Kunzea ericoides* Reichb.), kamahi (*Weinmannia racemosa* Dickison), and six exotic species (Daniel 1990; Dwyer 1962).

Limestone caves (Dwyer 1962; Daniel & Williams 1983; Appendix II), limestone cliffs (Griffiths, pers. comm.[1]), and man made structures such as bridges and farm buildings have also been used as roost sites for long-tailed bats (Dwyer 1960, 1962; Daniel and Williams 1981).

Few colonies of long-tailed bats have been studied in detail and relatively few large roosts were reported in the last 30 years (Daniel 1990). The number of bats in roosts vary. There are reports of "thousands" of bats inside felled trees last century (Buller 1893, Cheeseman 1894), but the majority of recently reported roosts range from one 1 to 50 bats, with a mean of 10 (Daniel 1990). Up to 300 bats were counted in Grand Canyon Cave (Daniel & Williams 1983; Appendix II). The only report of a long-tailed bat nursery colony (Daniel 1981) contained 20 bats and was located in a pine forest during January 1976 .

Few details are published about emergence behaviour. Daily emergence time from roosts has been reported as 10 - 30 minutes after sunset (Daniel 1990). The preferred tree species, tree age, tree location, tree size, cavity location and internal temperature for long-tailed bat roost sites is unknown.

There are several publications on the roosting behaviour of Australian *Chalinolobus* species. These have dealt mainly with the breeding of bats in cave or house roosts (Dixon & Huxley 1989; Simpson 1962; Dwyer 1965; Richards 1979). Data on roost tree location, roost cavity attributes, seasonality, roost size, roost tree species, occupants and predation on Australian *Chalinolobus* species that roost in trees has been reported by Lunney et al. (1985), Tidemann & Flavel (1987) and Hall (1970).

It is important to understand the roosting behaviour of New Zealand bats so habitat with suitable roosting sites can be preserved, potential roost predation can be identified, and if necessary, suitable predator exclusion techniques developed. A better knowledge of roosting behaviour would also increase the understanding of the breeding activities of the bats, and aid in developing indicators of breeding status, recruitment, population size and population health of bats.

There were two main aims in this study: (1) to investigate the roost trees

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[1]Richard Griffiths, Entomology and Animal Ecology Department, Lincoln University.

used by long-tailed bats in a North Island podocarp forest, with special emphasis on the roost location, favoured tree species and the roost cavity; (2) and to study the roosting behaviour of bats during the breeding season to gain information on their emergence behaviour, the number of occupants using roosts and roost site fidelity.

Methods

All data were collected from Balls Clearing Scenic Reserve, Puketitiri, Hawkes Bay. The reserve is dominated by mature podocarp species with areas of mature red beech (*Nothofagus fusca*). A detailed description of the study site is presented in Chapter 1.

Bats were captured in harp traps and mist nets (see Chapter 2). Short-life transmitters (up to 20 days) weighing 1.7 g were attached to the backs of 17 adult females, one adult male and one juvenile male between October 1994 and February 1995. Transmitters were attached by first trimming the fur between the shoulder blades with a small pair of scissors. A contact adhesive (Ados F2) was spread sparingly onto both the transmitter and the skin of the bat and allowed to dry for three to five minutes. The transmitter was then placed on to the bat and allowed a further five minutes to dry before the bat was released.

Radio-tagged bats were tracked to day roosts using directional receivers. Initial searches for radio-tagged bats were made within the reserve. If these were unsuccessful, then all likely locations within 5 km of the reserve were searched. The exact location of every day roost was recorded and the roost trees were numbered with identification pegs, and marked on an aerial photograph. The health of roost trees was classed as one of the following: (1) healthy with no visible cavities; (2) live with visible cavities; (3) recently dead with visible cavities and with branches and branchlets still attached; and (4) decaying with large cavities and with only large limbs remaining. These classes were also assigned to specific branches whenever there was a dead limb on an otherwise healthy tree. The height, location of the entrance, and circumference of communal roost trees were recorded. Cavity descriptions of two accessible communal roosts were made using a penlight and fibre optic equipment.

Roost trees were observed with the unaided eye before dusk and with night vision equipment after dusk. The location, height and orientation of the roost cavity was confirmed by observing bats leaving the roost. The number of bats using the roost, the time of emergence, and whether bats were entering or leaving the roost were noted using a hand-held counter and a voice-activated tape recorder.

Results

Two bats with transmitters were not located again after their release while 17 transmitters provided roosting data for periods of up to 17 days (mean = 6.88 days). One transmitter was recovered beneath a roost tree and had been chewed. The remaining transmitters were either left inside roost cavities that were not accessible, or could no longer be located within the study area.

Roost location

A total of 43 roosts were investigated in this study. Four were in red beech forest, while the remaining 39 were in podocarp forest. Of the roosts, 30 (70%) were solitary, the remainder, 13 (30%) contained more than five bats (Table 2). All roosts that were located in this study were within the mature native forest at Balls Clearing Reserve (Chapter 1). Roost sites varied from 10 m to 280 m from the bush edge. The greatest and shortest distances between consecutive, communal roosts were 770 m and 110 m respectively (mean: 360 m). There was no clear pattern in the choice of either individual or communal roost sites, although individual roosts were rarely closer than 100 m from the previously used roost, and were often on the opposite side of the reserve. One solitary juvenile male however roosted in three similar miro trees on three consecutive days. The trees were approximately 20 m from each other.

Table 1. Descriptions of communal roosts.

Roost Number	Dates occupied	Tree species	Tree health	Trunk circumference @ 1 m (cm)
1	12 & 13 Oct 1994	miro	just dead	238
15	10, 11, 13, 15, 16 Oct 1994	miro	healthy	243
3	5, 13 & 14 Nov 1994	miro	live with dead 2nd leader	214
4	24 - 26 Nov 1994	miro	live with cavities	290
7	19 Dec 1994	miro	live with cavities	146
14	17 Dec 1994 7 Jan 1995	kahikatea	healthy	275
12	3 & 4 Jan 1995	miro	rotten	220
16	12 Jan 1995	rimu	healthy	268
19	23 Jan 1995	miro	live with cavities	229
23	22 Jan 1995	matai	live with dead 2nd leader	391
31	23 Jan 1995	rimu	healthy	409
22	24 Jan 1995	red beech	live with cavities	399
24	26 -30 Jan 1995	red beech	live with dead 2nd leader	422

Roost tree size

There was considerable variation in the trunk diameter of the trees selected by bats as communal day-roosts (Table 1). The circumference at one metre above ground level ranged from 146 cm to 422 cm (mean = 290 cm). The largest trees that bats selected (31% were >350 cm circumference) tended to be either rimu, red beech (*Nothofagus fusca*), or matai (*Podocarpus spicatus*, Laubenf.), while smaller trees were mostly miro (*Podocarpus ferrugineus*, Laubenf) or kahikatea. All roosts were in canopy trees (approximately 35 m). Sub-canopy trees did not appear to contain suitable roost cavities.

States of trees with roost sites

Communal roosting bats appeared to prefer either recently dead trees with small and not very obvious cavities and entrances, or live trees with roosting cavities in dead or dying limbs. Half of the apparently healthy trees selected by communally roosting bats were rimu. In these, the bats roosted high in the canopy where the location and type of cavity could not be determined. One female bat however was located approximately 3 m up, under the flaking bark of a large, healthy rimu. Of 15 roost trees that were apparently healthy, 11 (73 %) were used by solitary bats and 4 (27%) were used by communally roosting bats. One of the beech trees used by communally roosting bats was an apparently healthy canopy tree with some small dead branches at approximately 9 -10 m above ground level. The other beech tree had one healthy trunk to canopy height, and one dead trunk in which the bats roosted. No roosts were found in very decayed or hollow trees.

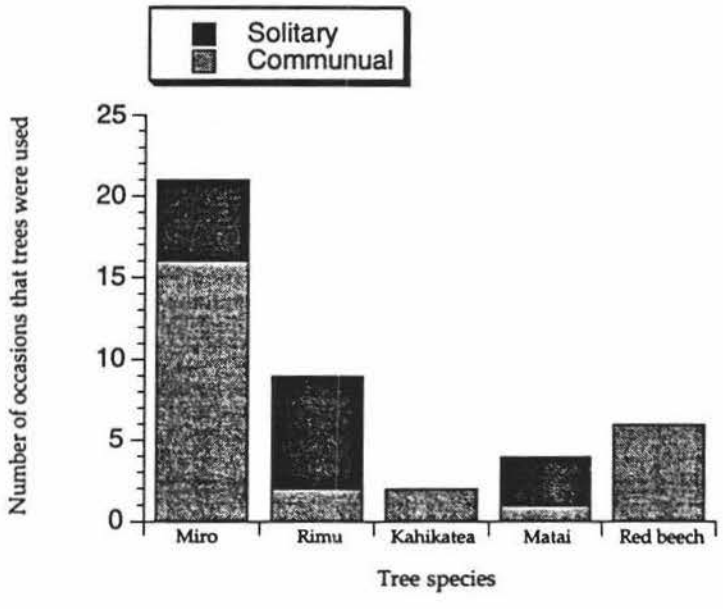

Figure 1. Use of roost tree species by solitary and communally roosting long-tailed bats at Balls Clearing, Puketitiri.

Table 2. Entrance details of communal roosts at Balls Clearing, Puketitiri.

Roost number	Entrance type	Entrance height	Entrance orientation	Number of bats
1	single small hole	8m	east	79+
15	single small hole	9m	south	61 - 208
3	open gash	5m	west	137+
4	3 small holes	6m	west	68 - 148+
7	5 holes, some large	5 - 8 m	south & south east	108 +
14	not determined	30 m approx	not determined	16 +
12	single small hole	7m	west	31 - 60 +
16	not determined	30 m approx	not determined	not determined
19	not determined	30 m approx	north	31 +
23	not determined	30 m approx	not determined	29 +
31	not determined	30 m approx	not determined	not determined
22	single small hole	9m	south	11
24	not determined	30 m approx	not determined	5 - 61+

Roost cavities

The entrances to the roost cavities were not located for single bat roosts because the departure of one bat is difficult to observe. In communal roosts the height of the entrance ranged from 5 m to canopy (35 m) height in trunk and branch cavities. The overall mean height of communal roosts was 15.9m while the mean height of non-canopy communal roosts (n = 7) was 7.2 m. The entrance was usually singular, small (6 -7 cm) and round, although three roosts had two or three larger entrances or one larger gash opening.

Two roost cavities that were in trees that were climbed were investigated. One, in a healthy red beech tree (Roost 22), was 9 m up, near the first branch. The entrance was approximately 6 cm in diameter and the cavity was essentially a tunnel of the same diameter that snaked into the trunk. The optic probe (approximately 50 cm) did not reach the end and no bats were visible within the cavity. The other roost (Number 7) was a vertical internal cavity with five openings 5 to 8 m above the ground. There was no clear pattern in the orientation of the opening of roost cavities selected by the bats in this study (Table 2).

Roost occupants

Large communal roosts were recorded from 13/10/94 to 26/1/95. All radio tagged bats roosted with other bats during the seven week period from early November (Figure 2a). No communal roosts were found during February. The number of bats counted on 19 occasions when they emerged from 13 different communal roost sites ranged from 5 to 208 (mean = 86), however bats were usually still emerging from these roosts when they could no longer be counted because of low light. Therefore, the numbers of bats counted during emergence are a minimum estimate of the actual number of occupants. The emergence time relative to sunset of the first bat tended to be earlier as the number of bats in the roost increased (Figure 2b).

Communally roosting bats also emerged earlier than solitary roosting bats. Solitary bats emerged between 2 and 40 minutes after sunset (Figure 2b) whereas the first bats that emerged from communal roosts were as early as 16 minutes before sunset. The emergence of bats from communal tree roosts was sporadic and tended to occur in groups. Occasionally bats were seen crawling as far as 1 m down the tree trunk before flying but most seemed to fly from the entrance itself. Although only one bat flew from each roost entrance at a time, groups of up to thirty bats tended to leave immediately one after another. These were interspersed with periods of up to five minutes where no bats emerged or when only occasional individual bats emerged. Emerging bats usually continued this behaviour for up to one hour depending on the number of bats in the roost. The number of bats emerging in each group decreased with time, with most bats emerging within 30 minutes after the first bat.

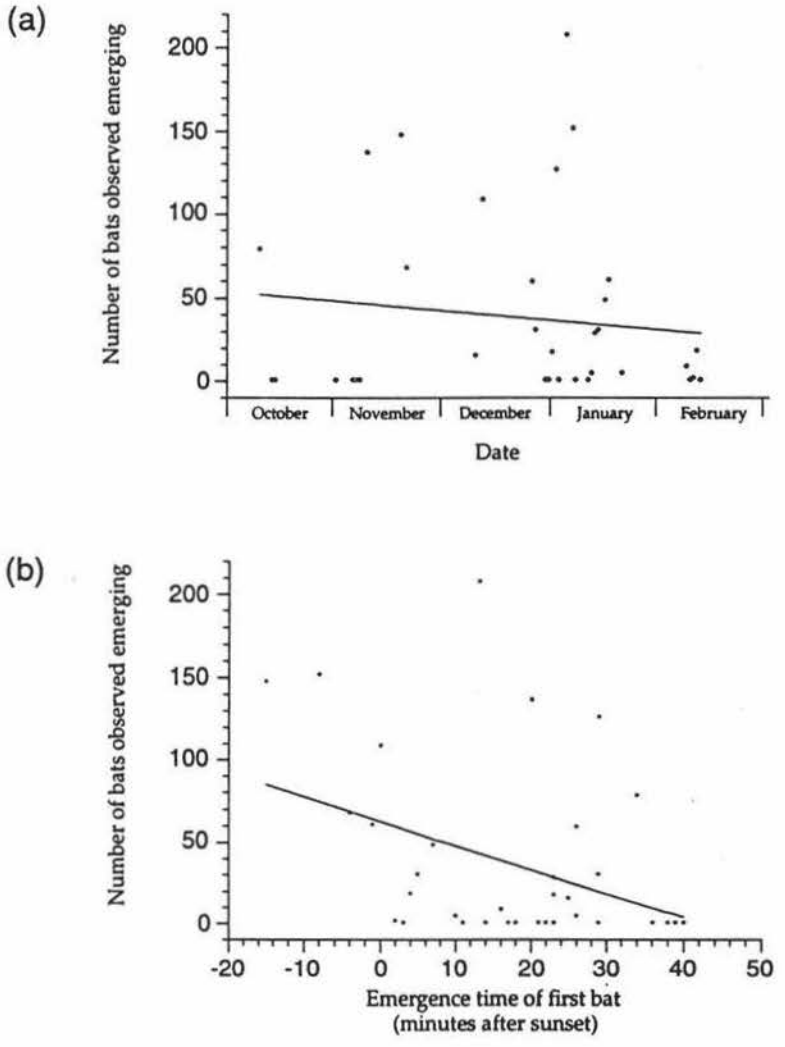

Figure 2. Variation in emergence behaviour of long-tailed bats at Balls Clearing, Puketitiri. (a) Seasonal variation in the number of bats observed emerging from roosts (R=0.125). (b) The relationship between the time of emergence and the number of bats observed emerging from roosts (R=0.367).

Bats usually began returning within the first hour of emergence and some returned while other bats were still emerging. Returning bats generally flew past the roost entrance, circling around, and occasionally landed briefly at the roost entrance. This circling and landing behaviour continued while

other bats flew into the roost. The frequency of circling decreased as more bats entered the roost. The last bat generally returned to the roost approximately two hours after the first bat emerged. Most bats that returned to roosts did not emerge again until early morning (usually between 3 and 5 am). However there was a continuous, steady but low rate of emergence and return activity during the night.

Radio-tagged bats rarely returned to the same day roost for more than two consecutive days. Of 43 occasions when bats were tracked to day-roosts, 28 of the roosts were used for only one day, 11 were used for two days, and 4 were used for three consecutive days. Communal roosts were used by other bats for up to three days after radio-tagged individuals had moved on suggesting that roosts have a changing occupancy by different bats.

Possible predation by morepork (*Ninox novaeseelandiae*) was observed on two occasions (14/11/94 & 13/1/95). On both occasions a single morepork flew up to the entrance of the roost cavity while bats were emerging. The bird landed for approximately one second before flying off. It was not confirmed whether the moreporks had taken any bats.

Discussion

Long-tailed bats appeared to use two types of roost trees at Balls Clearing. Recently dead trees or dead limbs on otherwise healthy trees were used by both solitary and communally roosting bats. The entrances of these roosts were usually small and at least 5 m up. Healthy trees are used by solitary bats more than by communally roosting bats. Bats generally roosted in the canopy of healthy trees. No bats were found in the hollows or cavities of rotten trees where only the trunks and large limbs remained. The types of roost tree selected by long-tailed bats at Balls Clearing differs from those reported in other studies (Daniel 1981; Daniel & Williams 1984) where most bats were found in hollow trees or under bark. The cavity size of native tree roosts at Balls Clearing is similar to a roost described in *Pinus radiata* by Daniel (1981) and for roosts of *Chalinolobus morio* in Australia (Tidemann & Flavel 1987). The roosts of long-tailed bats have other similarities with those occupied by Australian *Chalinolobus* species. Roost sites of the latter tend to be found in old, large trees (Lunney et al. 1985; Tidemann & Flavel 1987), and the mean height of roost cavities selected by *C. morio* (10.5 m)

was similar to that of communal roosts found at Balls Clearing. The orientation of the cavity entrance may be important in some Australian species for heat maintenance (Tidemann & Flavel 1987) but this did not appear to be the case for the long-tailed bats at Balls Clearing.

The fact that healthy trees were used more by solitary long-tailed bats than by communal bats probably relates to the cavity space that roosting bats require because such cavities tended to be found in aging trees. In contrast, the space necessary for a single bat may be found in both healthy trees as well as dead or dying trunks and limbs. Single roosting bats may rely more on being widely dispersed and less likely to be found by predators, while a large and more conspicuous group may require a restricted cavity entrance for protection.

The number of bats (mean = 86) that roosted in communal roosts during summer at Balls Clearing was much larger than those reported elsewhere. Daniel (1990) found that most roosts contain between 1 and 50 bats (mean = 10). The Balls Clearing roosts have more occupants than Australian *Chalinolobus* roosts during summer. Tidemann & Flavel (1987) found mean roost sizes of 37.6 bats for *C. morio* and 8-11 bats for *Chalinolobus gouldii*, while Lunney et al. (1985) found 15 female *C. morio* plus juveniles in a large tree roost in New South Wales. The number of bats observed at roosts in Balls Clearing was almost certainly less than the actual number using each roost. Roost counts were only made when there was sufficient light to allow reliable observations with night vision equipment. Therefore the number of bats recorded at roosts (Table 2) are conservative, minimum figures.

The sex ratio of bats at communal roosts is not known. Trapping of emerging bats was not attempted, but one radio-tagged male was located in a roost with radio-tagged females during December 1995. It is likely that most communal roosts were nurseries as heavily pregnant females continued to roost with others (both male and female) during the lactation period (see Chapter 3). The seven week period where all bats with transmitters used communal roosts coincided with the lactation period described in Chapter 3. Nursery roosts probably disbanded from February onwards because no communal roosts were found and a radio-tagged juvenile male was roosting alone after this period.

The lack of roost fidelity displayed by long-tailed bats at Balls Clearing suggests that lactating females transported non-volant juveniles from roost to roost every one to three days. Bats generally changed roosts between 3 and 5 am, after the females initial feeding activity during dusk and after their subsequent return for night roosting when presumably juveniles were suckling. How individual bats select where they will roost on any particular night or why they change roosts so frequently is unknown. There are several reasons given to explain low roost site fidelity in bats: the abundance of roost sites, the proximity of food resources, predation pressure, and human disturbance (Kunz 1982). There appears to be an abundance of suitable roost sites at Balls Clearing so bats may take advantage of this by changing roosts regularly to escape predation or mite infestation which was observed by Heath et al. (1987) in the short-tailed bat (*Mystacina tuberculata* Gray). The members in each group are likely to change as often as the bats change sites because untagged bats were still using one roost (Number 15) after a radio-tagged individual had moved on to roost with other bats. I could never watch two roosts at a time so could not confirm the use of many communal roosts simultaneously, however from preliminary results of a large survey conducted at Balls Clearing during December 1995 it appears this is the case. The circling and landing behaviour shown by returning bats may be an investigation of the roost cavities. Individual bats may therefore check a number of roosts until they locate one in use. Individuals probably move between many communal roosts rather than staying faithful to one group.

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Chapter 7

Conclusions and Recommendations

Overview

The general aim of this study was to investigate the morphology and behaviour of the New Zealand long-tailed bat. The combination of (1) the opportunities that Balls Clearing Scenic Reserve provided as a study site; (2) concentrated field work over spring and summer; and (3) supplementary sites (particularly Grand Canyon Cave) that complemented the work conducted at Balls Clearing, allowed me to detail five areas of research within this broad aim. (1) The morphology of adult male and female bats in the area was described and information about the development of juvenile bats was collected; (2) the timing and duration of parturition, lactation and the onset of volant juveniles was described; (3) the diurnal and seasonal patterns in long-tailed bat activity was described, along with an analysis of how bat activity is affected by changes in sunset, weather, moon phase and insect abundance; (4) the choice of roost trees, the emergence behaviour and the numbers of bats using roosts was described; and (5) prey taxa and prey size preferred by long-tailed bats was investigated.

The compilation of these separate areas gives a detailed overview of the changes in the morphology and behaviour of long-tailed bats during the breeding season at Balls Clearing. Analysis of bat guano from Grand Canyon Cave was completed during the winter before the data from Balls Clearing was collected. This provided information on which of the trapped insects should be used as an index of prey abundance and which method of trapping these insects was most suitable. Concurrent studies of the breeding season, roosting behaviour and the activity of the bats complemented each other.

This work has provided three major contributions to the understanding of the New Zealand long-tailed bat. There is a clear description of when parturition, lactation and juvenile volance occurred, with details on the post-natal development of juveniles. Variation in bat activity on a diurnal and seasonal basis was described, with information on how this relates to breeding and the environment. Roosting behaviour in podocarp forest was described with details about roost trees and cavity types that are preferred by long-tailed bats as well as detail of the occupancy of these roosts.

The morphological study of captured bats provided a base of data for future research at Balls Clearing and as foundation for comparative studies elsewhere. A higher sex ratio of captured adult female bats is probably a reflection of higher energy demands during pregnancy and lactation. The higher sex ratio of juvenile males and the sexual dimorphism of size exhibited in the population cannot be explained. The continued capture of bats through the season and the morphological data that were collected also provided valuable information on the breeding season of the bats.

Most females showed signs of pregnancy (ie. weight gains and more obvious nipples) during October and November. Weights amongst individual female bats were more consistent during the period of weight gain than during the period of weight loss. Therefore it is likely that fertilisation is initiated by extrinsic factors such as day length or environment rather than internal physiological triggers such as the accumulation of sufficient fat reserves. Bat activity was highest during the pregnancy period than later in the season, with more recorded bat passes per hour during the night and dusk periods . This may be a result of higher energy requirements during pregnancy, but is more likely to be a compensation for low prey insect abundance. Most female bats gave birth in mid-November when mean female weight was greatest and a marked increase in nipple size was evident. Insect abundance increased at this time so female bats may synchronise lactation with periods of high prey abundance. Bat activity levels decreased immediately following parturition and during lactation which probably reflects time spent suckling new born bats. The increase in prey during lactation probably allows more productive foraging during this period. The lactation period of the population (the period between mean parturition date and the capture of the first volant juvenile) lasted approximately eight weeks, but individual bats may have lactated for shorter periods. This could be confirmed by intense surveillance at a suitable permanent roost. All females that were tracked with radio transmitters used communal roosts during the lactation period, however pregnant females occasionally used solitary roosts during pregnancy and after juveniles became volant. Communal roosts may therefore have a more suitable roost temperature and provide more protection from predators while females are feeding. The end of the lactation period and the onset of volant juvenile capture occurred in early January when bat activity in the first hour increased. Total passes during the night, total passes per hour of darkness and prey insect abundance all showed marked increases during

February which is most likely a period when all bats are increasing fat reserves for the coming winter.

Explaining activity beyond the restraints of pregnancy and lactation is difficult. Combinations of variables best explained variation in bat activity patterns. The environmental variables that explained most variation were maximum temperature, sky cover, moonlight and wind strength, but there were no clear rules of thumb that could predict bat activity under any given conditions. It is difficult to isolate individual environmental factors that affect bat activity, while diurnal patterns of activity appear to vary under different conditions.

Long-tailed bats preferred tree cavities with small entrances which are found in recently dead, mature podocarp trees. Bats also changed roost sites every one to three days. Roost sites therefore may be a limiting factor in the distribution of long-tailed bats. In areas where limestone cliffs and caves are not available the habitat may need to contain mature trees with suitable roosting cavities for solitary and communal roosts. Balls Clearing has a small area of mature forest (36 ha), therefore the size of the area may not be as important for bats as the availability of suitable roosting sites.

Recommendations and the direction of future research

The diurnal and seasonal variation in bat activity must be taken into consideration when surveying bat activity. I suggest that sampling for bats is most productive during the first hour after sunset. During this time, bat encounters are most likely, so more detailed comparisons are possible between nights and sites. Also, direct observations of bats around dusk may also help in the identification of species. Weather details and an index of moonlight should be recorded and sampling methods should be standardised to allow comparisons to be made between sites. The stage of the breeding season should be considered at sites where human presence may unduly disturb the bats. Grand Canyon Cave is one colony that seems to have reduced in size over the course of my visits. There are reports of many visitors observing bats without permits (including a bus load of people on an organised field trip). Efforts should be made to tighten restrictions on cave visitors, perhaps allowing only essential visits be made from November through to February while bats are giving birth and

suckling their new born. Suitable alternative maternity sites may not be available near by and so disturbance during this period may affect recruitment. The features and the species of the roost trees that long-tailed bats prefer should be considered when sampling and attempting to capture long-tailed bats in similar habitat elsewhere. These factors should also be considered when protecting suitable long-tailed bat habitat.

As we understand more about the basic biology and ecology of New Zealand bats, the avenues for both conservation-orientated research and management will expand. Most work on long-tailed bats at present is concentrating on understanding the basic biology and ecology of the bats. The status of most long-tailed bat populations is unknown, mainly because a standard method of bat sampling has yet to be developed. The identification of species by echolocation alone is difficult, as is the capture of long-tailed bats at most sites. These areas will need to be researched so efficient population estimates can be made. Understanding the breeding biology and population recruitment of bats is essential if in the future we find there is a need for active management of the species. Further details of roosting ecology, particularly habitat type and roost cavity preferences in other areas, will provide information on which habitat types need protection as well as the potential to supply supplementary roost sites and develop predator exclusion techniques.

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Appendix I

Report on work at Grand Canyon Cave

Report on research conducted on the long-tailed bat (*Chalinolobus tuberculatus* Gray) at Grand Canyon Cave, Piopio.

INTRODUCTION

A study of the long-tailed bats at Grand Canyon Cave was to be conducted as part of a Masters project in cooperation with the Taupo/Tongariro and Hamilton Conservancies of the Department of Conservation. The intention of the study was to investigate roosting locations (inside and outside the cave), foraging flight distances, and prey species selection by bats as part of a comparative study on bats in a cave population with those in a forest population. Regular monitoring of emergence behaviour from the cave was to be conducted as part of the Department of Conservation's monitoring program.

Long-tailed bats proved to be extremely difficult to catch in the Tongariro area and so the original comparative study planned had to be modified into a concentrated study of long-tailed bat morphology, breeding and behaviour at Puketitiri, Hawkes Bay. The cave part of the study was continued with less intensity, and concentrated mainly on collecting data on day and night roosting behaviour, emergence surveys, and the collection of guano for analysis later.

METHODS

My initial research on the long-tailed bat population began in June 1993. The purpose of this first visit was to confirm that the population still existed in the cave and to assess the site's suitability as part of my study. Between June 1993 and April 1995, eight further visits were made to the cave. These usually involved a survey through the cave during the day, locating and recording where bats were roosting and where old and new guano deposits were. Population estimates were made at night by counting all bats leaving and entering the cave. Fresh guano samples were collected for faecal analyses (Chapter 5) and light trapping was conducted to gain an estimate of insect food availability. Data from bat surveys using bat detectors both near the cave and at local forest areas was also collected. In January 1994 a dusk till dawn cave entrance survey was conducted so that activity levels of the bats through the night could be investigated. From 9/3/94 more intense

work began in the cave and continued to 26/3/94. During this period daily surveys were made through the cave which gave consecutive day-roosting data. On one night (10/3/94) mist nets were set up at the south entrance and four bats were caught. Details including sex, weight and other morphometric data were collected. A radio transmitter was attached to one bat and all bats were released. Daily and nightly tracking of this bat continued until 26/3/94. Night surveys of the cave were also made during this visit. Summary reports of the early visits to the cave as well as all emergence and roosting data was reported to Department of Conservation, Te Kuiti, Waikato Conservancy.

Table 1. Details of visits to Grand Canyon Cave.

Date	Purpose of visit
6/6/93	Assess suitability of study site Cave survey Entrance count
7-8/11/93	Cave survey Entrance count
13 - 14/12/93	Cave survey Entrance count Survey likely feeding sites
29 - 30/1/94	Cave survey Dusk till dawn entrance count Roosting bat group observations
9 - 26/3/94 23 visits made	Day surveys Entrance counts Night-roosting surveys Mist net bats at Sth entrance Radio track tagged bat Survey sites within 5 km of cave
14 - 15/7/94	Cave survey Entrance count
6/8/94	Cave survey Entrance count
1 - 2/4/95	Day survey Harp trap bats at Sth entrance

RESULTS AND DISCUSSION

Day-roosting

The number of visible bats roosting in the cave during the day ranged from 0 to 64, with the mean = 14.74. On only five out of the 19 day-roost surveys were there more than 15 bats present in the cave. On these occasions there were always one or two large groups (between 20-64 bats) together with individual bats roosting in other areas.

As the presence of these large groups was more the exception than the rule, a second mean was calculated by omitting groups over 15 bats. Excluding the large groups of roosting bats, the mean number of bats using the cave during the day was 4.43. This is a more realistic estimate of the numbers of bats that can typically be found in the cave when most individuals are roosting separately.

Large groups of bats using the cave during the day tended to roost on the roof. Smaller groups (down to seven) were usually on the roof but sometimes under knobs or ledges near the roof, while individual bats seem to favour the walls at varying heights from 8m up to and including the roof (ca. 30 m).

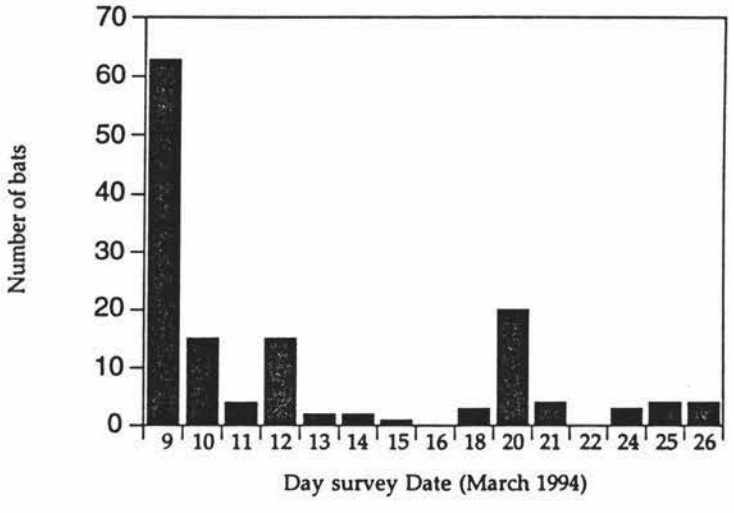

Figure 1. Change in the number of bats day-roosting in Grand Canyon Cave during March 1994.

There is no clear seasonal pattern explaining the variation in the number of bats using the cave as a day-roost during March 1994, although the largest numbers of bats observed during the day were during summer (64 bats on 13/12/93 and 63 bats on 9/3/94). Day-roosting data collected from 15 consecutive surveys (Figure 1) shows a decline in numbers with time. Even though these surveys were conducted by myself only and disturbance was kept to an absolute minimum it is still possible that torches and human presence caused some of the bats to roost elsewhere.

There are some areas in the roof that are hidden from view and so cannot be surveyed. It is possible that bats were roosting in such areas. Little Canyon cave was surveyed twice during this period. No bats were located.

For 13 consecutive days (during March 1994), one bat did not seem to move (day or night) from its individual roost (13 m up on the east wall, 256 m into the cave). There was no sign of movement when spotlighted for long periods. The bat was still in the same location during a later cave visit 12 months later (4/1/95) so it is most likely dead, mummified in the roosting position.

Night-roosting

During five night surveys, during March 1994, the cave was used as a night-roost by a large number of bats. The bats entered the cave at approximately 8.45 pm and formed an unsettled group on the cave ceiling. These groups were located between 85 m and 230 m from the North entrance and audible squeaks were usually heard before groups were sighted. Night-roosting groups would sometimes congregate on brown stained limestone while on other nights they did not. There was no evidence that the bats preferred these areas or that the stains resulted from regular use of these sites. On two consecutive nights (22 and 23/3/94) the group roosted in the same location on the roof (126 m from North entrance). The size of these large, night-roosting groups ranged from approximately 150 to 300 bats (determined by counting a portion of the group with binoculars then estimating total group size).

Approximately 150 bats were observed night-roosting together on 15/7/94. There were no large groups spotted during a day survey, but at 7.40 pm , the bats were observed roosting on the roof of the cave 88 m from the North entrance. The bats were still there at 10.35 pm. The bats in these groups

were easily disturbed and could be observed with a torch for only about ten seconds at a time.

As night roosting in this manner was recorded during both during summer and winter it is not likely to be related to a seasonal or breeding behaviour.

Bat captures

On 10/3/94 a mist net was set up at the south entrance. Four bats were caught between 8.45 pm and 9.30 pm.

Table 2. Measurements of the radio-tagged bat (mm), and weight only of three other bats.

Sex	Weight	L. forearm	R.forearm	Tail	Skull	Body	Wingspan
F	11.0g	42.8	42.7	38.4	12.95	32.85	28.25
F	11.0g						
F	11.5g						
M	10.5g						

The first bat was measured, and tagged with a short-life radio transmitter. The other three bats were sexed and weighed before release. The female fitted with the transmitter joined a large night-roost within the cave when released but was not located inside the cave the following morning. This may show that a large number of bats do actually leave the cave rather than roosting in areas not visible to observers. The tagged bat was located later in the day, roosting in Waitoru Bush (3.8 km from Grand Canyon Cave), the actual roost tree could not be located. The bush is dominated by rewarewa (*Knightia excelsa*), tawa (*Beilschmiedia tawa*), kahikatea (*Dacrycarpus dacrydioides*), with some totara (*Podocarpus totara*), hinau (*Elaeocarpus dentatus*), rimu (*Dacrydium cupressinum*), matai (*Podocarpus spicatus*) and miro (*Podocarpus ferrugineus*). Waitoru Bush is grazed by domestic stock.

Extensive searches were made for the next 16 days, both during the day and at night around local farm and forest areas up to 10 km from the Cave. The tagged female was not located again.

Dusk till dawn activity monitoring

Bat passes were monitored and recorded at the North and South entrance of the cave from 8.00 pm on the 29/1/94 to 7.00 am the following morning. At the North entrance, passes in and out of the cave were detected with a bat box and were recorded at five minute intervals. Passes were recorded as either in, out, or circle (out then in). Temperatures were recorded sporadically at the North entrance. The South entrance was monitored using a bat detector and a sound activated tape recorder. The direction of passes at either entrance was difficult to determine. Trial echolocation (when the direction of the bat was observed) were taped and used as a reference, but as the nature of the cave results in a lot of echoes, I could still not be absolutely certain about the direction of most passes.

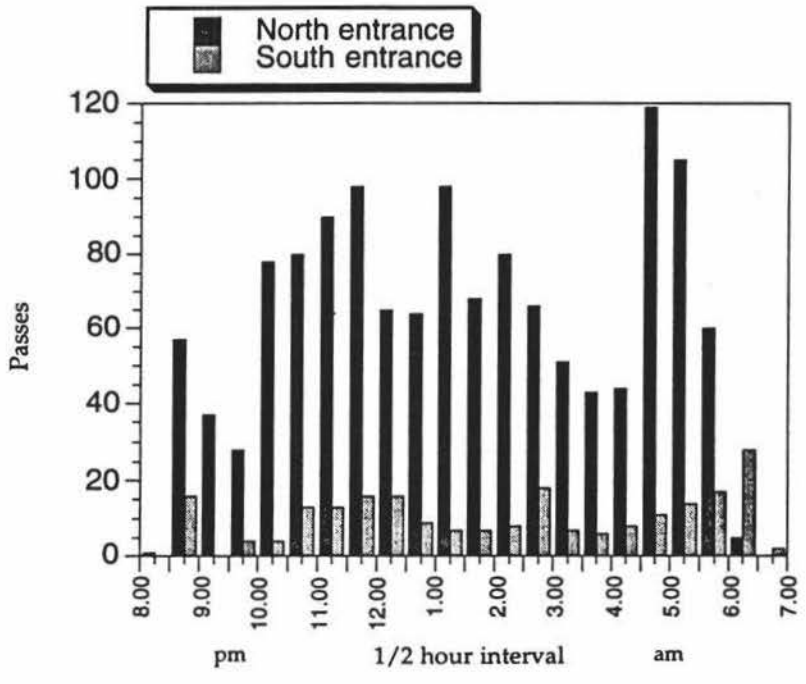

Figure 2. Total number of passes recorded at North and South entrances of Grand Canyon Cave from dusk on 28/1/94 till dawn on 29/1/94.

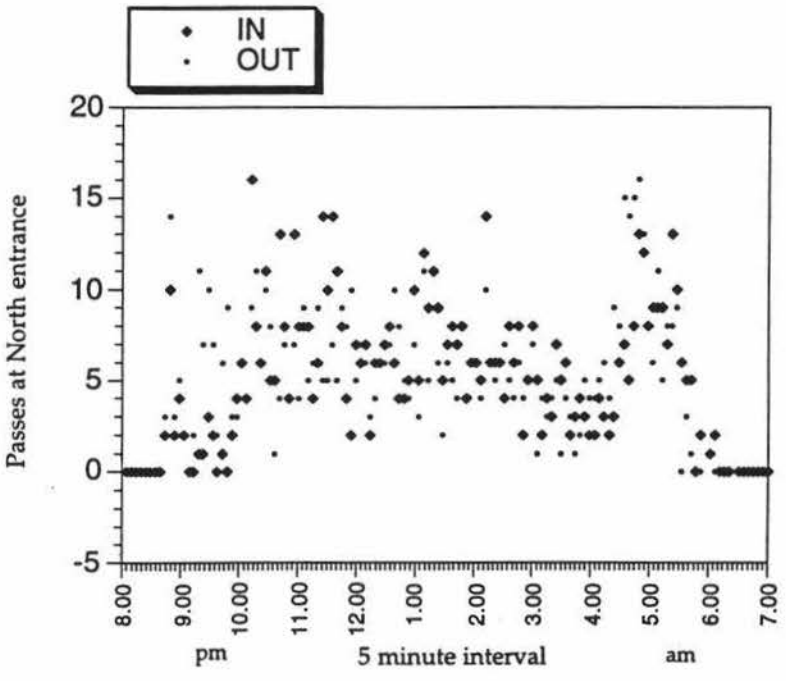

Figure 3. Passes in and out of the North entrance of Grand Canyon Cave from dusk on 28/1/94 till dawn on 29/1/94.

The relationship between passes out of the cave and passes in (Figure 4) are closely related during dusk, dawn, and the period in between. This means that as passes into the cave increased then so did passes out of the cave. Activity was reasonably intense during the entire night so the bats appear to have been making many short flights. It is possible that these may have been feeding flights to feed juveniles within the cave but there is no further evidence to support this.

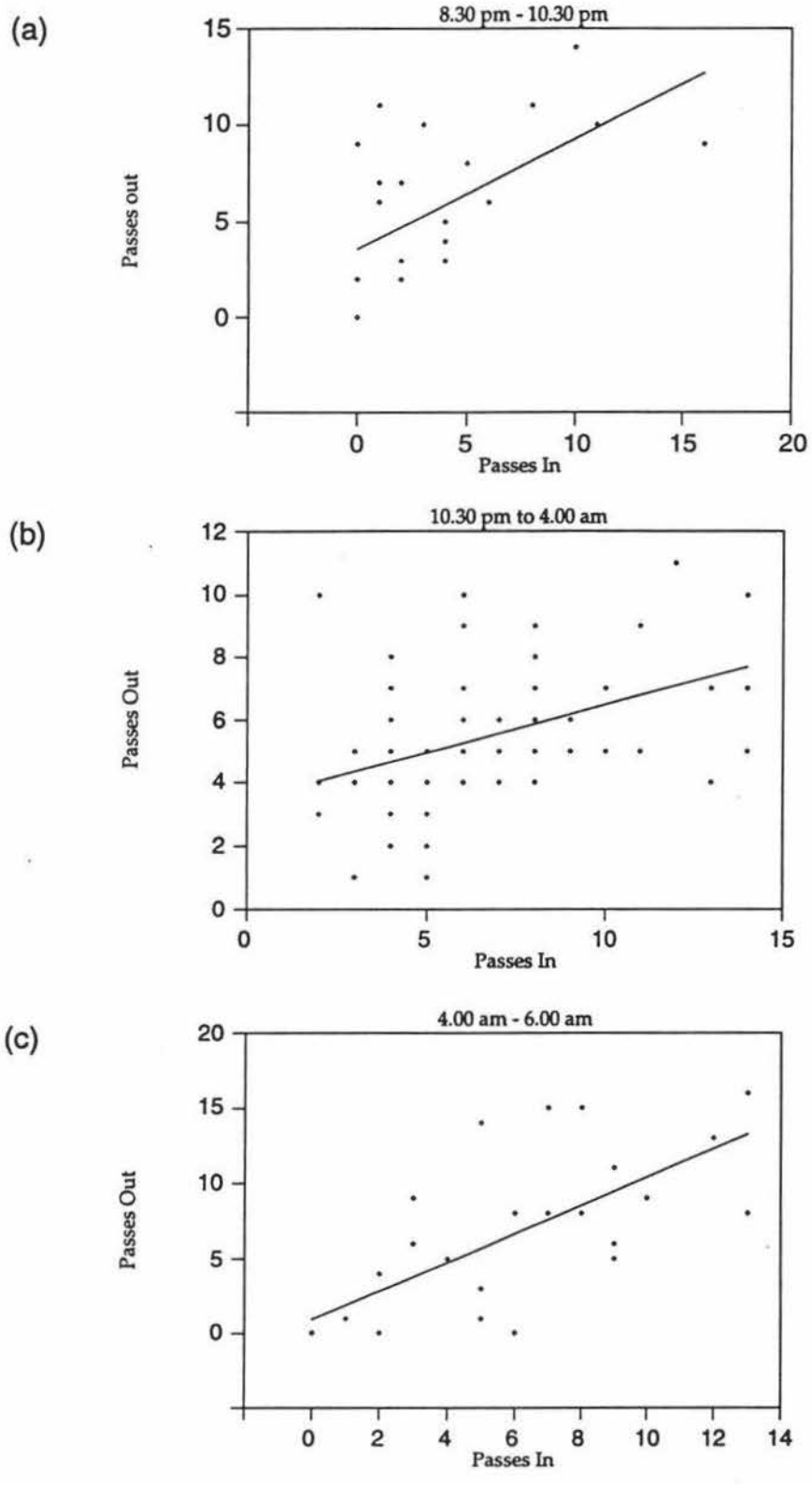

Figure 4. Relationship between passes in and out of the North entrance of Grand Canyon Cave (29/1/95) at (a) dusk (R = 0.593), (b) during the night (R= 0.399), and (c) dawn (R= 0.729).

Observations of a group

On 29/1/94 a group of what looked like 26 bats (counted with binoculars and a low powered torch) were located roosting in a crevice 8 m up on the west wall, 39 m into the cave from the North entrance. A cotton sheet was spread beneath the group, and the emergence behaviour was observed continuously from 8.30 pm until 9.43 pm with further checks at 10.00 pm, 10.25 pm and the following morning.

7.30 pm	Three droppings on sheet since 2.30 pm.
8.30 pm	Audible squeaks heard from group, bats making restless movements.
8.40 pm	Most bats still restless.
8.45 pm	One bat flies, other bats become more settled. Individuals near the edge of the group are more restless with forearms out moving, bats in the middle of the group are less restless with wings close to body. As a bat leaves the remainder become more settled.
8.47 pm	More squeaking, bats leaving group steadily one by one towards North entrance (out of cave) and South entrance. Much activity outside, bats that are farthest into crevice still settled.
8.50 pm	Squeaking.
8.56 pm	Bats on outer edge are all active while bats further into the crevice are slowly coming out.
9.03 pm	Two smaller groups now. One group far less active. Eleven bats remain.
9.06 pm	All remaining bats now active.
9.22 pm	Five bats remain.
9.28 pm	One bat on wall 4 m below roost.
9.30 pm	Four bats remain. Droppings on sheet. Some droppings are large (10 mm long) while others are small (2 mm long and thinner).
9.43 pm	Remaining bats along the inside of crevice
10.00 pm	As above
10.25 pm	All bats gone. Next morning six bats roosting in same crevice.

Some conclusions can be drawn from these observations. Bats on the outside of the group become active earlier than bats in the centre of the group. Although bats in the centre have periods of activity, they generally remain still until surrounding bats have departed. It took approximately two hours for all the bats to depart, but I cannot discount that my presence may have influenced this. The dull torch used to observe bats was turned on for quick observations with binoculars approximately every two minutes, depending on how active the bats were. There was no evidence of early departure which I would expect if the bats were disturbed.

The sex and the age of the individuals could not be determined.

Faeces collection

The main purpose of guano collection was so that the diet of the bats could be investigated but an effort was also made to determine when roosting bats defecate. This was done by spreading a large cotton sheet (2 m x 8 m) on the floor of the cave at several locations.

Bats in the cave very rarely returned to the same location so it was difficult to monitor defecation over a 24 hour period. The quantitative component of the study would be difficult to design as the number of bats in any particular group could not be determined precisely and usually changes during observation periods.

The only faecal data that were collected from a known number of bats was from the group that was observed (above). Although the number of bats in this group changed through time, making quantitative collection impossible, very few droppings were collected in the five hours up to 7.30 pm compared to the two hours from 7.30 to 9.30 pm when the bats became active.

Appendix II

Report on work in the Taupo/Tongariro Conservancy

Long-tailed bat survey.

Client: Department of Conservation, Taupo/Tongariro.

INTRODUCTION

Basic ecological research on the long-tailed bat (*Chalinolobus tuberculatus*) is essential in order to design appropriate population estimation methods and to provide valuable information for monitoring and protecting this species.

My initial investigations on the long-tailed bats began in early June 1993, and continued through to late November 1993. This consisted of a literature search, corresponding with other scientists and three field trips. The first two trips were to Grand Canyon Cave with stop-overs in the Taupo/ Tongariro Conservancy. The main aims of these trips were to confirm the existence of long-tailed bat populations both in Grand Canyon Cave and in Erua State Forest (Tongariro) and to discuss the possibility of research with the respective conservancies. The Grand Canyon Cave population was still resident in the cave and long-tailed bats were found in a number of sites in the Taupo/Tongariro Conservancy. A third field trip was made in 1993 to visit John McLennan and Tony McCann (Landcare Research) and a long-tailed bat research site at Balls Clearing in Hawkes Bay where mist-netting and bat handling techniques were learnt. Field research began in the Tongariro area on the 8th December 1993.

The main aim of this study was to attempt to trap bats using mist nets at suitable sites. Radio transmitters were then attached to adult female bats so that their movements could be tracked with directional receivers. Roost site selection and the breeding ecology was to be investigated as part of a comparative study of forest and cave dwelling populations. The occurrences of bats in both areas in which they were known to exist and areas from which they had not previously been recorded were recorded to obtain a more detailed picture of bat distribution in the Tongariro area. Weather conditions were recorded in order to assess under what conditions bats were most active, and hence which nights were best for mist-netting.

METHODS

1. Sites where bats were reported in Department of Conservation records were surveyed to determine locations where previous bat activity was highest, and where successful mist-netting would be more likely. Sites were also sought in areas where bats had not previously been reported. Potential mist-netting sites would also require appropriate vegetation or natural topography to increase chance of capture. Bat detectors were used manually and with sound-activated tape recorders to confirm the presence of bats.

2. Meteorological data was collected by direct observation and estimation of variables such as cloud cover, wind direction and rainfall. More accurate measures were obtained from thermometers, an anemometer and the meteorological service.

3. Prey species availability was sampled using a 12 volt black light trap. The light trap was set up at both mist-netting sites and other sites where bats were present. Insect sampling was to be compared with results from analysis of guano from local roosts.

4. Approximately every second night was spent mist-netting at sites where bat activity was highest, while every other night was spent surveying new, potential mist-netting areas.

5. A harp trap was used both on the ground and hoisted up large trees on four nights while in the Ohakune area.

RESULTS AND DISCUSSION

No long-tailed bats were captured in the Tongariro area. 137 hours were spent sampling sites and attending mist nets in the Tongariro area between 5/6/93 and 6/4/94. Most of this time was spent around dusk from December 1992 to February 1993. Surveying during dusk and in the first hour after dusk was considered more productive for two main reasons; this seemed to be when the bats were most active (30-60 minutes after first appearing the bats would leave the foraging area), and at this time bats could be seen silhouetted against the sky even if they were out of range of the bat detector.

In open clearings, the flight path of individual bats could be followed for distances of up to about 70 m.

52 evenings were spent surveying for bats in the Taupo/ Tongariro area and bats were seen or heard on 19 occasions. A number of new long-tailed bat sites were located in the Tongariro area and some sites seemed to have visits from bats on a regular basis. At one site (NZMS T19 429398) near Lake Rotoaira, up to seven long-tailed bats were seen regularly flying above the canopy and clearing. On five nights at this site bats were first sighted at the same time (8.57 pm) of day. Assuming that greater flight distances would produce more varied arrival times it is likely that the bats roost close by. However, systematic searches with a bat detector through the forest during emergence time did not result in the location of any roosts. Catching bats in these open areas was difficult because the bats did not appear to use the nearby stream as a flight path. Instead the bats flew at or above canopy height, foraging mainly above a large clearing.

The most promising site for netting bats was on a bluff (Siemonik's farm) in Erua (NZMS S20 082155). Two long-tailed bats regularly appeared at this site but were never caught. They were observed flying over, around and under the mist net while pursuing insect prey. Being a bluff there was often wind present so the net was constantly moving, this movement was probably detected allowing the bats to avoid the net. The net was also silhouetted against the sky during dusk. Most bats were seen or heard with the bat detector between 9.00 pm and 9.30 pm during summer (up until about thirty minutes after dark) at forest sites and up to 10.15 pm in more open areas (eg. the bluff site). The significance of this is not clear but it may be related to the distance between foraging sites and the roost. Regardless of site, more bats were detected within the first hour of darkness than later in the night.

At Pekapeka clearing (NZMS T19 429398) most bats were observed early and usually when there was some cloud cover. Air temperature at dusk, on nights when bats were most abundant, was also higher (18.1 to 22.9^{o}C).

There was less bat activity on nights that started with clear weather then clouded over, than on nights that were already overcast, even though the temperatures at 9.30 pm were often similar. Bats were observed foraging on warm wet nights but less bat activity was observed on cooler misty, or cooler wet nights. Long-tailed bats were observed flying in relatively strong wind

(7.4 m/s). An unidentified bat (probably short-tailed) was heard on the bat box at 1160 m above sea level at the new Blythe track footbridge, Ohakune.

Four short-tailed bats were caught in the Ohakune area but no long-tailed bats, which I was targeting, were either seen or heard. Continued intensive trapping and netting in the area (Brian Lloyd, pers. comm.[1]) has resulted in the capture of only a single one long-tailed bat. This gives some indication of the general difficulty of catching long-tailed bats.

CONCLUSIONS

Bats fly in a wide range of environmental conditions. No bats were caught in the Taupo/Tongariro area and so no information is available on flight distances and roosting behaviour. Insect light trapping was done in most areas but as no guano could be collected from local roosts it is not possible to draw any conclusions about the insect prey taken by the bats. Mist-netting should obviously be attempted in sites where bats occur regularly. However, in addition to having bats, the site needs to have the type of topography or vegetation where bats are forced low enough to be caught in nets, eg. stream flight paths or narrow, natural or man made corridors.

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[1] Brian Lloyd, Department of Conservation, Science and Research division. Tory St, Wellington.

Table 1. Sites surveyed in the Tongariro, Erua, and Ohakune areas.

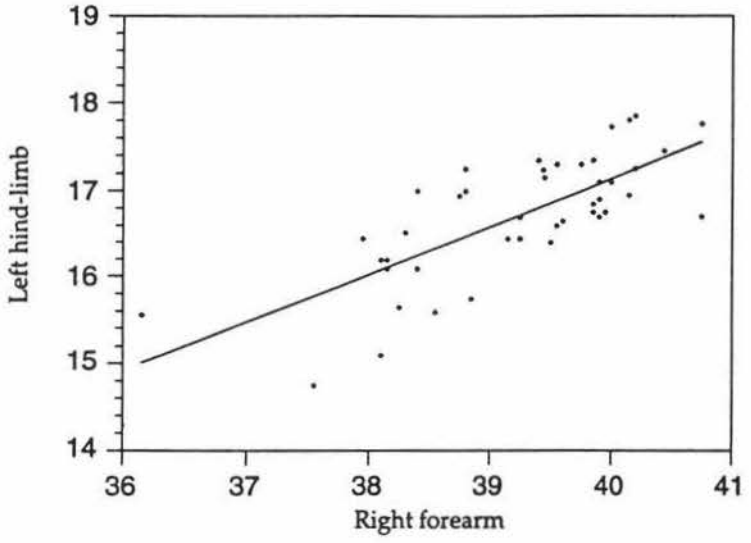
NZMS Map Reference	Location	Notes
T19 476458	Omoho Stream	Nothing
483458	" +1 km west	Nothing
433492	Powerstation lookout	Nothing
486438	Tupatomatua Stream	Nothing
475403	Hinemihi's Track	Passes
484417	Papanetu stream	Passes, nets up
480416	" "	Passes
473403	Te Pongana Saddle Rd	Passes
467396	Lake Rotopounamu	Nothing
467392	" "	Nothing
467387	" "	Nothing
465382	" "	Nothing
468379	" "	Nothing
456388	Opotaka	Nothing
430397	Pekapeka Clearing	Passes
428399	Pekapeka Stream	Passes, nets up
429403	"	Nothing
425400	West of "	Passes
422400		Passes
422402		Nothing
414400	Otara Stream	Nothing
411404	Otara Stream	Nothing
436419	Maungakatote	Passes, nets up
435422	"	Passes
434427	"	Nothing
437475	Kahuarua	Nothing
308368	Outdoor Pursuits	Nothing
309360	Ford	Nothing
307356	Dam	Nothing
495503	Poutu Canal	Nothing
490337	Ohunga Rd	Nothing
482337		Nothing
537378	Shag Pool	Nothing
536385	Admirals Pool	Nothing
693385	Kikio Rd end	Nothing
696385	"	Nothing
699385	"	Nothing
S20 155170	Waimarino Stream	Nothing
150172	" +500m west	Nothing
145170	Cuff Rd	Nothing
140160	Erua Rd	Nothing
136152	"	Passes
129146	"	Nothing
124135	"	Passes
115136	"	Nothing
105142	Airstrip	Passes
103146	"	Passes
097150	Erua Rd	Passes
082155	Trig	Passes, nets up

073155	Erua Rd	Nothing
249034	Blythe footbridge	Passes
231023	" carpark	Passes, harp-trap up
230023		Passes, nets up
253054	New Blythe footbridge	Passes, nets up
197092	Camp Rd end	Nothing
193984	Camp Rd bridge	Nothing
213008		Nothing
224014		Passes
224013		Passes, nets up,
221943	Rangatau ford	Nothing
269937	Lake Rotokura	Passes, harp-trap up
269937	"	Passes
270942	"	Passes
267937	"	Passes
271945	"	Passes, nets up
269934	"	Passes
224943	Rangatau swamp	Passes
233932	Karioi Railway Rd	Nothing
243926	"	Nothing
243924	"	Nothing
250962	Waiharuru Stream	Nothing, nets up
254962	"	Nothing
255955		Nothing
260952		Nothing
255935		Nothing
S19 172265	Makaretu Stream	Nothing

Appendix III

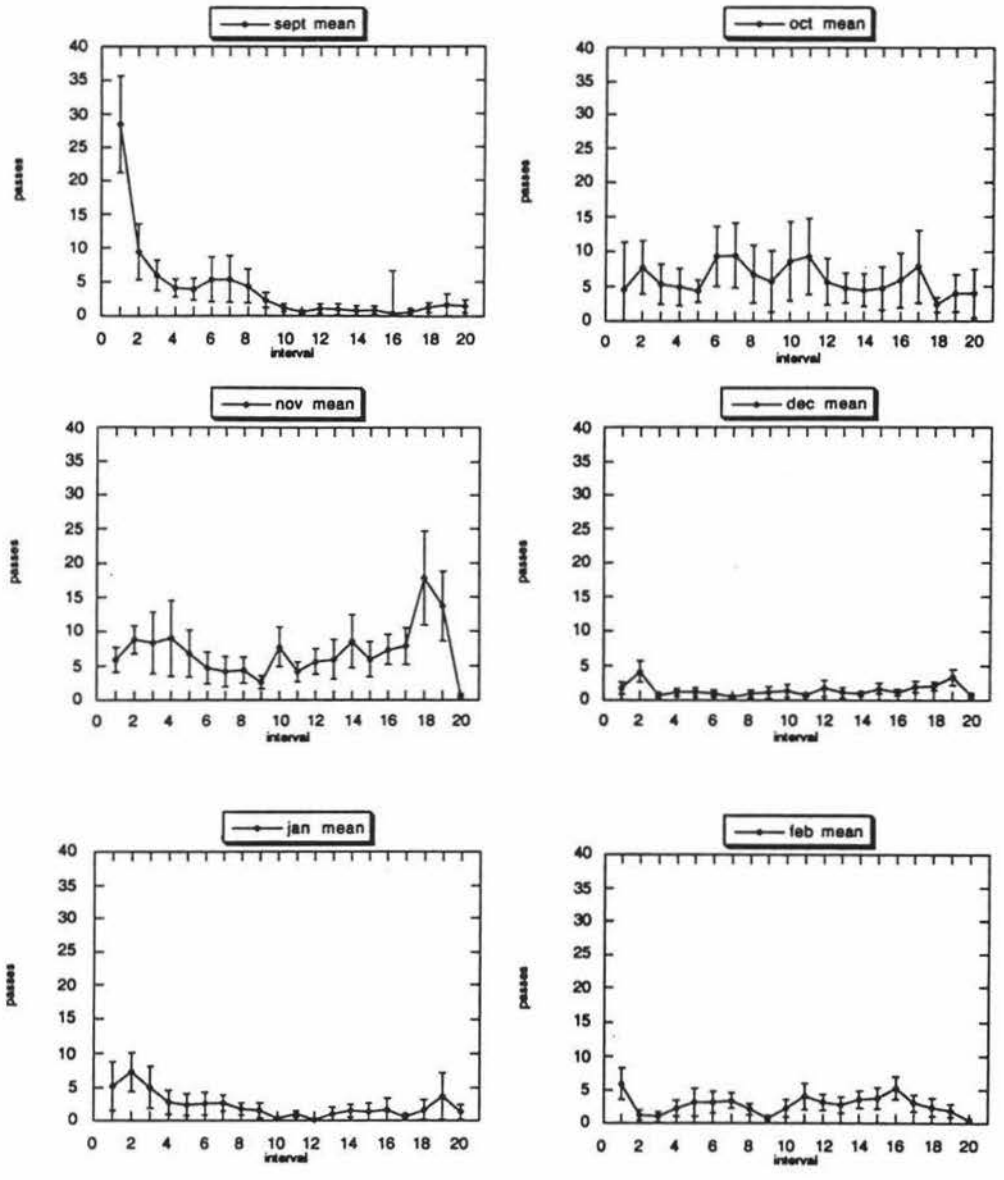
Graphs and Statistics

1. Morphology



Juvenile forearm length vs left hind limb length. (R= 0.74119)

2. Activity

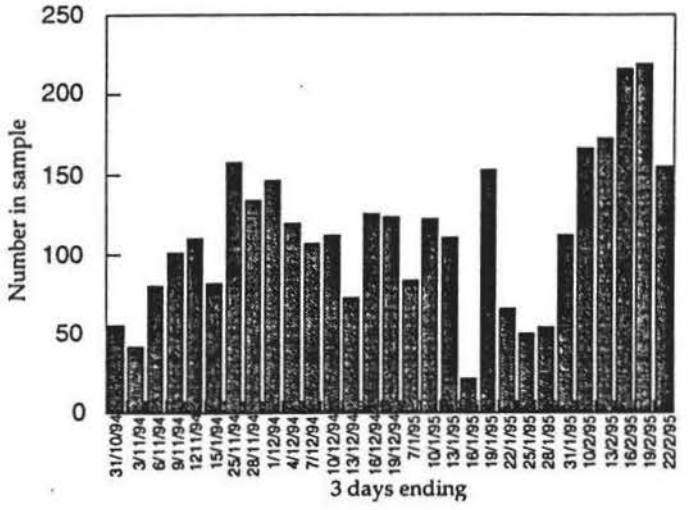


(a) Seasonal changes in long-tailed bat diurnal activity.

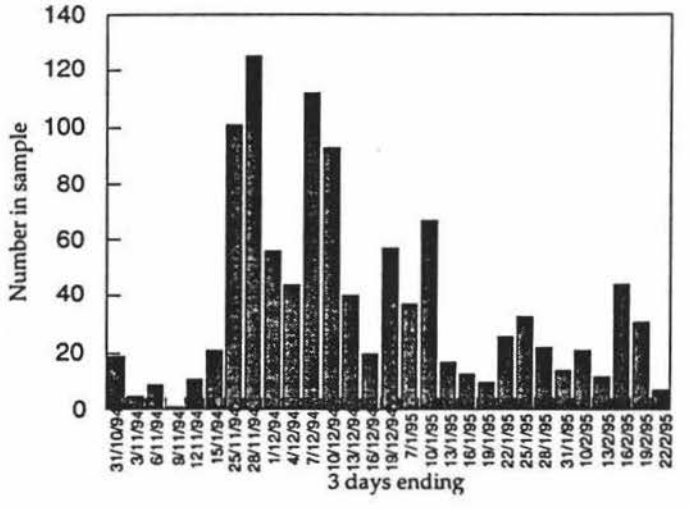
(b) Seasonal abundance of separate insect orders:

(a) Diptera
(b) Lepidoptera
(c) Coleoptera

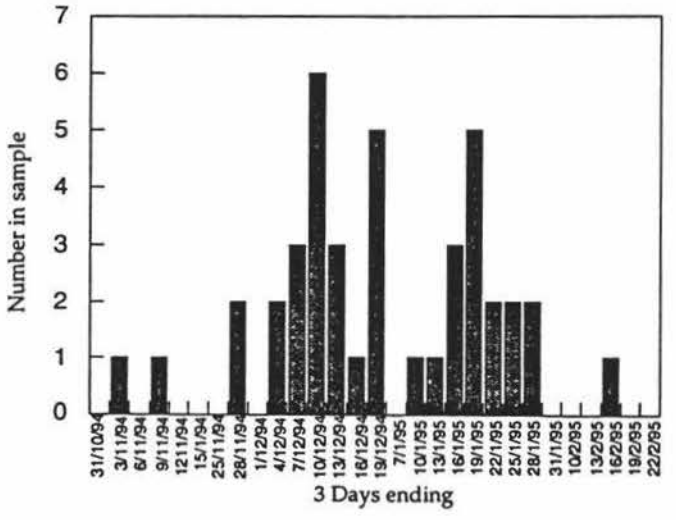
(a)



(b)



(c)



(c) Multivariate statistics.

(1) Total passes in night vs external variables.

(No variable met the 0.5000 significance level for entry into a stepwise procedure model).

Summary of forward selection procedure.

Variable	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
Min T	1	0.0387	0.0387	-0.4404	1.1685	0.2886
Rain	2	0.0241	0.0629	0.8932	0.7207	0.4031
Wind	3	0.0686	0.1315	0.9975	2.1328	0.1557

(2) Number of passes in first hour after sunset vs external variables.

Stepwise procedure.

Step 1 Variable (wind) entered R-square = 0.31152500 C (p) = 10.26726723

	DF	sum of squares	Mean square	F	Prob>F
Regression	1	5787.99599930	5787.99599930	15.38	0.0004
Error	34	12791.55955625	376.22233989		
Total	35	18579.55555556			

Variable	Parameter estimate	Standard error	Type II Sum of squares	F	Prob>F
Intercept	16.51421098	3.28894577	9485.20699290	25.21	0.0001
Wind	0.15442270	0.03937035	5787.99599930	15.38	0.0004
bounds on condition number	1		1		

Step 2 Variable (moon minutes) entered R-square = 0.43604099 C (p) = 4.62290709

	DF	sum of squares	Mean square	F	Prob>F
Regression	2	8101.44785885	4050.72392942	12.76	0.0001
Error	33	10478.10769671	317.51841505		
Total	35	18579.55555556			

Variable	Parameter estimate	Standard error	Type II Sum of squares	F	Prob>F
Intercept	1.5910891	6.29775386	20.47168722	0.06	0.8011
Moon min	0.04848910	0.01796381	2313.45185954	7.29	0.0109
Wind	0.18471311	0.03786942	7554.17335480	23.79	0.0001
bounds on condition number		1.096262	4.385049		

Step 3 Variable (month) entered R-square = 0.49081980 C (p) = 3.25989401

	DF	sum of squares	Mean square	F	Prob>F
Regression	3	9119.21373252	3079.73791084	10.28	0.0001
Error	32	9460.34182304	295.63568197		
Total	35	18579.55555556			

Variable	Parameter estimate	Standard error	Type II Sum of squares	F	Prob>F
Intercept	-28.84495945	17.49721841	803.44969495	2.72	0.1090
Month	2.24105034	1.20783078	1017.76587367	3.44	0.0728
Moon min	0.07024351	0.02092671	3330.94393271	11.27	0.0020
Wind	0.24104034	0.04750648	7610.80589637	25.74	0.0001

Summary.

Variable	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
Wind	1	0.3115	0.3115	10.2673	15.3845	0.0004
Moon min	2	0.1245	0.4360	4.6229	7.2860	0.0109
Month	3	0.0548	0.4908	3.2599	3.4426	0.0728

(3) Time of first pass vs external variables.

Step 1 Variable (Month) entered R-square = 0.28360123 C(p) = 15.95090754

	DF	sum of squares	Mean square	F	Prob>F
Regression	1	4716.70440252	4716.70440252	11.08	0.0024
Error	28	11914.76226415	425.52722372		
Total	29	16631.46666667			

Variable	Parameter estimate	Standard error	Type II Sum of squares	F	Prob>F
Intercept	-15.07735849	13.22602807	552.99218221	1.30	0.2640
Month	4.08490566	1.22694862	4716.70440252	11.08	0.0024
bounds on condition number	1		1		

Step 2 Variable (Max T) entered R-square = 0.51573299 C(p) = 4.35772677

	DF	sum of squares	Mean square	F	Prob>F
Regression	2	8577.39602416	4288.69801208	14.38	0.0001
Error	27	8054.07064250	298.29891269		
Total	29	16631.46666667			

Variable	Parameter estimate	Standard error	Type II Sum of squares	F	Prob>F
Intercept	-59.45401495	16.57662520	3837.26515610	12.86	0.0013
Month	4.21694168	1.02793471	5020.13963611	16.83	0.0003
Max T	3.67103422	1.02042646	3860.69162165	12.94	0.0013
bounds on condition number	1.001276		4.005106		

Step 3 Variable (Sky) entered R-square = 0.60117157 C(p) = 1.35461088

	DF	sum of squares	Mean square	F	Prob>F
Regression	3	9998.36495850	3332.78831950	13.06	0.0001
Error	26	6633.10170816	255.11929647		
Total	29	16631.46666667			

Variable	Parameter estimate	Standard error	Type II Sum of squares	F	Prob>F
Intercept	-49.87787966	15.85789434	2523.87728614	9.89	0.0041
Month	3.20061346	1.04362189	2399.51464199	9.41	0.0050
Max T	3.60471285	0.94410436	3719.15816602	14.58	0.0007
Sky	0.08011550	0.03394657	1420.96893434	5.57	0.0261
bounds on condition number		1.206751	10.24294		

Summary.

Variable	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
Month	1	0.2836	0.2836	15.9509	11.0844	0.0024
Max T	2	0.2321	0.5157	4.3577	12.9424	0.0013
Sky	2	0.0854	0.6012	1.3546	5.5698	0.0261

(4) Mean passes in first hour after sunset vs potential insect prey abundance.

Summary of stepwise procedure.

Variable	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
Total N° Prey items	1	0.1279	0.279	9.3505	2.6396	0.1216
Prey weight	2	0.1029	0.2308	8.3585	2.2748	0.1499

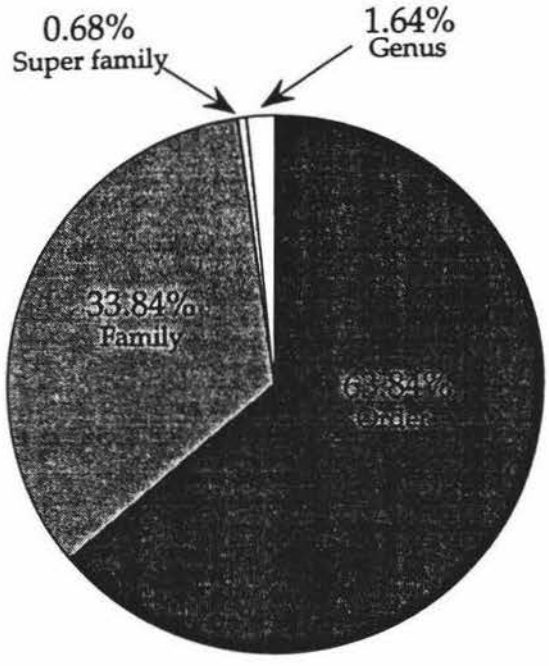
(5) Mean total passes in night vs potential insect prey abundance.

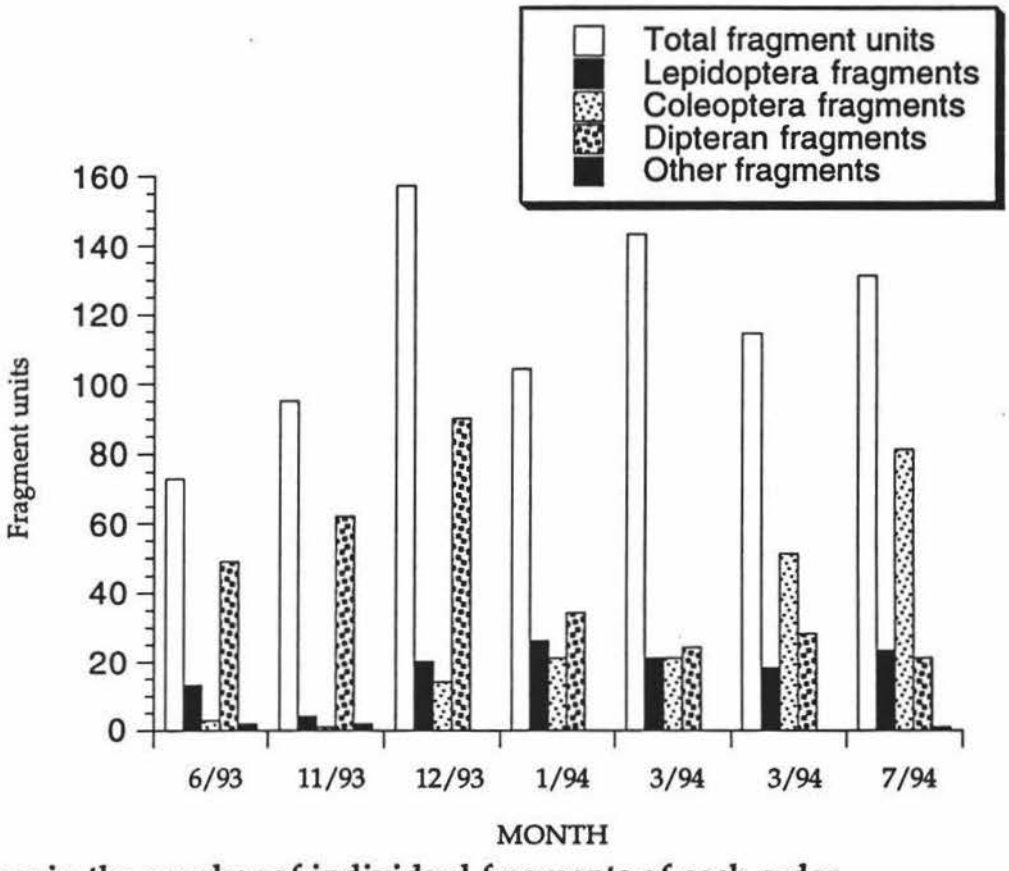
Summary of stepwise procedure.

Variable	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
N° of Coleoptera	1	0.1485	0.1485	8.4677	2.9638	0.1033
Month	2	0.1408	0.2892	6.5881	3.1690	0.0940

3. Faecal analysis

(a) Percentage of each taxonomic group that fragments were identified to.





(b) Change in the number of individual fragments of each order.