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**Ecology and Reproductive Biology of
the North Island Brown Kiwi
(*Apteryx australis mantelli*)**

Murray Alan Potter

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A thesis presented in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy in Zoology at
Massey University, Palmerston North.



FRONTISPIECE: Six-day old North Island brown kiwi chick at the entrance to its nest, Paerata Wildlife Management Reserve, Tangiteroria, Northland. February 1987.

To Acta

You gave much and
knew not that you gave
at all.

(Modified from K. Gibran 1923)

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ABSTRACT

The spacing behaviour, habitat use, pair bonding, breeding biology and reproductive endocrinology of the North Island brown kiwi (*Apteryx australis mantelli*) are investigated. Twenty-six kiwi (10 males and 16 females) were fitted with radio transmitters and tracked for two and a half years in a forest remnant in Northland.

Spacing behaviour: Home ranges overlapped extensively. One 1-ha grid square was used by at least 13 different kiwi. All range-estimate methods were sensitive to the number of fixes obtained. The average range size calculated by the field worker method was 30.7 ha. Males and females had similar home range sizes.

Habitat use: Kiwi spent over 80% of days in burrows or natural earth cavities when roosting with their mate - over twice the proportion of days spent in these types of roosts when alone. Pairs roosted together on 22% of days. This increased to over 35% of days between April-July, up to four months before females started laying. Eighty-three percent of the kiwi made use of the numerous bush remnants scattered over farmland outside the reserve. All remnants isolated by less than 100 m of pasture were used by kiwi. The maximum distance kiwi ever walked between bush remnants was 330 m. Longer migrations of up to 1.2 km from the reserve were made by kiwi using small bush remnants as "stepping stones".

Pair bonding: The kiwi were sequentially monogamous and had an extraordinarily high annual divorce rate of around 50%. Most divorces occurred between January and April - the non-breeding season. No relationship was apparent between the breeding success of a pair and their likelihood of divorce. The forest contained an unbalanced sex ratio with females outnumbering males by 1.3-1.4 : 1.

Breeding: Eggs were laid over eight months of the year from July to February. Males were found incubating in all months except May and June. Pairs averaged 1.5 eggs/pair/year and no females laid more than two eggs in a season. Clutches that failed were not immediately replaced. Eighteen of 20 nests were in burrows 45-125 cm long. Males did all the incubating and emerged every night to feed except one to two days before their chicks hatched. Incubating males spent an average of 3.6 hours off their nest each night - less than half the active time of non-incubating kiwi. In both sexes body weights tended to peak in winter at the start of breeding. Females lost about 9% of peak body weight for each egg they laid, while males that incubated full-term lost about 17% of peak body weight. Only six of 26 eggs laid over three seasons hatched. Five chicks fledged. At fledging three of these chicks were known to be 15-20 days old. The average productivity was 0.3 chicks/pair/year.

Endocrinology: Plasma samples were collected from the radio-tagged kiwi and analysed by radioimmunoassay for testosterone (T), progesterone (P) and estradiol-17 β (E). Male T concentrations increased sharply in Autumn, rising from near basal levels in April to peak at over 2.2 ng/ml in May. Male T levels remained high through winter and then declined to low levels (0.15-0.42 ng/ml) between October and the following April. Plasma T levels peaked (1.8-2.8 ng/ml) in males 12-4 weeks before their mates laid, and dropped significantly (to 0.21 ng/ml) during the four weeks before egg laying. Females showed no significant monthly variation in T levels. Plasma T concentrations were highest (0.21 ng/ml) in females 4-2 weeks before laying, but even during this period T levels in females did not significantly exceed minimum (brooding) levels in males. Plasma P levels did not vary significantly between months or reproductive stages in either sex. P levels were almost always higher in males than in females. Males also obtained extraordinarily high plasma E levels. Both sexes showed an enormous increase in E in autumn, with plasma concentrations rising from near minimum detectable levels (6 pg/ml) in March to average over 1.6 ng/ml in males and 2.6 ng/ml in females in April. E levels were higher in incubating males (0.30 ng/ml) and males during the 12 weeks before egg laying (0.60-1.40 ng/ml) than in non-breeding males (27 pg/ml), suggesting that E may facilitate the development of incubating behaviour in these birds. Breeding females had significantly higher E levels than non-breeding females from 16 weeks before egg laying until two weeks after egg laying. Males and females E levels did not differ significantly from each other during any reproductive stage prior to egg laying. These results indicate that sex-role reversal in the brown kiwi is not accompanied by a reversal of the normal male/female androgen levels, but that male kiwi have remarkably female-like estrogen cycles.

Management: Recommendations on the conservation and management of the North Island brown kiwi are presented. Kiwi reserves need to be large if they are to contain populations with long-term viability (500-1000 individuals). Just how large may vary between 750-1500 ha in different regions. Smaller populations also are of conservation value and should not be neglected. Bush corridors and "stepping stones" can be used to reconnect separated islands of habitat. Regular predator monitoring and control programmes must be instigated in prime kiwi refuges.

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INTRODUCTION

1.1 BACKGROUND

Kiwi are unusual birds in several aspects of their morphology, anatomy, physiology and behaviour. Even among ratites they have been considered peculiar (Handford & Mares 1985). In particular, their egg weight to body weight ratios are extremely large (Reid 1971a; Calder 1978, 1979; Rowe 1980); their 74-84 day incubation period is exceeded only by the large albatrosses (Lack 1968; Rahn & Ar 1974; Calder *et al.* 1978); and relative to their size and metabolic rate kiwi lead all birds in the amount of energy invested in the egg (Reid 1971b; Calder *et al.* 1978). Incubation tends to be performed solely by the male in the little spotted kiwi (*Apteryx owenii*) and brown kiwi (*A. australis*) (J. Jolly pers. comm.; McLennan 1988), although exceptions may occur in the Stewart Island brown kiwi population (*A. a. lawryi*) (Soper 1976; Sturmer & Grant 1988). In the great spotted kiwi (*A. haastii*) incubation is sometimes shared between the male and female (Eason 1988; J. McLennan pers. comm.). Kiwi have very large olfactory bulbs (Craigie 1930) and a highly developed sense of smell (Wenzel 1968), and they are unique among birds for having their nostrils located at the tip of their long beak. Kiwi have small rudimentary eyes. Contrary to earlier reports that kiwi are myopic (short sighted) (Walls 1967; Davis & Greenwell 1976), Sivak & Howland (1987) have recently shown that kiwi are slightly hyperopic (long sighted) or emmetropic (zero refractive error). Along with other ratites kiwi are completely flightless.

Until recently, most research on kiwi has concerned their taxonomy and phylogenetic relationships (Oliver 1955; Bock 1963; Sibley & Frelin 1972; Cracraft 1974; Reid & Williams 1975; Rich 1979; de Boer 1980; Sibley & Ahlquist 1981; Diamond 1983; Stapel *et al.* 1984; McGowan 1985; Houde 1986), anatomy (Owen 1841, 1849, 1871; Parker 1888a,b, 1891, 1892; Craigie 1930; Kinsky 1971; McCann 1973; McGowan 1979, 1982, 1985; Vanden Berge 1982; Beale 1985), physiology (Farner *et al.* 1956; Shorland & Gass 1961; Calder & Rowe 1977; Calder & Dawson 1978; Calder *et al.* 1978; Calder 1979; Beale 1985), and parasites and diseases (Clay 1972; Tandan 1972; Smith *et al.* 1973; Harris 1975; Andrews 1977; Clark & McKenzie 1982). Knowledge of their reproductive biology and feeding habits has come largely from the study of birds in captivity, or the analysis of dead birds (Gurr

1952; Robson 1958; Bull 1959; Wenzel 1968; Reid 1970, 1971a, 1972a,b; Reid *et al.* 1982; Kinsky 1971; Watt 1971; Rowe 1974, 1978; Goudswaard 1986; Eason 1988). The diet of wild kiwi has also been studied by faecal analysis (Kleinpaste & Colbourne 1983; Colbourne & Powlesland 1988).

With the exception of Buller's (1888) general account, little was published on the behaviour of wild kiwi until this decade. The paucity of information on wild kiwi behaviour is partly attributable to the inherent difficulties involved in studying these shy nocturnal birds in their often dense New Zealand forest and shrubland habitats. The first information on kiwi spacing behaviour came from vocalisation surveys (Corbett *et al.* 1979; Jolly 1983; Taylor & Calder 1983; Colbourne & Kleinpaste 1984; Rasch & Kayes 1985), and from an extensive banding study (Colbourne & Kleinpaste 1983). In the early 1980's significant advances in radio telemetric techniques facilitated the first intensive studies of the day-to-day movements of tagged individuals (Jolly 1983; McLennan *et al.* 1987). These studies indicated that kiwi are both territorial and monogamous. They also raised concern about inadequacies in both the size and quality of current kiwi habitat (Jolly 1985a (also see Atkinson & Daniel 1985; Jolly 1985b); McLennan *et al.* 1987). A recent workshop on kiwi research and conservation (Powlesland 1988) highlighted the deficiencies in our current knowledge of kiwi ecology, and the lack of information necessary to answer basic management questions such as: what are the habitat requirements of kiwi?; how should reserves be designed?; and will kiwi use corridors or move over open country between reserves? Recent observations on the devastating effect of a single ravaging dog on the Waitangi State Forest kiwi population (Taborsky 1988a,b) emphasises the urgent need to design and implement effective conservation strategies for kiwi.

A desire to conserve the kiwi for its own sake is enhanced by the realisation that study of their unusual behavioural and physiological characteristics could make a valuable contribution to the wider understanding of avian biology. Male uniparental care is rare among birds (Ridley 1978), occurring only in the ratites (except the ostrich); some charadriiforms; some gruiforms; a few galliforms; and nonparasitic cuculiforms (Oring 1982). The rarity of male-only incubation has led to considerable interest in determining the conditions under which it evolves (Jenni 1974; Emlen & Oring 1977; Gaul *et al.* 1977; Oring 1982, 1985). Sex-role "reversed" species, such as the brown kiwi, provide test cases for these theories. They also provide an opportunity to study the endocrine regulation of incubation and brooding independent of the complications of the ovarian cycle (eg. Oring *et al.*

1988). Breeding and endocrine systems are interlinked in a complex way. To understand these systems studies are required that investigate the interactions between the biotic and abiotic environment, breeding biology, and endocrinology (see Wingfield 1983). Here these interactions are explored in the North Island brown kiwi (*A. a. mantelli*).

1.2 AIM OF THE STUDY AND THESIS PLAN

Aim

The primary aim of this study is to describe environmental and physiological requirements for reproduction in the North Island brown kiwi to aid the design of effective conservation strategies for the species. This is tackled by investigating spacing behaviour, habitat use, pair bonding, breeding biology, reproductive endocrinology, and the interactions between these variables.

Thesis layout

The study site and methods applying to the whole of the study such as kiwi capture and telemetry techniques are described in Chapter 2. Methods specific to just one section are described there.

Following the general methods section (Chapter 2), the thesis is presented in six chapters. The first (Spacing Behaviour and Habitat Use; Chapter 3) concerns kiwi movements, and interactions between kiwi and their environment. Range size, roost selection and nocturnal use of habitat by kiwi are examined and compared with data from other populations.

Chapter 4 presents data on the use by kiwi of small bush remnants outside Paerata Wildlife Management Reserve (Paerata), and the distances they travelled over pasture to reach these remnants. The implications of these findings for the design and enhancement of kiwi reserves are discussed.

Kiwi pair bonding is investigated in Chapter 5. The formation and stability of the pair bond are examined and interpreted in the light of the preceding results on spacing behaviour.

Findings on the fecundity and breeding biology of kiwi are presented in Chapter 6. Comparisons are made between the Paerata kiwi and those studied elsewhere, both in the wild and in captivity.

The reproductive endocrinology of the kiwi is investigated in Chapter 7. These data are related both to the seasonality of breeding, and to specific stages of the breeding cycle. The endocrine control systems of the kiwi are compared with those of other sex-role reversed species.

Finally, results from the preceding chapters are drawn together in Chapter 8 and used to formulate recommendations on the future conservation and management of the North Island brown kiwi.

STUDY SITE AND GENERAL METHODS

2.1 STUDY SITE

The study was undertaken at Paerata Wildlife Management Reserve (Paerata), Tangiteroria, Northland (35°47'S, 174°02'E) between September 1985 and April 1988. Paerata is one of only two reserves specifically created for kiwi. The other is the Ecological Reserve in Waitangi State Forest.

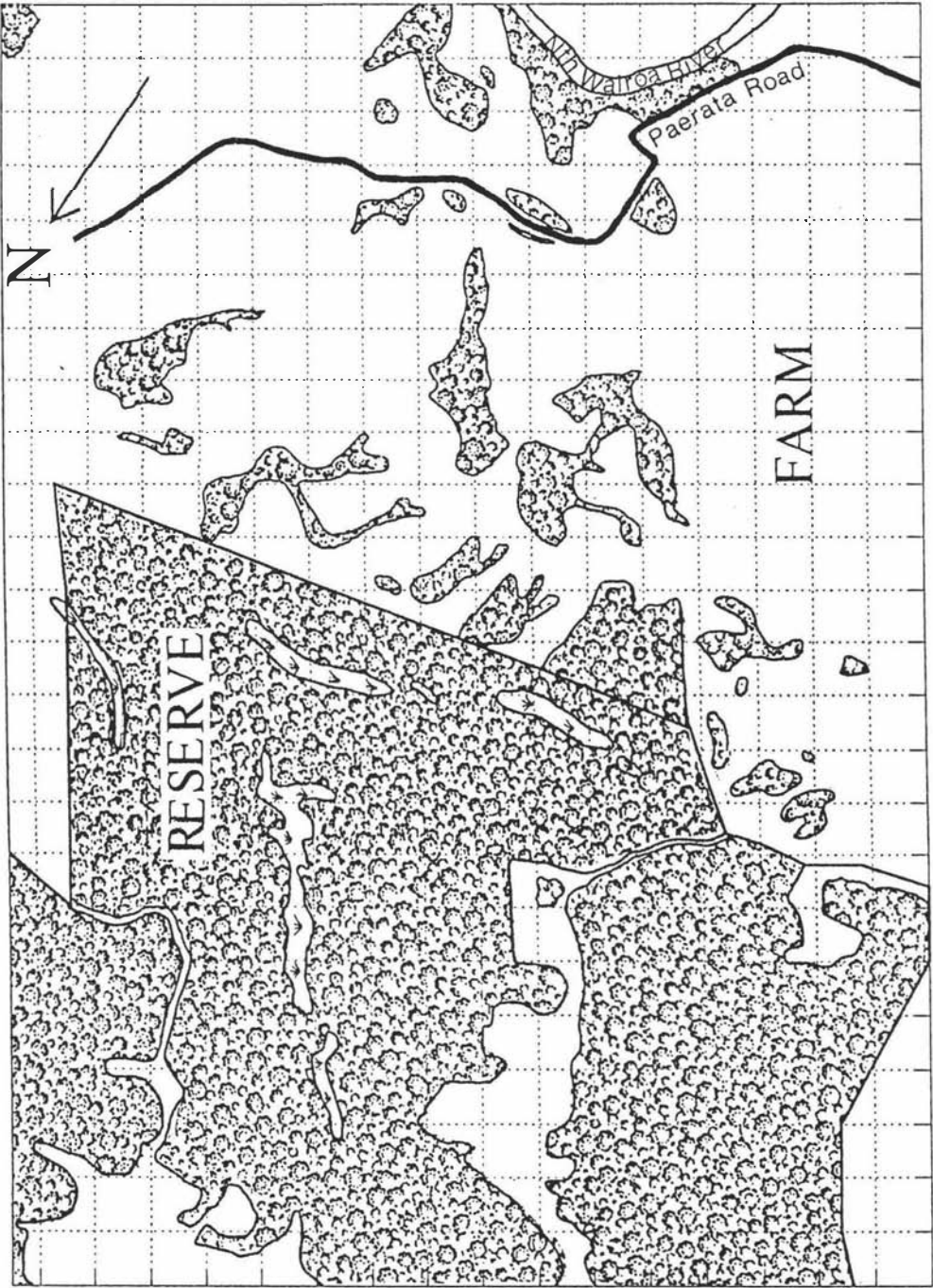
Reports from local farmers, and resulting surveys by the New Zealand Wildlife Service in 1976 and 1978 (reported in Reid 1983), indicated that the Paerata/Mangakahia area contained a high density of kiwi. These blocks were subsequently purchased by the Crown in three parts: the first block of 161.1 ha was gazetted in 1983; a second block of 40 ha was acquired in 1984; and a final 9 ha block was added in 1988. The resulting 210 ha reserve comprises a complex mosaic of grassland, manuka (*Leptospermum scoparium*) and kanuka (*Kunzia ericoides*) scrub, and regenerating podocarp/broadleaf forest. This patchwork of vegetation (Figure 2.1) is the product of a history of land clearance and grazing.

Originally the Paerata site was covered by lowland kauri (*Agathis australis*) forest, but only a few scattered kauri now remain. The area was cleared first by milling, then for gum digging, and most recently (in the 1920's and 1930's) for farm development. Hall's totara (*Podocarpus cunninghamii*) is now the dominant tree species, with scattered patches of kohekohe (*Dysoxylum spectabile*), tanekaha (*Phyllocladus trichomanoides*) and putaputaweta (*Carpodetus serratus*). Several stands of raupo (*Typha muelleri*) occur in the reserve's two large swampy valleys. Large tracts of land adjacent to the reserve were cleared during the 1960's. Between 1975 and 1980 120 ha of scrub near the Mangakahia River was the last large block of land to be cleared near Paerata. Before this clearance a series of recovery operations removed over 80 kiwi from the block (M.B. Tapp pers. comm.).

The land now comprising Paerata has been grazed continually by cattle (*Bos taurus*) during the past 40-50 years. During the course of the study the reserve was grazed in two blocks. The larger 161 ha block was stocked with 90 cattle, while the remaining 40 ha block contained 25. In October 1987 the stocking rates of these two blocks were reduced to 45 and 15 cattle respectively (M.B. Tapp pers. comm.). Paerata also contained feral goats (*Capra hircus*) and brush-tailed possums

FIGURE 2.1: Map of the study site at Paerata Wildlife Management Reserve, Tangiteroria, Northland (35°47'S, 174°02'E). The southern boundary of the reserve is shown as a heavy line down the centre of the map. Grid cells are 100 m² (1 ha).





(*Trichosurus vulpecula*). During the study Paerata contained areas of bush with very thick undergrowth despite its history of land clearance, grazing and browsing. Numerous small areas of bush and scrub remained, especially in the gullies, on the private farmland surrounding the reserve. Many feral cats (*Felis catus*) and several ferrets (*Mustela putorius*) were seen in and around the reserve during the study.

Topographically Paerata consists of low rolling hills, with a high point of only 122 m (400 ft) a.s.l. The climate is subtropical, with warm humid summers and mild winters. Annual rainfall ranges between 1500-2400 mm (Tomlinson 1976). The reserve's two main valleys are swampy and remain damp for all but brief periods in late summer.

The study was concentrated in the southern third of Paerata (Figure 2.1). Twenty-eight kiwi were caught within this area between September 1985 and August 1987. The whole of Paerata Wildlife Management Reserve contained 80-90 kiwi, or about one bird per 2.5 ha. This estimate allows for home range overlap and birds I failed to catch. This density is comparable with Waitangi State Forest (approximately 5 ha per pair (Colbourne & Kleinpaste 1983)), but about 10 times greater than the density of one pair per 55 ha reported for Hawkes Bay (McLennan *et al.* 1987).

Paerata Wildlife Management Reserve offered both a high density kiwi population and an excellent opportunity to investigate habitat use by kiwi in an environment fragmented by land clearance and farm development - an environment now typical of much of the remaining North Island kiwi habitat.

2.2 GENERAL METHODS

2.2.1 Introduction

This section details the general methods used in the study. Catching and tracking techniques are described, and the number of kiwi captured and the periods over which they were tracked are given.

2.2.2 Capture techniques

The majority of kiwi were caught using a Labrador bitch 'Belle' specifically trained for the task, and muzzled to prevent injury to the birds. Belle was used both to locate birds in their daytime roosts, and to catch birds that were moving about

at night. Kiwi were also caught by spotlighting and running them down at night without the aid of a dog. This was most successful when the birds were on grass or in open bush. Following capture each kiwi was banded (New Zealand National Banding Scheme size 'R' bands), fitted with a radio transmitter, weighed and measured (beak length, tarsus width, breadth and length, and toe length (Appendix)), and then released.

2.2.3 Radio telemetry

Radio telemetric techniques and transmitter design were similar to those described in McLennan *et al.* (1987). All radio transmitters used here were of the external whip aerial type and operated around 160 MHz. These were powered by a 750-900 mA-h lithium cell battery, and had an average field life of 10-16 weeks. Several SIRTRACK VI transmitters (Ecology Division, D.S.I.R.) were also used, and these had a field life of around 25 weeks. A CE12 receiver (Custom Electronics of Urbana Inc.) and a three element hand-held Yagi aerial were used in tracking. Signals could be detected at distances of 10-2000 m when kiwi were in their daytime shelters, and from 200-2000 m when they were active at night.

The major problem encountered with the transmitters was in maintaining water-tightness. This problem was solved by coating each transmitter and its battery in paraffin wax. The battery and transmitter were then encased in epoxy resin which also anchored a U-shaped aluminium strip covered with heat-shrink tubing. This strip was used to attach the transmitter to the kiwi's tibio-tarsus with two plastic straps (hospital identification bands). These bands were soft and pliable, and caused no noticeable injury to the birds' legs. The straps broke naturally after 10-30 weeks in the field, freeing the bird from long-term encumbrance should either the transmitter or battery fail. The complete package weighed 30-35 g (less than 2% of body weight) and measured approximately 40 x 35 x 20 mm.

Daytime roosts of radio-tagged kiwi were located by following the path of increasing signal strength until the type of shelter being used was seen. Night-time locations were determined by triangulation. Familiarity with the study site enabled most daytime fixes to be recorded to within 10 m of the true location, while night-time fixes were usually accurate to within 20 m. The fixes were plotted on a large-scale map and subsequently converted to Cartesian coordinates for computer analysis.

2.2.4 Number of kiwi captured and length of tracking period

Thirty-two kiwi (11 males, 20 females and 1 juvenile) were caught and banded between September 1985 and August 1987 (Figure 2.2). Five chicks too small to band were also found. Twenty-six kiwi (10 males and 16 females) were fitted with radio transmitters and tracked for periods ranging from two days (for a female whose transmitter failed almost immediately), to 116 weeks. The 10 males were tracked for periods of 16-116 weeks (median = 58 weeks), and 14 of the females were tracked for 12-96 weeks (median = 72 weeks). At least nine kiwi carried functional transmitters for each of the 25 months from March 1986 to March 1988. A minimum of 16 kiwi were tracked each month between June 1986 and June 1987 (Figure 2.2).

2.2.5 Frequency of tracking and handling

Radio-tagged kiwi were located on 375 days between September 1985 and April 1988. Kiwi were tracked in all but two (March 1987 and January 1988) of these 32 months. Mainly daytime records were made during the first ten months of the study, as nights were spent trying to catch new birds. From August 1986 kiwi were located during the day, and again 1-3 times most nights. A total of 3543 location records were collected, comprising 2096 daytime, and 1447 night-time fixes. Records were kept of the date, the type and location of roost site used by each bird each day, whether it was alone, and whether itself, its mate, or another bird had been found in that site previously. For night-time fixes the date and time were recorded, a note kept of the type of vegetation each bird was in, and its location with respect to neighbouring birds.

Radio-tagged kiwi were recaptured every 4-10 weeks for weighing (Section 6.2.3), blood sampling (Chapter 7) and to check on and change damaged straps and transmitters with old batteries. Kiwi were variable in their response to being caught and handled. Some kiwi fled the capture area once released, while others remained close to their release site and showed little outward sign of stress from their ordeal. The most extreme home range movements were never the obvious result of my interference or presence (Chapter 3).

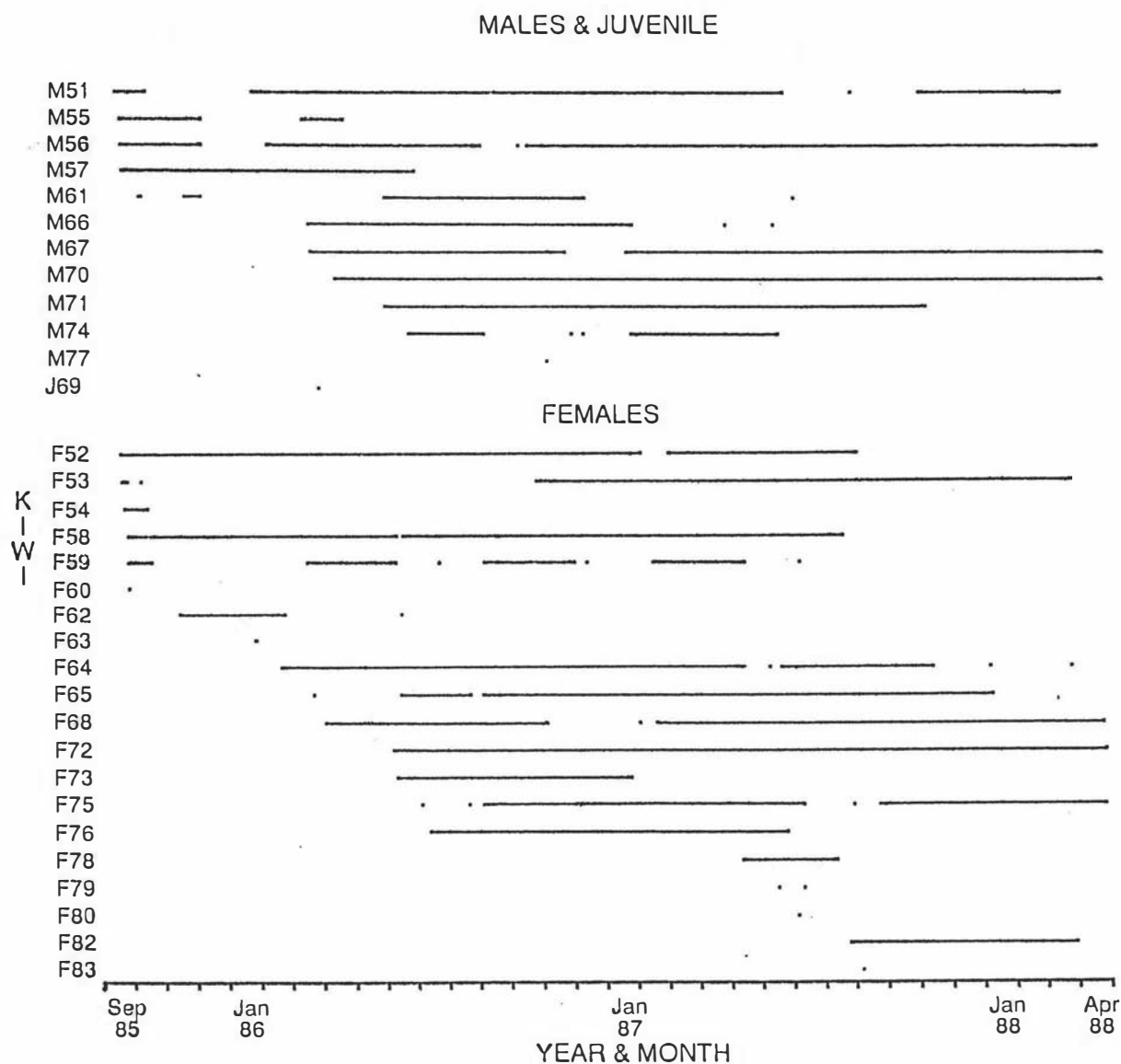


FIGURE 2.2: Date of capture and length of time each kiwi was radio-tagged at Paerata. M = male; J = juvenile; F = female. The identity number of each kiwi is the last two digits of their New Zealand National Banding Scheme size 'R' bands. The prefix was R 350-.

SPACING BEHAVIOUR AND HABITAT USE

3.1 INTRODUCTION

Land clearance during the past century has fragmented the North Island brown kiwi population into many small discrete sub-populations concentrated in three geographic regions: Northland; Taranaki-King Country; and Urewera-Hawkes Bay (Bull *et al.* 1985). Two previous studies (Colbourne & Kleinpaste 1983; McLennan *et al.* 1987) have shown that kiwi population densities can vary by an order of magnitude across this range. Using radio telemetric techniques McLennan *et al.* (1987) were able to give a detailed account of the habitat use, roosting and spacing behaviour of kiwi in two sites in Hawkes Bay. If we are to manage successfully the North Island brown kiwi across its entire range, comparative data from different populations are needed to determine the degree of ecological uniformity or diversity existing between regions. The aim of this section is to investigate the range size, roosting behaviour and habitat use of brown kiwi in a high density population in Northland.

3.2 METHODS

For details of study site, number of kiwi captured and tracking techniques see Sections 2.1 and 2.2.

3.2.1 Estimation of range size

Diverse methods have been developed for estimating the size of an animal's range. Reviews of the various techniques are given in van Winkle (1975); Macdonald *et al.* (1980); Voigt & Tinline (1980); Rhoades & Langham (1984); and Samuel *et al.* (1985). Each method has its strengths and weaknesses, and Macdonald *et al.* (1980) warn that more mathematically complex models do not necessarily give greater biological insight. To enable comparison between kiwi in Northland and Hawkes Bay, the only other population for which comparable data are available, the home range estimate methods of McLennan *et al.* (1987) are used

here. These are: the convex polygon method; the grid cell method; and the field worker method. In addition, the outer boundary of chronologically linked observations (OBCLO) (Rhoades & Langham 1984), a modified convex polygon method, is also employed.

The convex polygon method is defined as the smallest convex polygon enclosing all the points (Mohr 1947). Although this method is generally considered to give a good indication of the shape of an animal's range (Hough 1982), it is very sensitive to movements on the periphery of a range, and may include large areas which are never visited. This error grows as the shape of the range becomes increasingly irregular.

The OBCLO method involves plotting and linking observations chronologically, and then determining the area within the outer boundary of these linked observations. The resulting area is sensitive to the interval between fixes. OBCLO estimates will tend towards the convex polygon estimate when the range is reasonably circular in shape, or the tracking intervals too long. However, with my data it was less sensitive to movements around the edge of the home range than the convex polygon method, effectively excluding large areas that the kiwi were known never to visit.

The grid cell method, in contrast to these polygon methods, does not rely on a single contour around the boundary of a home range. Instead it is based on the sum of "used" grid squares or polygons (Adams & Davis 1967). A 20 x 20 m grid, appropriate to the accuracy with which the kiwi could be located at night (when fixes were most inaccurate), is used here. A cell was considered part of the range if a kiwi was recorded in it, or in an immediately adjacent cell. After plotting the fixes, islands of use were connected to their nearest neighbours on the assumption that the kiwi had taken the shortest route when moving between them. All cells traversed by this route, but not their immediate neighbours, were then also considered part of the range.

The field worker method was considered by Macdonald *et al.* (1980) often to be the most biologically meaningful, and McLennan *et al.* (1987) argued that for kiwi this method gave the most accurate estimate of home range. The field worker method estimates home range size and shape by drawing a shape that takes into account radio fixes, topography, and knowledge about the probable routes taken by a bird when moving about its home range.

Home range estimates are presented only for kiwi located at least 20 times over a period of not less than 12 weeks. The field worker estimate was equated to

the convex polygon estimate when kiwi were located less than 50 times, or tracked for less than six months, as it was considered that these birds were not known well enough to make a distinction between these methods.

3.2.2 Daytime roost and night-time habitat description

Confusion has developed over what to call kiwi daytime shelter sites. Colbourne & Kleinpaste (1983) use the term 'burrow' for these shelters. This is unsatisfactory because a 'burrow' in general usage refers to a hole or tunnel excavated by an animal for dwelling, and excavated dwellings are only one of several types of shelter used by kiwi. McLennan *et al.* (1987) used the terms 'den' and 'roost' interchangeably for these shelters. 'Den' usually refers to the lair of a large mammal. Despite Calder (1978) awarding "this remarkable bird the status of an honorary mammal" (sic) kiwi remain birds, so I prefer the term 'roost' to describe their daytime shelters.

Paerata roosts included burrows (excavated by kiwi), natural cavities, surface vegetation, and hollow logs. Where possible the length of the burrows and natural cavities, and whether the site had been used previously were recorded. Night-time fixes were ascribed to one of the following vegetation descriptions: thick bush; open bush; long grass/reeds/swamp; and bush/grass edge (= 5 m either side of the actual bush edge).

All location records were plotted and then the habitat composition of each "field worker home range" was determined with a compensating planimeter, or by tracing and weighing. The trace and weigh method involved tracing an outline of each habitat type onto paper from a large scale aerial photograph. These sketches were then cut out and weighed. Their weights were proportional to area, and the conversion was readily made by comparison with the weight of a reference sheet of paper corresponding to a known area on the aerial photograph. The amount of bush edge was determined with a mapping wheel micrometer.

3.2.3 Statistical analyses

Home range sizes were compared using one-way analyses of variance. Chi square analyses were used to compare roost use by kiwi roosting alone versus with their mate, and the observed and expected night-time use of habitat. Seasonal and individual differences in roosting behaviour and night-time habitat use were

investigated with an SPSSx loglinear analysis package (SPSS Inc. 1983) on Massey University's Prime computer. This analysis is a log likelihood ratio test based on the G statistic (Sokal & Rohlf 1981).

3.3 RESULTS

3.3.1 Range size and overlap

The length of the maximum axis of individual home ranges varied between 320 m and 1600 m ($n = 23$; median = 920 m). Home range estimates, as determined by the four techniques, are summarised and compared in Table 3.1.

The convex polygon method gave the largest average estimate of home range size (mean = 40.5^{ha}) for the 23 radio-tagged kiwi. This is probably an over estimate as large areas known never to have been visited by the kiwi were often included in their range estimate. The smallest estimates of home range size were usually generated by the grid cell method (Mean = 15.8^{ha}). This method probably tended to underestimate the true range size because of its strong dependence on the number of grid cells in which the kiwi were located, while placing little importance on areas lying between these grid cells. Manual tracking of many individuals over long periods of time could locate each kiwi in relatively few of the total number of grid cells probably used. A realistic measure of home range would be obtained by this method only if an extremely large data set was available such as that generated by an automatic tracking system.

The OBCLO estimates (mean = 22.4 ha) usually fell between the convex polygon and grid cell estimates, but the OBCLO method was conservative compared with the field worker method (mean = 30.7 ha). The field worker estimates tended to be larger than the OBCLO estimates because the latter did not take account of the topography and the most likely routes taken by kiwi moving about their range.

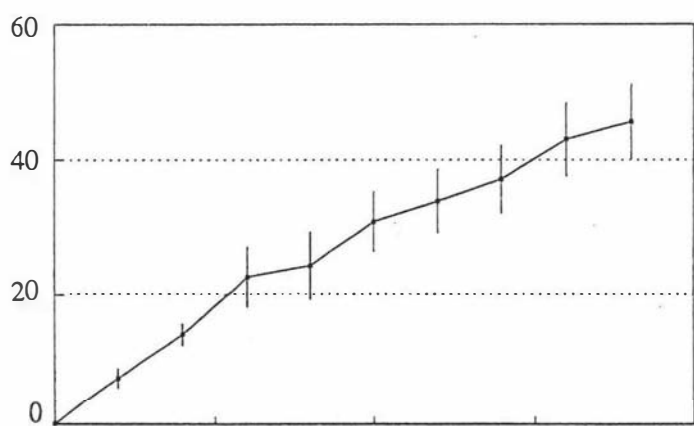
Range size estimations derived from the convex polygon, OBCLO and grid cell methods were all influenced by the number of fixes (Figure 3.1). Consequently, intra- and inter-population range size comparisons can be made accurately only from set numbers of observations per individual collected by a uniform tracking procedure. Compared this way, male and female range sizes did not differ significantly from each other for any of the six 20-observation intervals between 80 and 180 radio fixes per bird (Table 3.2).

TABLE 3.1: Range sizes (ha) of kiwi in Paerata Wildlife Management Reserve located 20 times or more. Estimates of home range were calculated by the convex polygon method, the outer boundary of chronologically linked observations (OBCLO) method, the grid cell method, and the field worker method (SE = standard error).

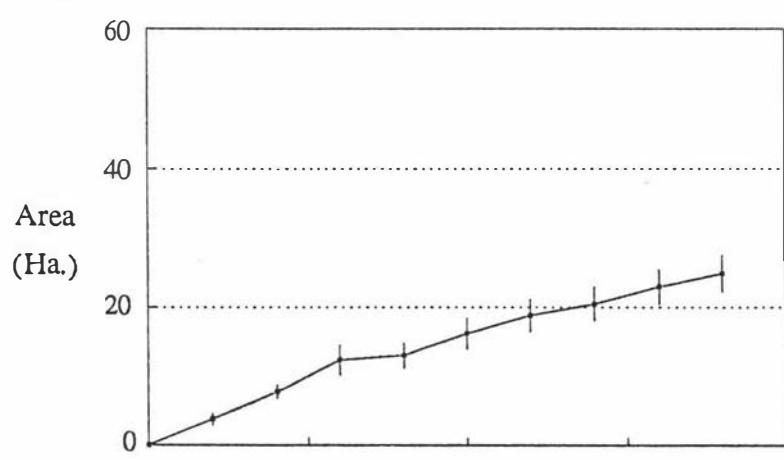
Bird	Weeks tracked	No. fixes	Convex polygon area	OBCLO area	Grid cell area	Field worker area
MALES						
M51	95	299	92.5	36.2	25.3	53.6
M55	16	63	35.6	9.9	7.3	35.6
M56	116	253	35.0	26.6	20.1	34.0
M57	40	57	4.0	3.1	4.1	4.0
M61	29	100	32.7	21.6	12.6	31.7
M66	43	143	39.5	20.2	12.8	27.2
M67	98	221	63.5	29.0	25.2	42.8
M70	103	246	38.5	31.9	21.9	31.4
M71	73	234	33.8	17.9	17.9	23.9
M74	30	64	13.2	7.7	8.8	13.2
Mean ± SE	64.3	168	38.8 7.8	20.4 3.4	15.6 2.4	29.7 4.4
FEMALES						
F52	95	192	72.3	40.6	20.8	52.9
F53	72	90	56.0	37.7	19.3	43.3
F58	95	150	26.6	17.9	12.6	25.3
F59	39	117	26.4	16.5	12.6	26.2
F62	14	27	17.0	7.2	8.0	17.0
F64	82	181	51.8	34.0	20.6	36.6
F65	77	248	91.5	47.5	27.2	53.5
F68	89	212	27.8	14.5	16.7	22.9
F72	96	226	55.9	20.0	21.6	37.8
F73	31	85	12.4	6.5	8.8	12.4
F75	72	108	65.7	43.3	20.2	44.4
F76	48	136	22.8	14.4	12.8	19.1
F78	12	37	17.1	10.4	6.1	17.1
Mean ± SE	63.2	139	41.8 7.0	23.9 4.0	15.9 1.7	31.4 3.9
Grand mean ± SE	63.7	152	40.5 5.1	22.4 2.7	15.8 1.4	30.7 2.9

FIGURE 3.1: The relationship between the number of fixes obtained and the home range size of Paerata kiwi estimated by: a) the convex polygon method; b) the outer boundary of chronologically linked observations (OBCLO) method; and c) the grid cell method. (mean \pm SE; n = 10).

a)



b)



c)

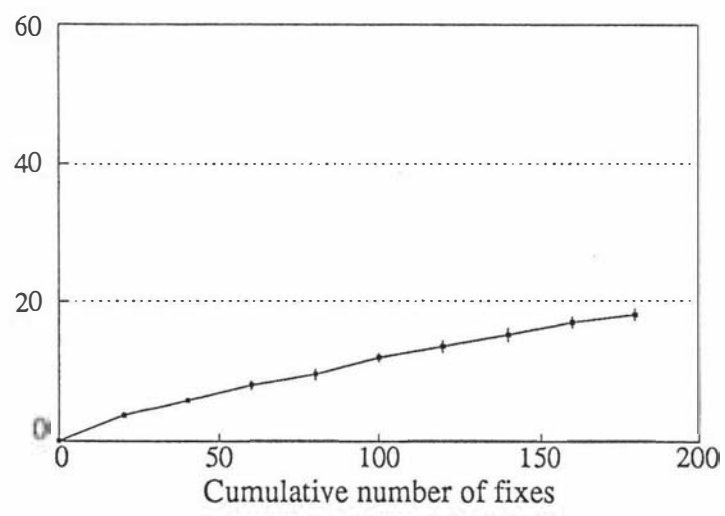


TABLE 3.2: F values calculated by analyses of variance on male vs. female kiwi home range sizes determined for set numbers of accumulated radio fixes by the convex polygon, OBCLO, and grid cell methods.

No. fixes	No. males	No. females	df	F		
				Convex* polygon	OBCLO*	Grid* cell
80	7	11	1,16	0.12	0.15	0.01
100	7	9	1,14	0.44	0.03	0.10
120	6	7	1,11	1.15	0.11	1.15
140	6	6	1,10	0.68	0.21	1.22
160	5	5	1,8	0.20	0.01	0.86
180	5	5	1,8	0.00	0.12	0.00

*All $P > 0.05$

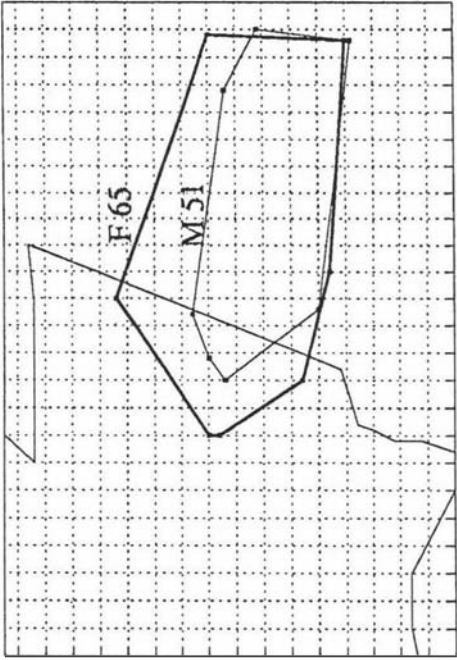
Field worker estimates are also influenced by the number of radio fixes obtained. However, they do not lend themselves to being broken down by observation interval in the same way that other methods do. This is because retrospective field worker estimates, based on limited numbers of earlier observations, could be biased by knowledge of the birds' subsequent movements. For this reason male and female field worker home range size comparisons are based only on the final estimates (Table 3.1). Field worker estimates of male and female kiwi range sizes, based on all data available for each bird, did not differ significantly ($F_{[1,21]} = 0.06$, $P > 0.05$).

Pair range comparisons were complicated by several individuals changing mates, and hence range shape and pattern of use, during the course of this study (Chapter 5). The similarity and degree of overlap in the home ranges of pairs during stable periods was variable (Figure 3.2 (Note: All bird locations are shown on a standard 100 m grid. See Figure 2.1 for a habitat map of the study area based on the same grid system)). One pair (Pair 4) overlapped in less than one third of their combined convex polygon range. The home ranges of some individuals tended to drift and change with time while others remained quite stable (Figure 3.3).

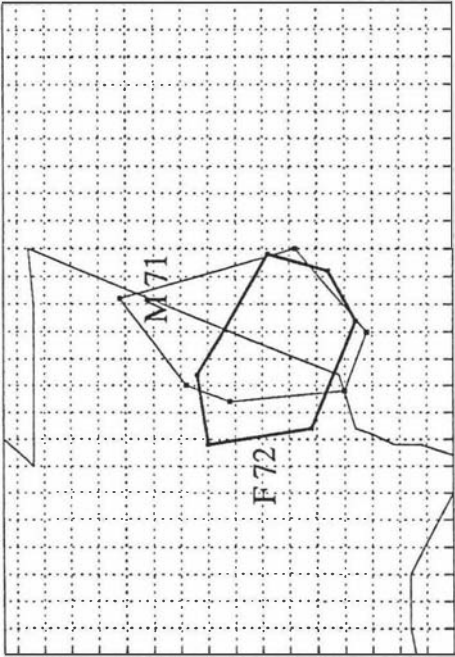
The kiwi varied in their response to being handled. Some tended to flee, either immediately or later that night, from the location where they were caught. Others remained in the vicinity of the release site and showing little outward sign of stress. When birds did flee they usually returned to their previous area of use within 48 hours. In no cases were the most extreme points within the home range obviously attributable to my presence or interference.

FIGURE 3.2: Convex polygon home range comparison of the male and female in four pairs of kiwi at Paerata during periods when their pair bonds were stable. The southern boundary of Paerata Wildlife Management Reserve is shown on each plot. Grid cells = 100 m^2 (1 ha). See Figure 2.1 for a habitat map based on this grid system.

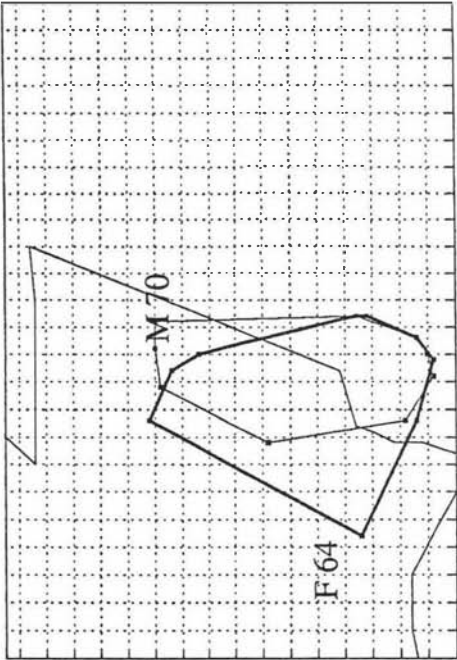
Pair 1



Pair 2



Pair 3



Pair 4

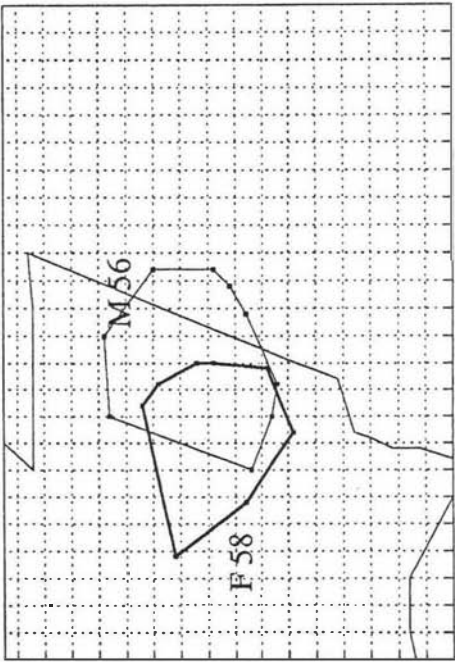
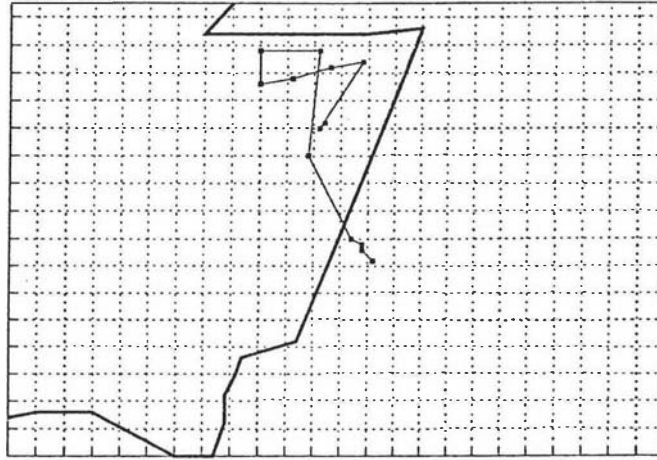
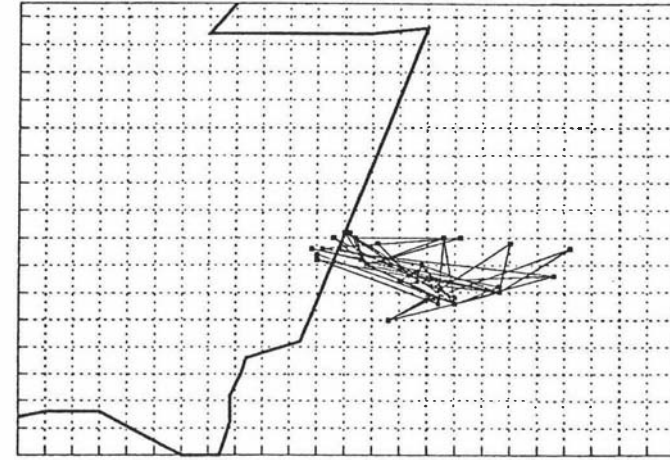


FIGURE 3.3: Home range stability comparison between: a) M51; and b) M over four 6-month intervals between September 1985 and August 1987. Radiofixes for each time period are linked chronologically. The southern boundary of Paerata Wildlife Management Reserve is shown on each plot. Grid cell 100 m^2 (1 ha). See Figure 2.1 for a habitat map based on this grid system.

M 51: Sep 85 - Feb 86

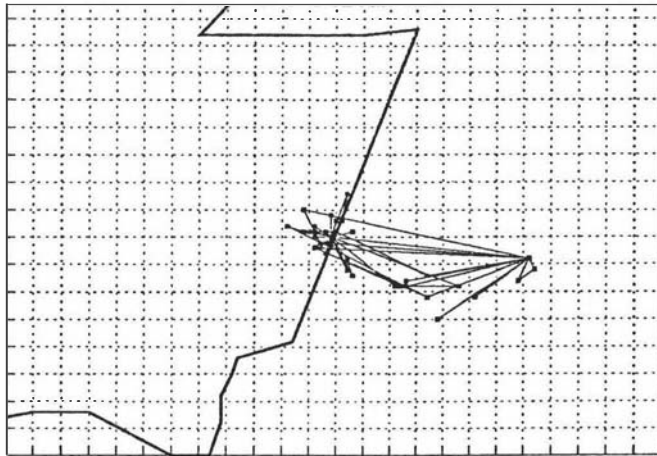


M 51: Mar 86 - Aug 86



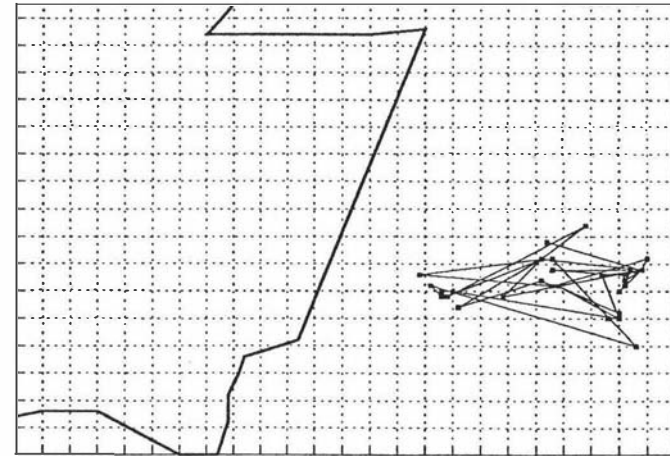
a)

M 51: Sep 86 - Feb 87

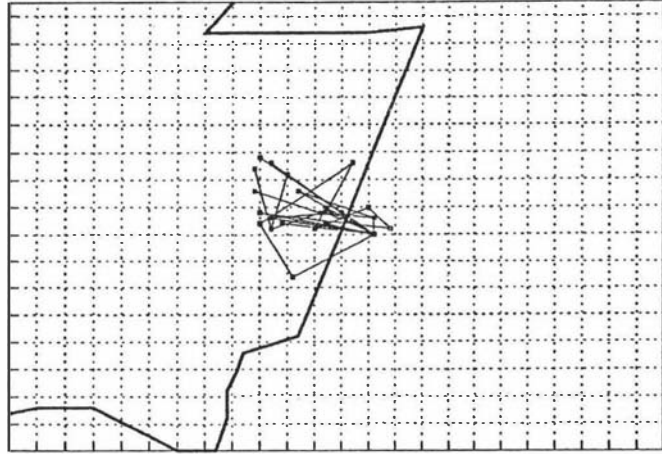


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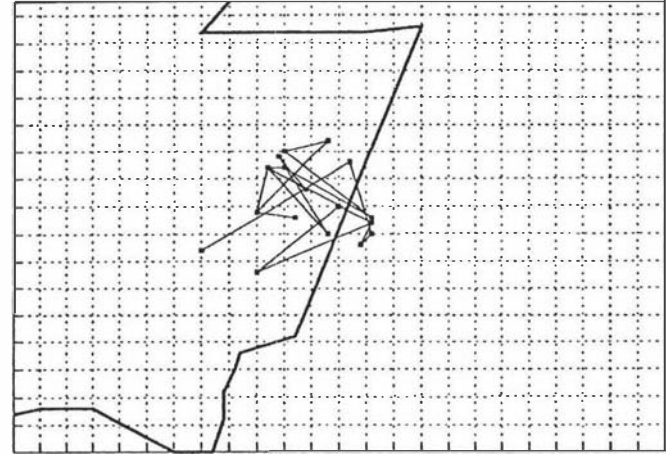
M 51: Mar 87 - Aug 87



M 56: Sep 85 - Feb 86

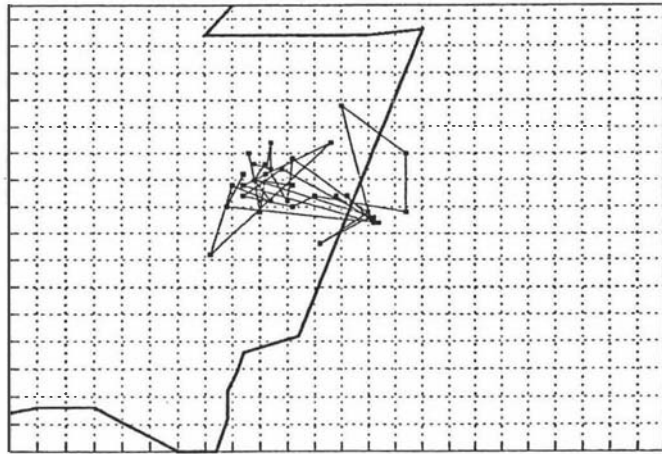


M 56: Mar 86 - Aug 86



b)

M 56: Sep 86 - Feb 87



M 56: Mar 87 - Aug 87

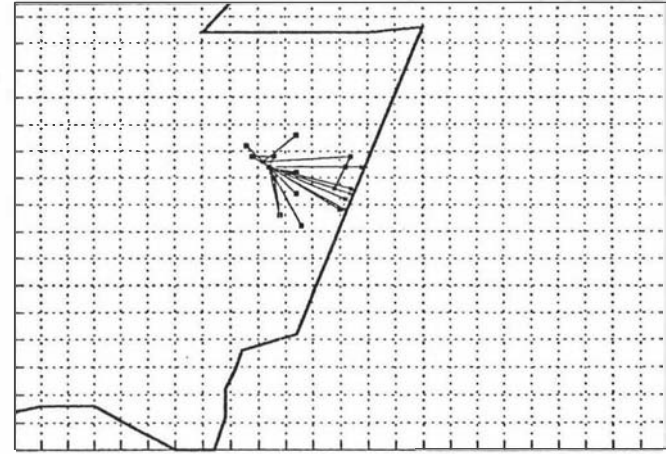


Figure 3.3 continued

Home ranges overlapped enormously. Fifty-two of the 70 1-ha grid squares (74%) within the southern third of Paerata Reserve were used by 4 or more kiwi. One 1-ha grid square was known to have been used by at least 13 kiwi. The extent of home range overlap, and the variability in the shape of these ranges, is indicated in Figure 3.4.

3.3.2 Daytime roost selection

The kiwi were highly variable in the types of roosts they used. In a loglinear analysis of individual bird vs. season vs. roost, removal of the overall interaction term (bird x season x roost) significantly reduced the goodness of fit of the saturated model (bird + season + roost + bird x season + bird x roost + season x roost + bird x season x roost) (19 kiwi, 4 seasons, 4 roost types; Likelihood Ratio Chi Square = 506.86; df = 163; $P < 0.001$). Any sexual differences that may have existed were obscured by the degree of individual variation.

Surface vegetation was the most frequently used roost type (45.6%) followed by burrows (26.1%), natural cavities (24.2%) and hollow logs/tree stumps (4.1%) (n = 2116 comprising 747 records for 9 males and 1369 records for 14 females). Although not significant (loglinear analysis above), burrows tended to be used most in winter and spring, natural cavities most in summer and autumn, and logs and stumps most in spring and summer (Figure 3.5).

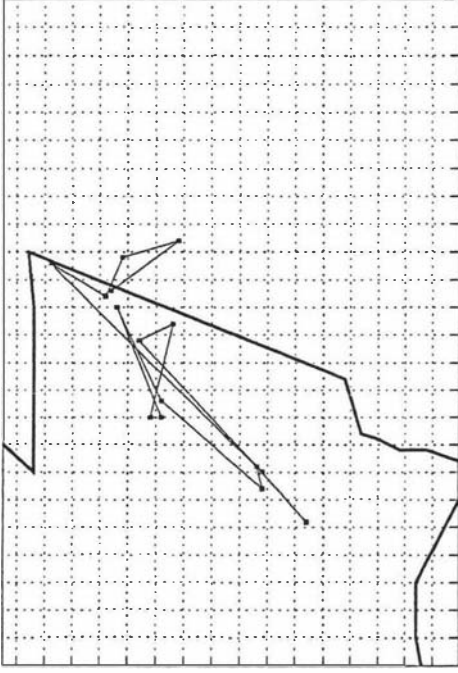
The type of roost kiwi used was significantly influenced by the presence or absence of their mate (Chi square = 137.2; df = 3; $P < 0.001$; Table 3.3) (Note: For this analysis roost counts for pairs roosting together were halved to avoid biasing the result through double counting).

TABLE 3.3: Selection of roosts by kiwi roosting either alone or with their mate. N = number of observations.

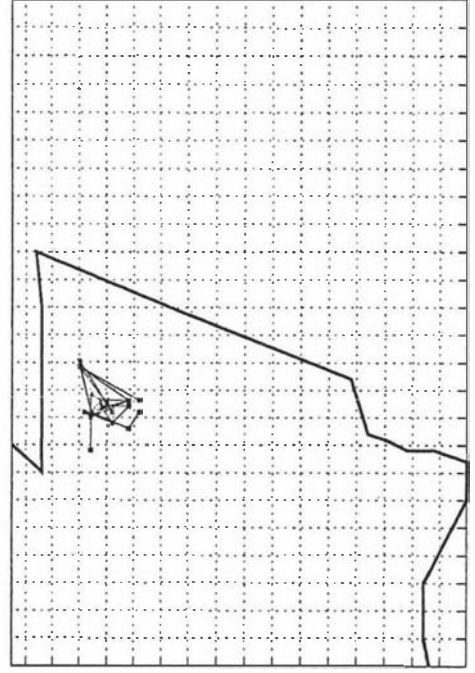
	N	% of observations in			
		Burrow	Natural cavity	Surface vegetation	Log/stump
Alone	1360	21.2	18.7	55.3	4.8
With mate	466	41.2	39.5	17.2	2.1

FIGURE 3.4: Home range and location records for all 32 kiwi caught Paerata. Radio-fixes for each kiwi are linked chronologically. M = male, F female, J = juvenile. The southern boundary of Paerata Wildlife Manageme Reserve is shown on each plot. Grid cells = 100 m² (1 ha). See Figure 2.1 for habitat map based on this grid system.

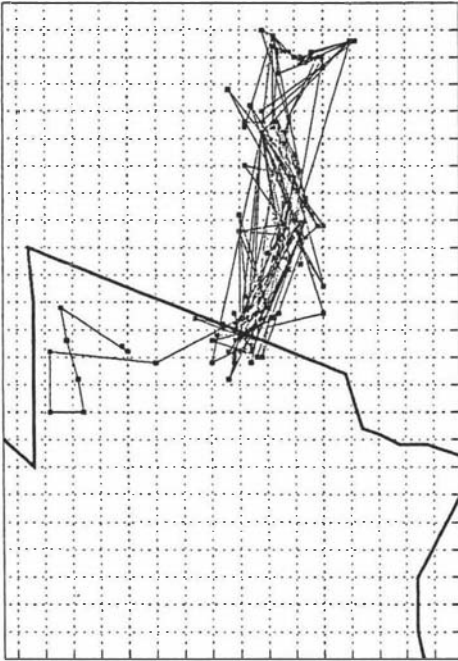
M 55



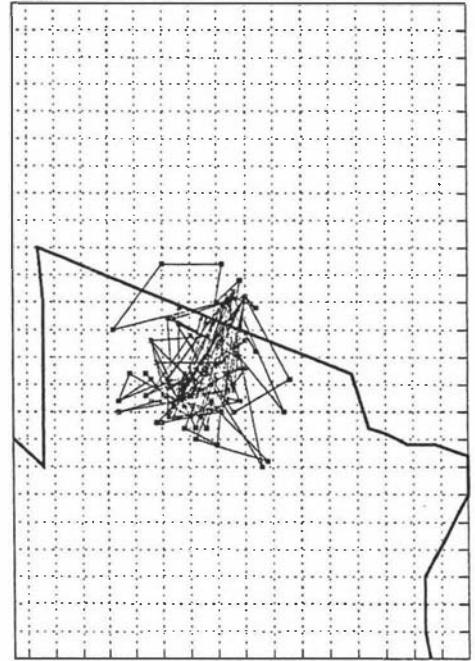
M 57



M 51

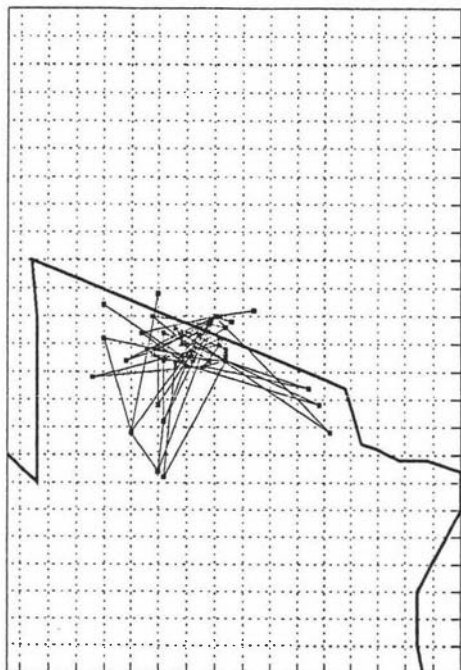


M 56

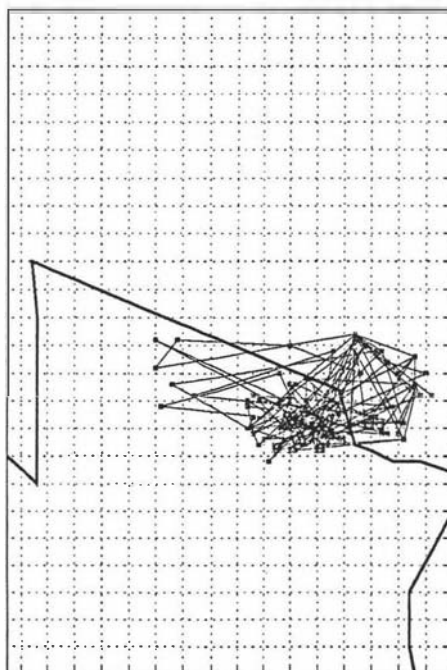


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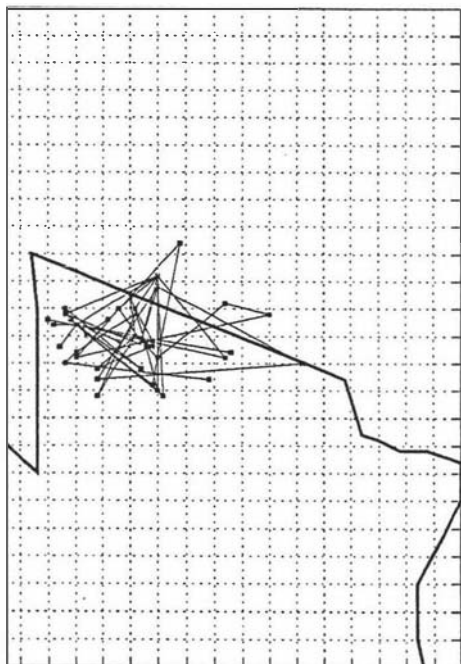
M 66



M 70



M 61



M 67

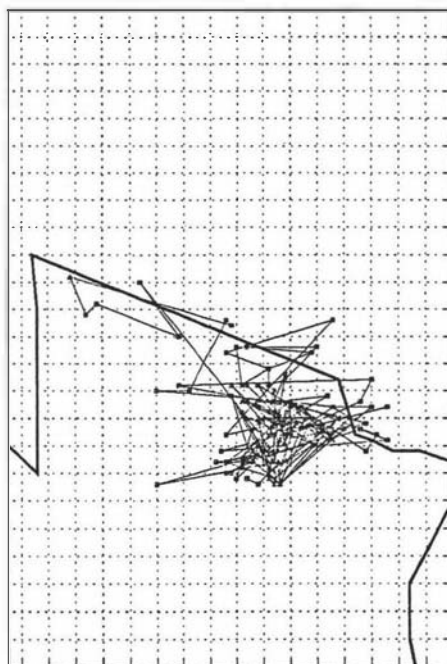
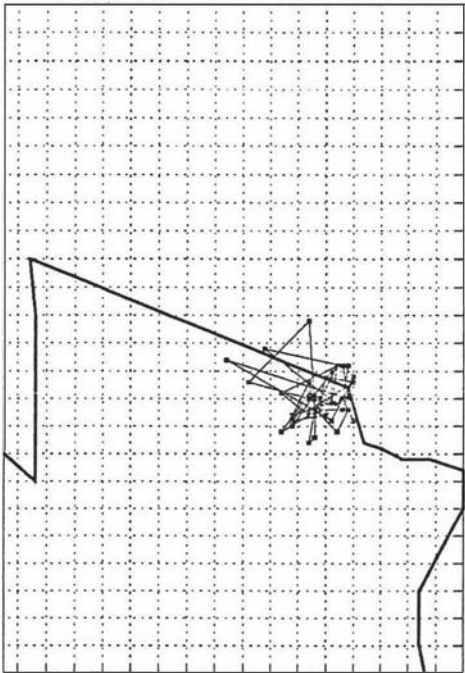
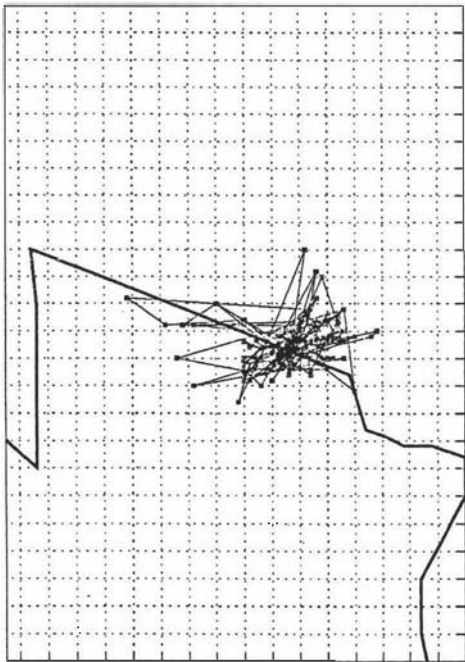


Figure 3.4 continued...

M 74



M 71



M 77 & J 69

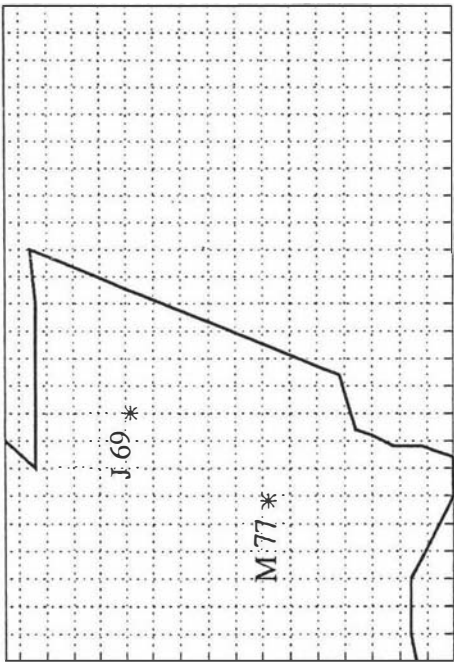
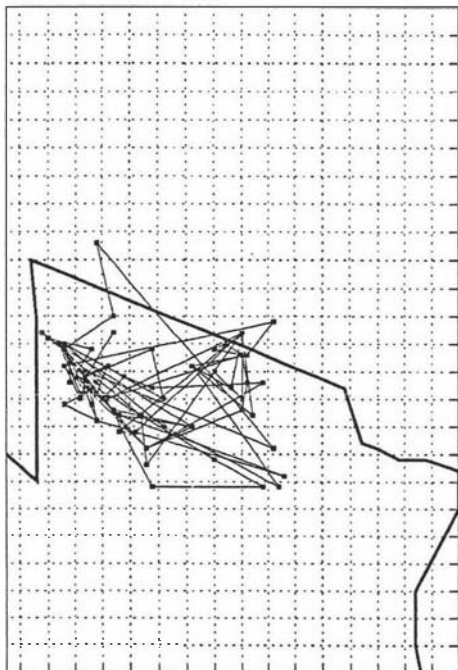
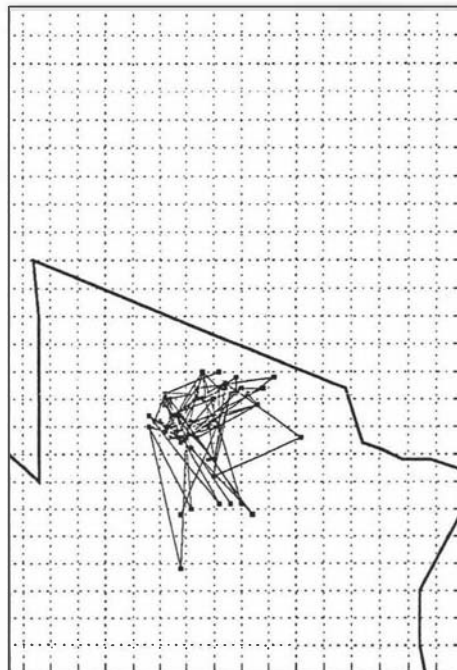


Figure 3.4 continued...

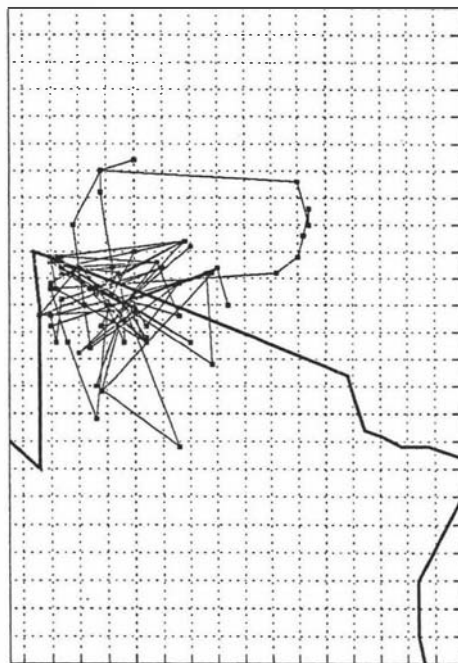
F 53



F 58



F 52



F 54

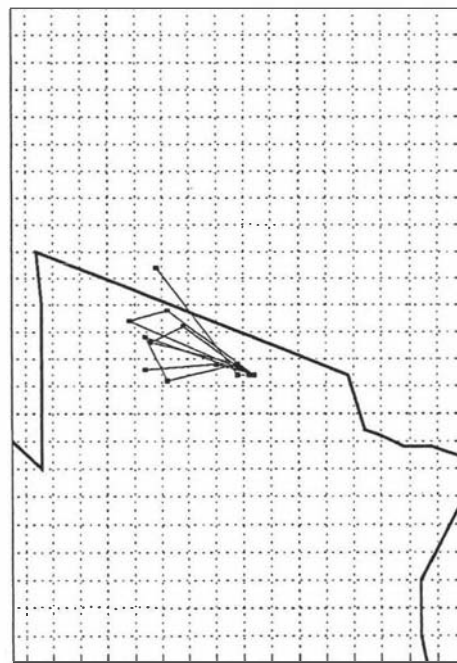
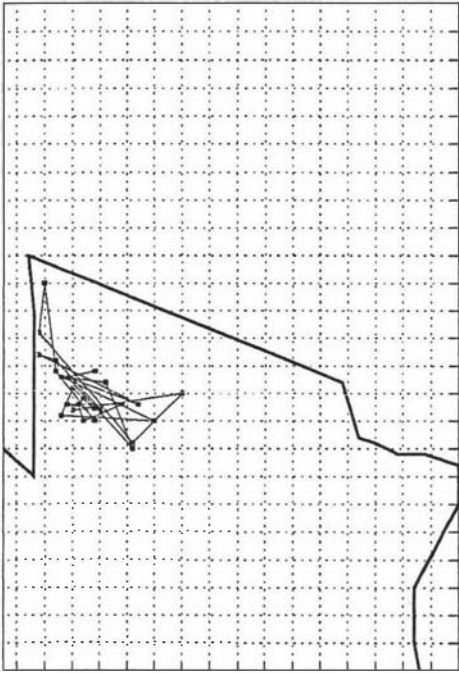
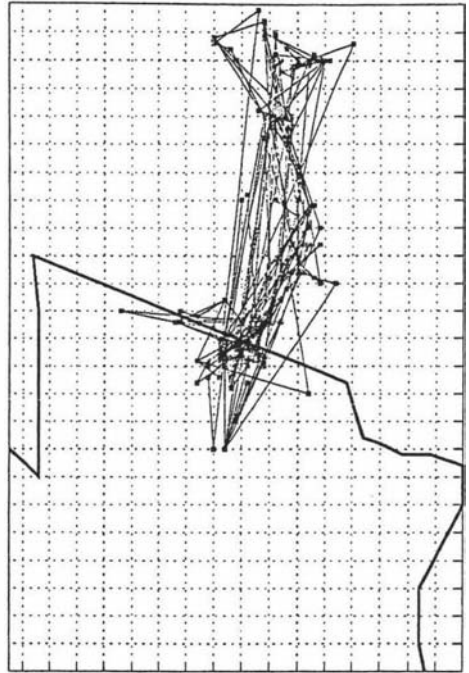


Figure 3.4 continued...

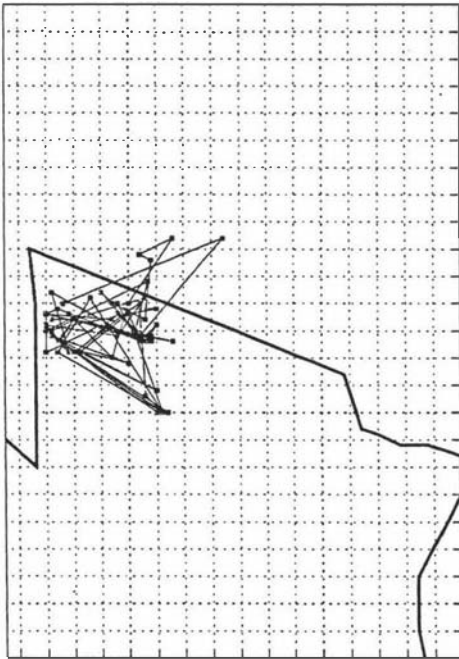
F 62



F 65



F 59



F 64

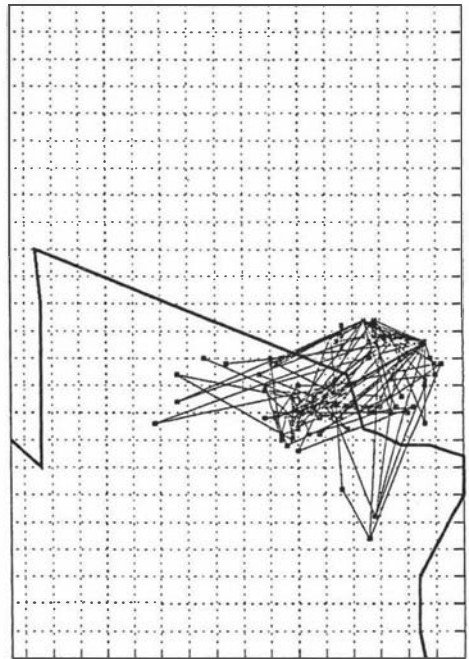
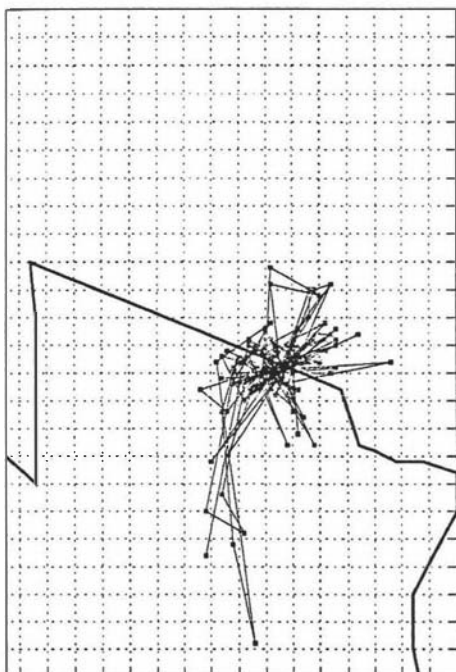
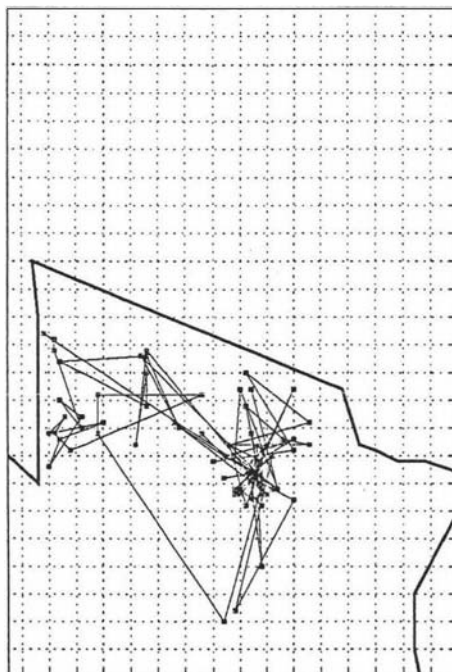


Figure 3.4 continued...

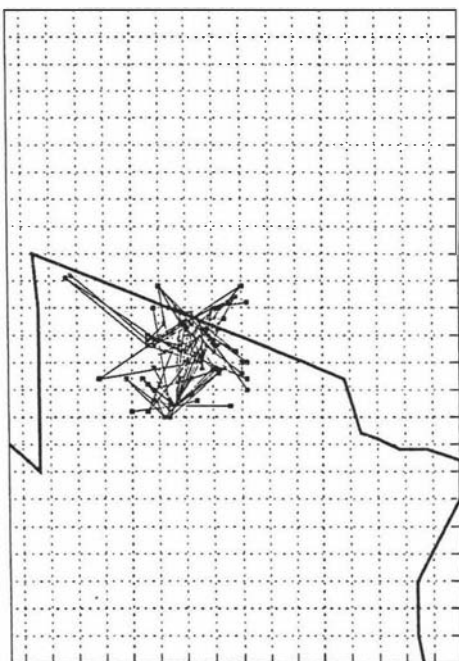
F 72



F 75



F 68



F 73

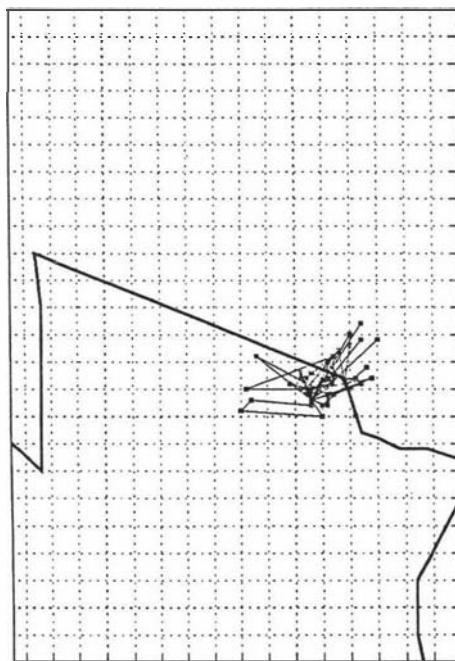
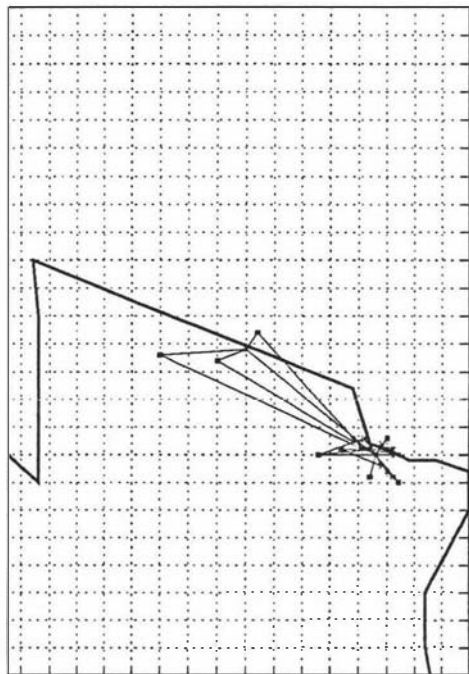
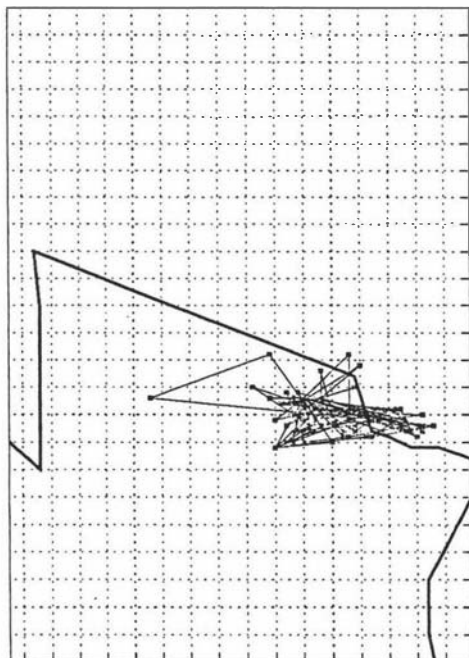


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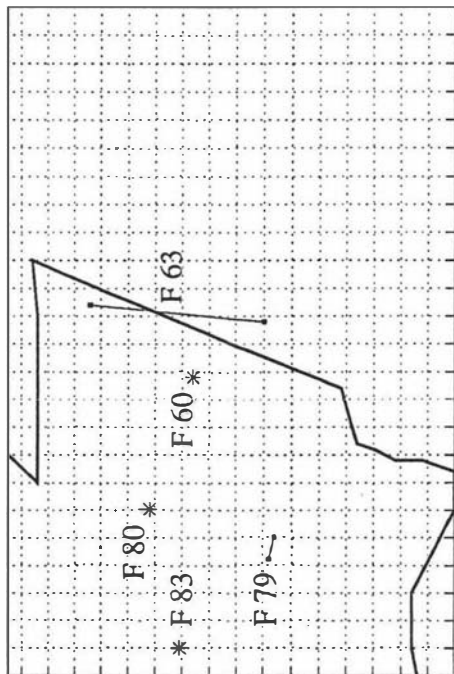
F 78



F 76



Other females



F 82

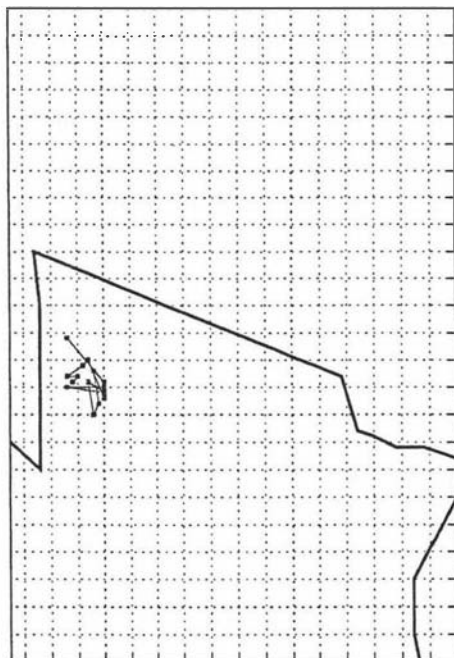


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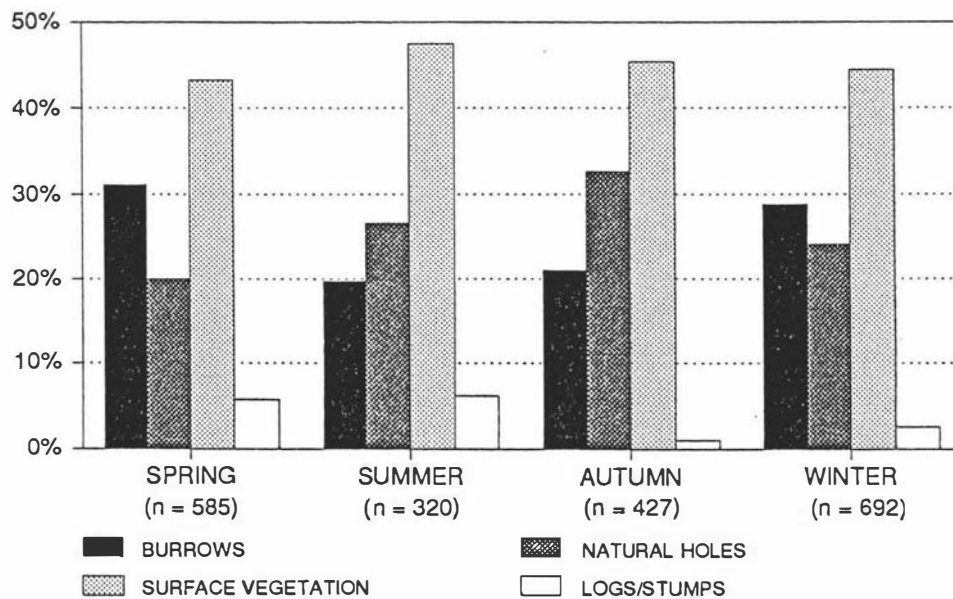


FIGURE 3.5: Seasonal use of different roost types by kiwi at Paerata.

Kiwi spent over 80% of occasions in burrows or natural earth cavities when roosting with their mate. This was over twice the proportion of days spent in these types of roosts when they were alone. Pairs of kiwi roosted together on 22% of days. This increased to over 35% of days during April, May, June and July with the start of breeding (Section 5.2).

The kiwi were variable in their pattern of roost use. One male (M67), located 53 times during a six-month period, used 34 different roosts in this time. He spent no more than three consecutive days in any site. One roost was used seven times, 1 four times, 4 three times, 3 twice, and 24 once only. This contrasts with one female (F68) which was recorded in only five different roosts during a six-month period when she was located 40 times. She used one roost 34 times, 2 twice, and 2 once only. She was recorded in her preferred roost on 20 consecutive occasions spanning three months, and probably used this natural cavity every day during that period. The roost was a 4-m long natural washout in a dry stream bed. Another pair used a natural cavity that extended for over 5 m underground. Some of the burrows excavated by kiwi were also quite long; one extending for over 2.5 m. Many of these burrows and natural cavities may have been used and enlarged by successive generations of kiwi, and were the type of roost used most intensively. However, some surface vegetation roosts were also used intensively. Over one 10-week period one male (M66) was recorded 22 times, out of 31 observations, roosting in surface vegetation. This roost was under a compacted pile of totara slash just outside the reserve boundary. Several other kiwi frequently roosted under similar small piles of cut scrub that had been pushed into ditches on the farmland adjacent to the reserve.

Almost all intensively used roosts had several features in common. They provided good cover from the elements, sheltered the bird in the dark or semi-dark during the day, and made the kiwi inaccessible to stock, to predators such as dogs and possibly cats, and to kiwi researchers! There was, however, no evidence to suggest that the use of these roosts increased with my handling of the birds. In contrast to these intensively used roosts, one-day-only shelters tended to be under more sparse cover, and occasionally kiwi were completely visible at the base of a tree or under scattered fern fronds.

Some roost sites were used sequentially by several kiwi. Sixteen roosts were known to have been used by 4 or more individuals (Table 3.4).

TABLE 3.4: The numbers of different roost types known to have been used by four or more kiwi.

	Roost type		
	Surface vegetation	Burrow	Natural cavity
Used by 4 kiwi	4	2	3
Used by 5 kiwi	2	0	2
Used by 6 kiwi	1	1	1

Most kiwi did not reuse roosts from which they had been removed for handling until at least three months later. Kiwi tended to return more quickly to roosts from which they were captured as they emerged at night, as opposed to roosts from which they were removed during the day. One female (F68) was caught as she emerged from the same roost on three different nights. On each occasion she reused the roost within two days.

3.3.3 Night-time habitat use

Kiwi were selective in their use of habitat while active at night. All 12 kiwi for which sufficiently large cell counts were available for analysis showed significant differences between their observed and expected use of habitat (Table 3.5). Expected use was determined by the relative proportions of each habitat type within their home range. Thick bush and pasture were both under utilised, while open bush, and bush edges (a 10-m wide strip running 5 m either side of the true bush edge) were used more than expected from their relative abundance. The average habitat composition of radio-tagged kiwi and the proportions of times they were recorded in each habitat type are summarised in Table 3.6.

TABLE 3.6: The average composition of kiwi ranges in Paerata compared with the average amount of time the kiwi spent in these habitats at night (N = 1022 comprising 439 observations for 8 males and 583 observations for 11 females).

	Thick bush	Open bush	Long grass/ swamp	Pasture	Bush edge
% Available	56.9	12.0	3.4	17.0	10.7
% Use	47.0	24.7	5.5	9.6	13.2

TABLE 3.5: Observed night-time use of habitat compared with the expected use determined from the habitat composition of each kiwi's home range. Chi square (df = 3) and P values are listed. As the expected values for long grass/swamp use were all low, these values were combined with those for open bush for analysis. M = male; F = female.

Kiwi	No. records	Observed & (Expected) use of habitat					χ^2	P ^a
		Thick bush	Open bush	Long grass/swamp	Pasture	Bush edge		
M51	97	35 (28.8)	31 (19.2)	14 (3.2)	8 (33.3)	9 (12.5)	44.34	***
M56	47	30 (32.5)	10 (2.8)	2 (1.9)	0 (4.7)	5 (5.1)	13.88 ^b	***
M67	72	37 (52.8)	11 (1.0)	0 (2.7)	14 (8.1)	10 (10.0)	24.34	***
M70	91	49 (45.2)	20 (13.0)	5 (2.3)	5 (20.6)	12 (9.9)	18.73	***
M71	85	28 (42.3)	31 (15.3)	2 (3.2)	7 (14.6)	17 (9.6)	25.86	***
F52	32	15 (15.0)	11 (5.8)	3 (1.0)	1 (5.7)	2 (4.5)	12.89	*
F64	67	19 (34.4)	25 (6.0)	3 (2.3)	7 (18.1)	13 (6.2)	67.92	***
F65	117	40 (28.9)	39 (25.6)	6 (3.5)	13 (44.3)	19 (14.6)	36.36	***
F68	59	32 (43.5)	7 (4.4)	2 (1.2)	3 (4.0)	15 (5.9)	19.39	***
F72	90	33 (41.9)	30 (19.1)	4 (2.2)	10 (18.0)	13 (8.8)	15.02	**
F75	41	19 (30.3)	14 (3.4)	1 (1.8)	7 (2.3)	0 (3.2)	23.09 ^b	***
F76	52	21 (34.3)	10 (3.3)	1 (1.4)	11 (7.3)	9 (5.7)	17.39	***

^a * P = 0.005; ** P = 0.002; *** P < 0.001

^b For these analyses pasture and bush edge counts were also combined (df = 2)

Loglinear analysis of individual and seasonal variation in habitat use showed a great deal of individual variability, as had the analysis for roost use. Removal of the overall interaction term (bird x season x habitat) significantly reduced the goodness of fit of the saturated model (bird + season + habitat + bird x season + bird x habitat + season x habitat + bird x season x habitat) (19 kiwi, 4 seasons, 5 habitat types; Likelihood Ratio Chi square = 288.35; df = 218; $P = 0.001$). The sexes were analysed separately and remained highly variable. Removal of the overall interaction term (bird x season x habitat) significantly reduced the goodness of fit of the saturated model for both males (8 birds, 4 seasons, 5 habitats; Likelihood Ratio Chi square = 114.27; df = 84; $P = 0.016$) and females (11 birds, 4 seasons, 5 habitats; Likelihood Ratio Chi square = 163.69; df = 120; $P = 0.005$). Analysing the sexes independently removes intersexual variation, but this failed to alter the outcome of the analysis. We can then assume that the observed individual variability was not related primarily to sexual differences in habitat preference.

Although kiwi varied in their use of habitat, they tended to be recorded in thick bush more in spring and summer than autumn and winter, and in open bush least in summer (Figure 3.6). They also tended to be recorded in open pasture more in summer and autumn than in winter or spring.

Some kiwi often commuted 3-400 m between where they roosted and where they spent most of the night feeding. One pair (M51 and F65), spent a lot of time in bush remnants outside the reserve and often travelled over 1 km during the first hour of darkness, and then frequently returned to their previous day's roost later that night.

3.4 DISCUSSION

3.4.1 Range size and overlap

The home range sizes of brown kiwi in Paerata were remarkably similar to those in Hawkes Bay (McLennan *et al.* 1987). Paerata home range sizes did not differ significantly from those in Hawkes Bay when determined by either the field worker method ($F_{[1,24]} = 0.87$; $P > 0.05$), or the convex polygon method based on the first 80 radio fixes for each bird ($F_{[1,22]} = 0.07$; $P > 0.05$). The Paerata kiwi grid cell estimate for 80 fixes per bird was, however, significantly less than the same estimate for Hawkes Bay kiwi ($F_{[1,22]} = 4.78$; $P < 0.05$). The difference here may

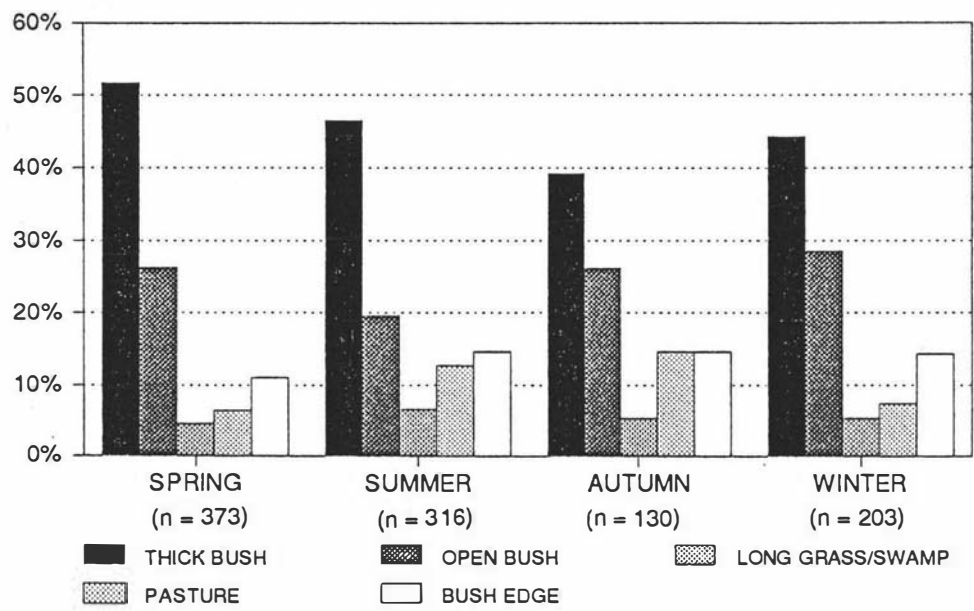


FIGURE 3.6: Seasonal use of different habitat types by kiwi at Paerata.

reflect the different patterns of roost use between these populations. Paerata kiwi reuse their roosts far more intensively than kiwi in Hawkes Bay. This would result in a less rapid increase in the number of grid cells recorded for Paerata kiwi than Hawkes Bay kiwi, producing a corresponding difference in their estimated grid cell range for a set number of radio fixes.

The field worker estimates of about 30 ha per bird in both Paerata and Hawkes Bay contrast with home range estimates of about 5 ha per adult pair reported for brown kiwi in Waitangi State Forest (Colbourne & Kleinpaste 1983). That study relied on a very different method of data collection. Kiwi were caught, banded, and individually colour coded with reflective markers. On subsequent nights they were searched for by torch light. The 84 kiwi caught and banded in Waitangi were resighted on average less than 4 times each. The home range estimate of 5 ha per pair was based on kiwi "recaptured 15 times or more" (Colbourne & Kleinpaste 1983). This was extremely few observations compared with the numbers obtained by radio telemetric means in Paerata and Hawkes Bay. All range estimate methods are sensitive to the number of fixes obtained (Figure 3.1). Therefore, Colbourne & Kleinpaste (1983) may have underestimated the home range size of kiwi in Waitangi State Forest. This possibility is supported by the findings of a recent radio telemetric study in this same forest (M. Taborsky pers. comm.).

The extent of kiwi home range overlap observed in Paerata exceeds any overlap previously documented, and is discussed further in the section on spacing behaviour (Section 3.4.4).

3.4.2 Daytime roost selection

Paerata kiwi reused roost sites far more often than Hawkes Bay kiwi (McLennan *et al.* 1987). They also showed a marked dichotomy in the types of roosts used when alone or with their mate. When roosting with their mate they preferred those sites offering the greatest shelter and security. These were also the roosts for which there was greatest competition, as indicated by the numbers of different kiwi that roosted in them. The extent of competition for some roosts suggests that quality roosts may have been at a premium in Paerata. If so, the defence of prime sites may explain why some kiwi intensively used some of their roosts. The different patterns of roost use for solitary birds and those with a mate suggests that quality roosts may be important to pair bonding (Section 5.4.5).

3.4.3 Night-time habitat use

Paerata kiwi were selective in their use of habitat at night. Kiwi have previously been recorded feeding on pasture invertebrates (Watt 1971) and on numerous occasions were observed feeding in pasture around Paerata. However, they spent much less time in this open environment than expected from the amount of pasture included in many of their home ranges. In contrast, open bush and bush edges were used significantly more than expected from the relative abundance of these habitats.

Kiwi are extremely difficult to observe for extended periods and so it was not possible to determine absolutely in which of these habitat types kiwi most often fed. However, when kiwi were observed in open bush or at bush edges they were frequently seen feeding. Paerata has a history of being grazed by cattle. Comparative invertebrate counts in the different habitat types were not made, but if the preference kiwi showed for open bush and bush edges was food-related the cattle indirectly may have been beneficial to the kiwi through maintaining these habitats. The advantages and disadvantages of having cattle in kiwi reserves deserves further investigation.

The tendency for Paerata kiwi to use open bush slightly less and long grass and swamp slightly more in summer than winter supports Colbourne & Kleinpaste's (1983) assertion that during dry periods kiwi tend to feed in damp areas where the ground is more penetrable and soil invertebrates more available.

3.4.4 Spacing behaviour

Previous studies on brown kiwi in Waitangi State Forest (Colbourne & Kleinpaste 1983) and Hawkes Bay (McLennan *et al.* 1987), as well as on little spotted kiwi on Kapiti Island (J. Jolly pers. comm.) have indicated that kiwi are territorial (*sensu* Mace *et al.* 1983, i.e. they maintain non-overlapping areas from which other individuals are actively excluded). Colbourne & Kleinpaste (1983) observed fighting and birds calling repeatedly at each other in Waitangi State Forest. This type of behaviour was not obvious in either Paerata or Hawkes Bay (McLennan *et al.* 1987). Bouts of calling were frequently heard in Paerata but it was not clear to whom the calls were directed. Breitwisch & Whiteside (1987) have recently shown that mockingbird song, traditionally interpreted as a territorial warning from one

male to another, is predominantly directed at actual or potential mates (also see Lewin 1987). Eriksson & Wallin (1986) have similarly demonstrated that in some flycatchers male song is largely a mate attractant. Colbourne & Kleinpaste (1984) reported that female kiwi frequently called in response to their mate's call. In Hawkes Bay an aggressive response could be readily induced in kiwi by simulating kiwi calls on a whistle, or by playing tape recorded calls. Resident kiwi would frequently respond to these calls by calling themselves and then running, often noisily, towards the source of the call (pers. obs.). This response was extremely useful in catching kiwi in Hawkes Bay, but failed almost completely in Paerata. When simulated or recorded calls were played near radio-tagged kiwi in Paerata the resident kiwi either remained motionless or fled, but (with one exception) never approached. This hide or flee response implies an aggressive component to the call, but without further study it is not possible to quantify how calls contribute to territory defence and pair bonding.

The relationship between optimal territory size, food density and intruder pressure is complex (Schoener 1983). Colbourne & Kleinpaste (1983) and McLennan *et al.* (1987) equated home range with territory, but many other possibilities exist (Mace *et al.* 1983; Kaufmann 1983). Although the home range sizes of Paerata kiwi were comparable with those in Hawkes Bay, the population density was nearly 10 times as great. The resulting overlap in ranges prohibits the equating of home range and territory for the Paerata kiwi. Intruder pressure in Paerata may have been so great as to render uneconomic the defence of a complete home range. If Paerata kiwi were actively defending areas, these 'territories' must have been far more restricted in time and space than was apparent in Hawkes Bay.

The density and distribution of kiwi in the Paerata area must have been affected by the local history of land clearance and habitat modification. Land clearance can lead to species crowding into remaining patches of bush (Lovejoy *et al.* 1986), but whether this accounts for the observed density of kiwi in Paerata is uncertain. Whatever the proximate cause of Paerata's high density of kiwi, similarly high densities may once have been widespread. C. O'Donnell (reported in McLennan *et al.* 1987) recently found that brown kiwi on Stewart Island also occupy overlapping ranges, with one 10-ha patch of kanuka being used by at least 23 different kiwi. And Buller (1888) describes kiwi hunts last century in which "a hundred or more" were caught with the aid of a dog in a single night. Buller (1888) believed kiwi to be gregarious, going together "in companies of six to twelve". There is no evidence now of such groups, but even allowing for exaggeration and

misinterpretation, kiwi were formerly present in very high densities compared with those observed now.

There is growing evidence that the North Island brown kiwi population is in decline (McLennan 1988). To reverse the trend we need to stop further destruction of kiwi habitat and to identify the other factors causing this population decline. We also need to understand why the density of kiwi in Northland forests is so much greater than that in other parts of the North Island.

DISPERSAL BETWEEN BUSH REMNANTS

4.1 INTRODUCTION

Large-scale land clearance during the past century has greatly reduced the distribution of many bush dwelling members of the New Zealand avifauna, including the North Island brown kiwi. Only three enclaves of the brown kiwi remain in the North Island. These are in Northland; Taranaki-King Country; and Urewera-Northern Hawkes Bay (Bull *et al.* 1985). Many of the surviving birds are now restricted to small islands of bush and scrub separated by large tracts of pasture. McLennan *et al.* (1987) expressed grave concern about the inadequacies in the physical size, and hence the carrying capacity, of the indigenous forest reserves in Hawkes Bay. Although brown kiwi in Northland can reach population densities 10 times those reported in Hawkes Bay (Section 3.4.4), the small size of many of the remaining North Island forests containing kiwi should be of general concern.

Habitat fragmentation has two components, both of which can cause extinctions: first, absolute reduction in habitat area (which primarily affects population sizes and hence extinction rates); and second, dissection of the remaining area into separated fragments (which primarily affects dispersal and hence immigration rates) (Wilcove *et al.* 1986). Many of New Zealand's endemic species, including brown kiwi, have large area requirements (East & Williams 1984). Unfortunately, the opportunity to create large new reserves has all but passed, and we need now to develop ways of enhancing and improving what is left.

If management of the fragmented populations of brown kiwi is to be effective, we need to know more about how the pattern of vegetation affects the movements of kiwi between bush remnants. In particular, we require data on how far kiwi will travel over open pasture between patches, and on the design and potential effectiveness of vegetated corridors linking patches of kiwi habitat. We also need information on land use practices that will allow kiwi to live, at least marginally, in land surrounding reserves. This will help provide buffer zones and enhance the carrying capacities of existing reserves.

Home range data obtained from radio-tagged kiwi in Paerata Wildlife Management Reserve are used here to investigate management strategies and reserve design for kiwi.

4.2 METHODS

For details of the study site, number of kiwi captured and radio tracking techniques see Sections 2.1 and 2.2.

Where data are available the maximum distance traversed between bush remnants by a given kiwi is determined from the known route the kiwi took. When a kiwi was known to use a bush remnant on farmland adjacent to the reserve, but the actual route taken by the bird was not observed, the estimate was calculated to be the minimum distance between the bush remnant and the nearest bush within the reserve. Similarly, when the exact movements of a kiwi were not known, and a series of bush "stepping stones" were available to travel between a visited remnant and the reserve, I assumed the kiwi took the shortest available route between these.

4.3 RESULTS

The kiwi tracked in this study were fairly evenly distributed along the 1200 m southern boundary of Paerata Reserve, and occupied about one-third of the reserve area. Numerous bush remnants of at least 0.1 ha were scattered over the farmland within 1 km of the southern fence line of Paerata Reserve (Figure 2.1). Twenty-three of these remnants were considered potentially accessible to kiwi from the reserve; that is, they were not isolated by large streams or rivers, or any other obvious physical barrier other than pasture.

4.3.1 Bush remnant use

Paerata kiwi made extensive use of bush remnants on farmland adjacent to the reserve. Of the 23 birds intensively tracked only four were never recorded outside the reserve. One pair spent 83% of their time over two years in bush remnants outside the reserve. This pair occasionally travelled up to 1200 m from the reserve by moving through three intermediate bush remnants to reach a fourth. Another pair regularly moved up to 350 m from the reserve in a similar way. The other 15 birds travelled between 50 - 280 m from the reserve.

4.3.2 Inter-remnant distance

Two of the 23 bush remnants of at least 0.1 ha within 1 km of the southern boundary of Paerata were contiguous with the reserve. The other remnants were separated from the reserve, and each other, by up to 550 m of pasture. The most remote remnant included in this study was 2.7 ha in area and lay 750 m south east of the reserve.

Figure 4.1 shows the maximum width of pasture each kiwi crossed when moving between remnants. This figure is based on the known, or most probable, route each kiwi took between remnants. This route was not always the shortest available. Kiwi often covered quickly the open ground between bush remnants. For instance, the pair that walked the greatest distance between remnants often covered the 330 m in less than 10 minutes.

Although 19 of the 23 kiwi tracked (83%) occasionally used bush outside the reserve, only seven kiwi (30%) ever crossed more than 120 m of grassland (Figure 4.1). One pair regularly walked 330 m between two bush remnants but they may have been encouraged to do so by the local topography. When moving between these remnants this pair invariably walked down a steep-sided swampy gully. This gully was in the middle of an open paddock but there were several scattered patches of rush and blackberry which may have provided the kiwi with some cover. Another female, however, was once observed 280 m from the nearest bush in completely open pasture. This observation is not included in Figure 4.1 because the female walked out of, and back to, the same bush patch. Excursions of this type should be expected if kiwi actively seek out new areas of bush.

4.3.3 Remnant size and vegetation type

The area of each of the bush remnants and their separation from other bush areas that could serve as "stepping stones" are shown in Figure 4.2. All remnants isolated by less than 100 m of pasture, regardless of size, were used by kiwi. However, only three of the nine remnants separated by more than 100 m of pasture were used, and then only by a single pair.

The bush remnants near Paerata Reserve were dominated by manuka and kanuka scrub, Hall's totara of various ages, and tree ferns. Two remnants contained small raupo swamps. These remnants were not fenced but most contained some dense scrub cover despite moderate to heavy grazing by stock. In Northland totara

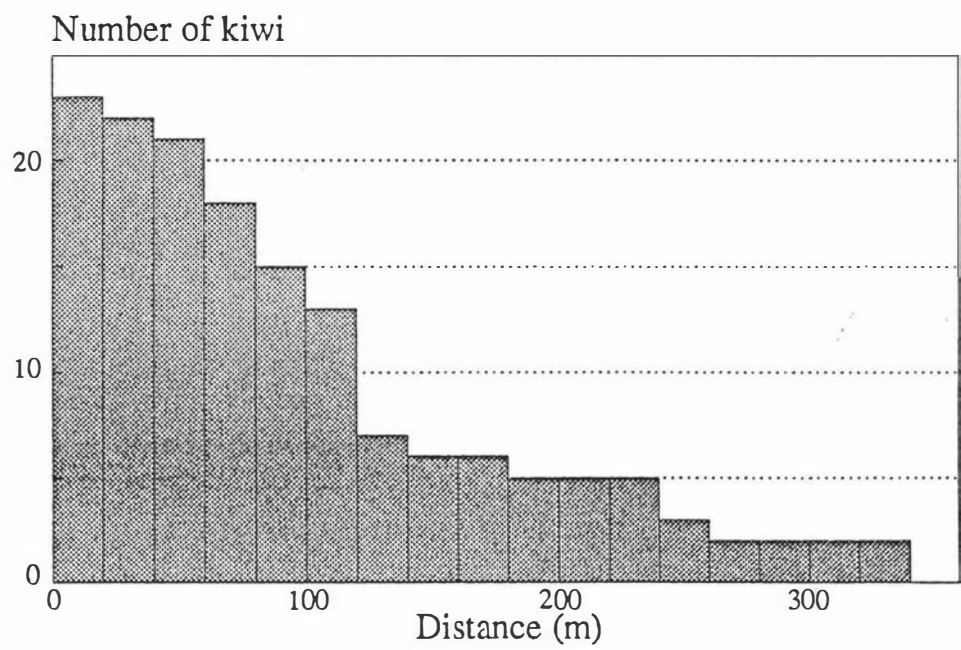


FIGURE 4.1: The maximum distance (metres) between bush remnants travelled by 23 kiwi at Paerata.

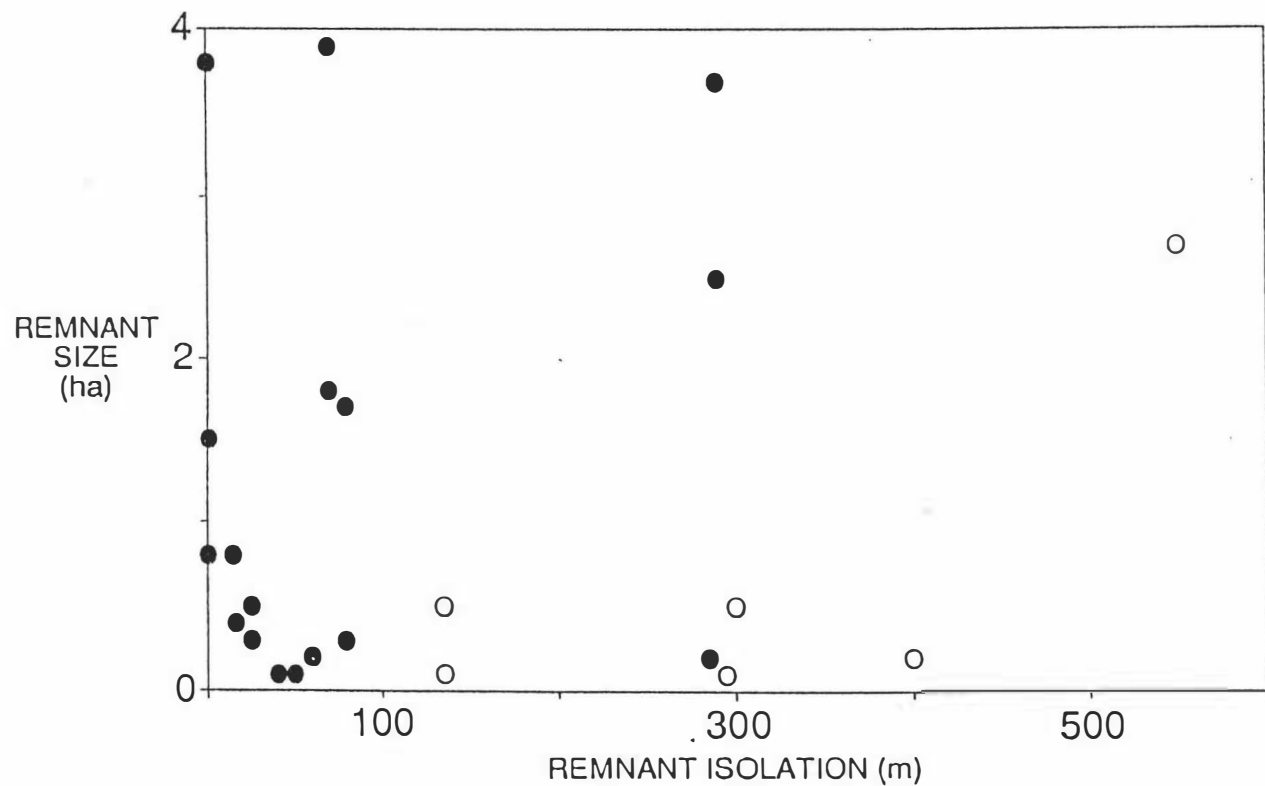


FIGURE 4.2: The size and separation of bush remnants from other bush remnants that could serve as "stepping stones" at the southern end of Paerata Wildlife Management Reserve, and their use by kiwi.

● used by kiwi; ○ not used by kiwi.

seems to be particularly resilient to grazing, and can often regenerate under the combined onslaught of cattle, sheep and goats. Kiwi are adaptable birds, and some of the remnants used consisted of little more than large patches of toetoe (*Cortaderia* sp.) and bracken (*Pteridium aquilinum*). A lot of totara slash lay on the ground near many of the bush remnants, and this dead vegetation was used by kiwi for daytime shelter (Section 3.3.2).

4.4 DISCUSSION

4.4.1 Inter-remnant distance

Paerata kiwi made extensive use of remnant patches of bush within 100 m of the reserve, and occasionally crossed up to 330 m when moving between remnants. Observations of how far kiwi will move away from bush cover in other areas are provided by the study of brown kiwi in Hawkes Bay (McLennan *et al.* 1987). There two kiwi were observed at least 200 m from the nearest bush. These kiwi had moved onto land that had recently been cleared, burnt, and planted in pines. Although this land was not as clear and open as developed pasture, it was considerably more open than the bush with which kiwi are generally associated.

From these observations it seems reasonable to conclude that a large proportion of kiwi (perhaps > 50%) will travel up to 100 m across open pasture between remnants, but few (perhaps < 10%) will cross distances of up to 300 m or more. Caution must be exercised in treating these findings as anything more than guidelines. How far kiwi would ultimately walk in open pasture could be influenced by their need to do so, which in turn could depend on the quality and quantity of resources available in their current habitat. Kiwi from healthy, expanding populations, or from artificially condensed ones as might result from land clearance (Lovejoy *et al.* 1986), could be subject to greater resource competition than low density or declining populations. Therefore they may also show a greater tendency to migrate or disperse away from their parental habitat. The high density of kiwi in Paerata may therefore mean that the observed distances of dispersal of these kiwi may be near the upper limit of what could be expected to occur elsewhere.

4.4.2 Remnant size and vegetation type

The theory of island biogeography (MacArthur & Wilson 1967) predicts that larger islands have a greater chance of being found by migrating species than small islands. The same principles can apply to bush birds migrating between habitat remnants in a sea of cleared land (Frankel & Soulé 1981). Although few remnants at Paerata were separated by more than 100 m of pasture, with one exception, the more remote remnants used by kiwi were relatively large. The relationship between remnant size and the likelihood of kiwi using them requires further investigation.

The remnants used by kiwi in Paerata comprised several vegetation types. The actual vegetation may be of minimal importance to kiwi so long as two vital requirements are met: i) the area has a rich surface and soil invertebrate fauna; ii) the area provides dense cover for shelter and roost sites. Kiwi are abundant in several exotic *Pinus radiata* forests in Northland (Colbourne & Kleinpaste 1983; Reid 1983). Kiwi are much less common in pine forests further south, but the possibility clearly exists for kiwi reserves to be enhanced and buffered with both native and exotic plantings.

4.4.3 Reserve design and enhancement

In designing a reserve for a target species the aim is to reduce the risk of local extinction of that species. Good reserve design does not remove the need for ongoing monitoring and management, but it can reduce the intensity of management required (Gilbert 1980). How large a reserve needs to be depends on the specific habitat requirements and "minimum viable population" size of each species (Franklin 1980; Soulé 1980; Frankel & Soulé 1981; Shaffer 1981, 1983; Gilpin & Soulé 1986; Soulé & Simberloff 1986). Frankel & Soulé (1981) calculated that most populations need to contain 500 - 1000 breeding individuals to have long-term viability. McLennan *et al.* (1987) used this as a guideline for determining the size requirements for brown kiwi reserves in Hawkes Bay. They estimated that reserves in that part of the North Island need to be between 7500 to 15000 ha each to meet this requirement. Although some kiwi populations may reach densities nearly 10 times higher than those found in Hawkes Bay, they still require reserves of considerable size (750 to 1500 ha). The creation of such large reserves is no longer possible in many areas because of land clearance. The best alternative is actively to manage the kiwi populations that remain. Our options for very small and very

isolated populations may be limited to:

- (i) leaving the kiwi where they are to face potential inbreeding depression (Allendorf & Leary 1986) and high risk of local extinction,
- (ii) mounting costly and time consuming salvage operations to recover and relocate to larger areas as many individuals as possible, or
- (iii) to instigate a programme of artificial migration by moving kiwi between reserves so as to maintain gene flow.

In other locations, however, we have a fourth option: to supplement and enhance the available habitat, and the effective population size, by linking remnants together. We have seen that some kiwi will travel up to 1200 m from a reserve using bush remnants as "stepping stones" or corridors. The possibility therefore exists that some remaining islands of bush within 1 - 2 km of each other could effectively be linked by enhancing existing bush "stepping stones", or by creating new ones. If new bush "stepping stones" or corridors for kiwi are to be planted they should be as close as possible - no more than 100 - 300 m apart. Preferably new plantings should comprise local flora. However, the effectiveness of other species, including exotics, could be worth investigating. A potential problem with creating bush corridors linking larger areas of kiwi habitat is that it may expose kiwi to greater risk of predation. For this reason corridors should be kept as large as possible. Ongoing population monitoring and predator control is vital (see Taborsky 1988a,b; Diamond 1989).

The bush remnants around the southern end of Paerata Reserve effectively contributed over 20 ha of useful kiwi habitat to the main 210 ha reserve. The effective size of existing reserves can, therefore, be greatly enhanced by planting shelter belts, or by protecting existing remnants. Fencing of bush remnants may not be necessary in all locations, but must be a prime consideration where regrowth is restricted or unlikely; for instance, where stock have access to the reserve. Fencing may be minimally effective in discouraging dogs from roaming through these areas. The standard seven-wire fence is not a major obstacle to kiwi.

Many management questions are not yet adequately answered. These include the effects on kiwi of grazing by stock; the effects of predation on kiwi recruitment; the regional genetic variation between kiwi populations; and the dispersal patterns of kiwi chicks. While these questions need attention, it is important not to let ignorance of these matters prevent us from acting now on the information we have (Diamond 1986). I have shown that kiwi will use bush "stepping stones" and corridors, and that kiwi habitat can be enhanced if land owners are encouraged to

retain and protect bush remnants near kiwi reserves. We need to apply these principles elsewhere, and learn to be as concerned about the composition of the surrounding habitat as we are about reserves themselves (Janzen 1986). Remaining inactive may send many of our remaining kiwi populations to extinction.

PAIR BONDING

5.1 INTRODUCTION

One of the many distinctive features of ratites is the apparent universality of male parental care (Handford & Mares 1985). Male and female ostriches share incubation (Bertram 1980), but in all other ratites care of eggs is provided primarily by the males (Oring 1982). Sex-role reversal, such as this, is rare in birds (Ridley 1978), and is often associated with polyandry (Jenni 1974; Emlen & Oring 1977; Oring 1985). However, the evolution of a particular mating system is dependent not only on the nature of the parental investment, but also on the specific ecological conditions of the species (Emlen & Oring 1977; Graul *et al.* 1977; Rubenstein 1980). Male parental care in ratites is associated with a diverse array of mating systems ranging from monogamy to mixed polygyny/polyandry (Handford & Mares 1985).

The view that the kiwi may be polyandrous has persisted since Buller (1888) recorded this as a Maori belief. Falla (1979) considered that the laying capacity of captive female kiwi could exceed the ability of a single male to incubate, and interpreted this as supporting evidence for the possibility of polyandry. However, recent field studies on brown kiwi (Colbourne & Kleinpaste 1983; McLennan 1988) and little spotted kiwi (J. Jolly pers. comm.) have found them to be monogamous, and their pair bonds to remain intact for many years. The kiwi in these studies lived in comparatively exclusive territories (Colbourne & Kleinpaste 1983; McLennan *et al.* 1987; J. Jolly pers. comm.). The possession of all-purpose exclusive territories greatly reduces the problem of maintaining pair bonds as males and females are always together (Rowley 1983). Retention of the same mate each year often has advantages for the individual in terms of improved reproductive success (Rowley 1983; Coulson & Thomas 1983). In some situations, however, these advantages may be minimal, and pairs may remain together primarily because of limited opportunities to acquire new mates (Freed 1987). Divorce (see Section 5.2.1), when it does occur, often results in differential dispersal of the sexes (Greenwood 1980, 1983). In most bird species this dispersal is female biased.

Mating systems can show a considerable degree of variability because they are dependent on the local environment, population density (Emlen & Oring 1977),

and sex ratio (Oring 1982; Hannon 1983). The extensive overlap of brown kiwi ranges in Paerata Wildlife Management Reserve (Section 3.3.1) provides conditions under which variations from monogamy and long-term pair bonding are perhaps most likely to occur.

In this section, the mating system and stability of pair bonds are investigated in this high density population of brown kiwi. The effects of mate change on home range movements are also examined.

5.2 METHODS

Details of the study site, number of kiwi captured, and tracking techniques are presented in Sections 2.1 and 2.2.

5.2.1 Terminology

The terminology used here is that of Rowley (1983). Re-uniting is re-mating with the same partner. The divorce rate is calculated as the percentage of pairs surviving from year one to year two that do not re-unite. Re-pairing is taking a new mate. Re-pairing after loss of a partner is mate-replacement.

5.2.2 Pair determination

Mated pairs were identified by their repeated roosting together (Section 3.3.2), and by their night-time proximity to each other. Pairs were considered divorced after prolonged (2-3 months) disassociation with each other, or when one member of the old pair was found to have re-paired.

5.3 RESULTS

5.3.1 Pair bond stability

During 1985/86 and 1986/87 50% of pairs of known fate ($n = 12$) failed to re-unite the following season. Two out of four pairs (50%) identified during the 1985/86 breeding season divorced before the 1986/87 season. Four out of eight

pairs (50%) identified in the 1986/87 breeding season and known to be still alive during the 1987/88 season divorced (Table 5.1). The female from one pair (M74/F73) died in January 1987. Her widowed mate replaced her within 3 months with a female (F76) from an adjacent pair. This left F76's previous partner (M67) without a mate. By June 1987 he had paired with a female (F75) living near him, apparently after desertion by her previous (unbanded) mate.

TABLE 5.1 Pair bond stability and annual breeding success. M = male; F = female; ? signifies missing or unconfirmed data; UB = unbanded bird.

Season	Pair (M/F)	No. eggs	No. chicks	Following season		
				Same mate?	Male with:	Female with:
1985/86						
	51/53	1	0	No	F 65	Unmated
	55/52	1	1?	No	?	Unmated
	56/58	0	0	Yes		
	61/59	1?	0	Yes		
1986/87						
	51/65	2	1(2?)	Yes		
	56/58	2	1*	No	F 68	?
	61/59	2	0	Yes		
	66/68	2	1	No	?	M 56
	67/76	?	0	No	F 75	M 74
	70/64	2	0(1?)	Yes		
	71/72	1	0	Yes		
	74/73	2	0	F died	F 76	-
	UB/75	?	?	No	?	M 67

*This chick died on hatching

5.3.2 Divorce and breeding success

No obvious relationship existed between the breeding success of a pair and their likelihood of subsequent divorce (Table 5.1). However, there are few pairs for which information is available. Of the nine occasions where a pair's breeding success was known for certain, one pair remained stable and one pair divorced after fledging a chick. Four pairs which failed to fledge a chick in a season remained stable, while three others divorced.

5.3.3 Timing of divorce

All of the observed divorces occurred between September and June, with most occurring between January and April (Table 5.2). This corresponds with the non-

breeding period (Section 6.3.1). Within a season females were never observed to lay eggs for more than one male.

TABLE 5.2 Time periods during which known pairs divorced, based on the months when members of the pair were last seen together, and first seen with a new mate. M = male; F = female; UB = unbanded bird.

Old pair (M/F)	Last recorded together	New pairs (M/F)	First recorded together
51/53	Jan 1986	51/65	Jun 1986
55/52	Apr 1986		
56/58	Jan 1987	56/68	Apr 1987
66/68	Jan 1987	56/68	Apr 1987
67/76	Nov 1986	67/75	Jun 1987
		74/76	Apr 1987
UB/75	Sep 1986	67/75	Jun 1987

5.3.4 Sex ratio

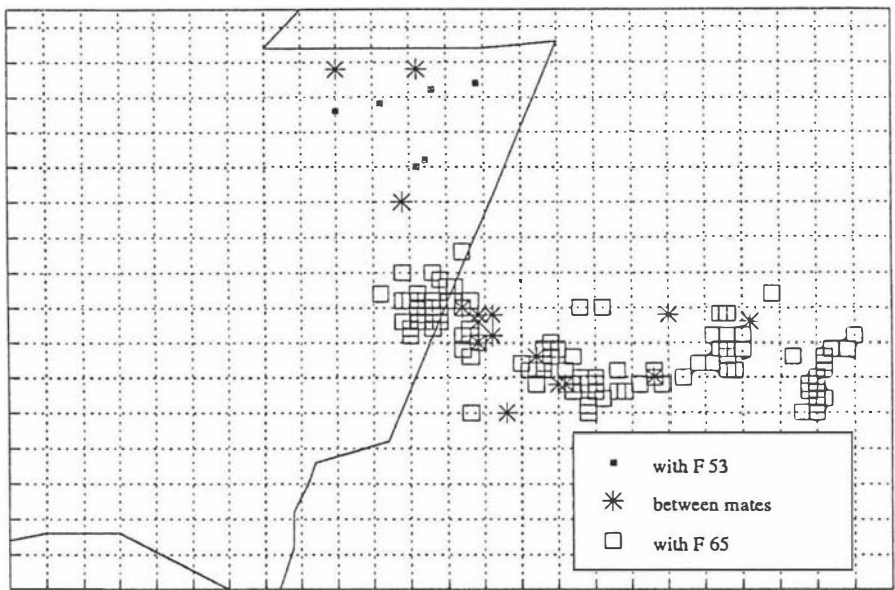
During the study 32 kiwi (11 males, 1 juvenile, 20 females) were caught and banded (Section 2.2). The mated status was determined for 10 males and 13 females. Each breeding season all radio-tagged males, but not all females, had a mate. Two females (F52 and F53) that divorced their mates after the 1985/86 breeding season did not breed or form pair bonds during the following 1986/87 or 1987/88 breeding seasons. Two other females (F78 and F82), tracked for one season each, also did not breed or appear to have mates during this time. This suggests that part of the bias in the number of females caught reflects a real bias in the sex ratio (see Section 5.4.4). From knowledge of the breeding statuses of the radio-tagged kiwi females outnumbered males by about 1.3-1.4 : 1.

5.3.5 Home range changes associated with divorce

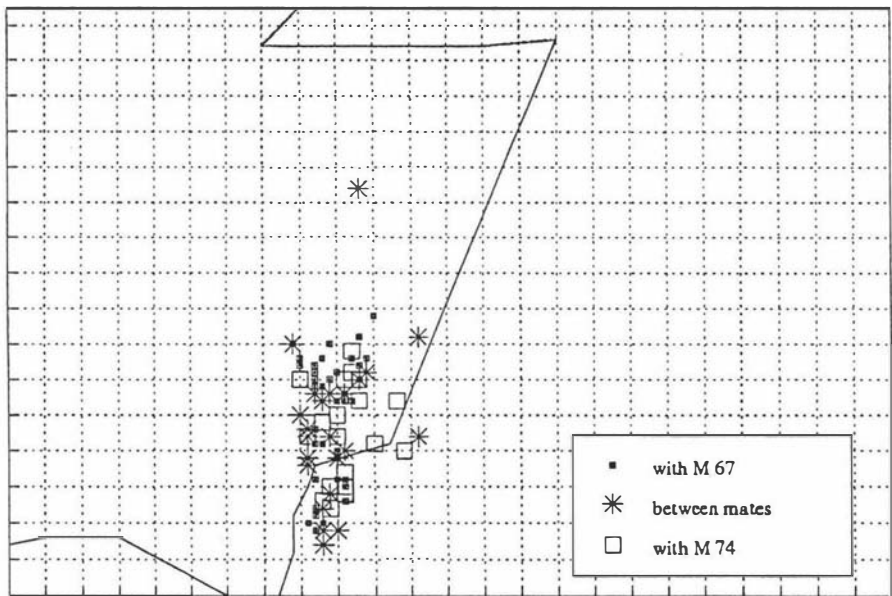
Divorce and mate change was associated with a temporary or permanent change in the home range movements of the affected kiwi in all six cases where adequate data were available (Figure 5.1). The period between divorce and the formation of a new pair bond was associated with extreme movements away from their previous range for four birds (M51; M67; F75; F76). This propensity to move was not clearly associated with one sex more than the other. Even though individuals often wandered widely following divorce, with only one exception

FIGURE 5.1: Home range changes associated with divorce and re-pairing in six kiwi at Paerata. M = male, F = female. Radio-fixes obtained from each kiwi before, during and after mate changes are indicated on each plot, as is the southern boundary of Paerata Wildlife Management Reserve. Grid cells = 100 m² (1 ha). See Figure 2.1 for a habitat map based on this grid system.

M 51

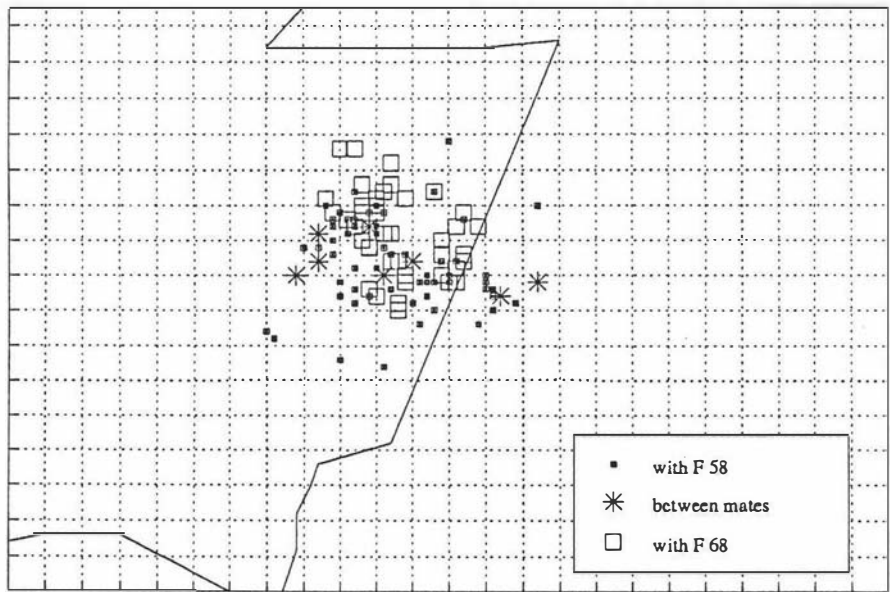


F 76



/ ...

M 56



F 68

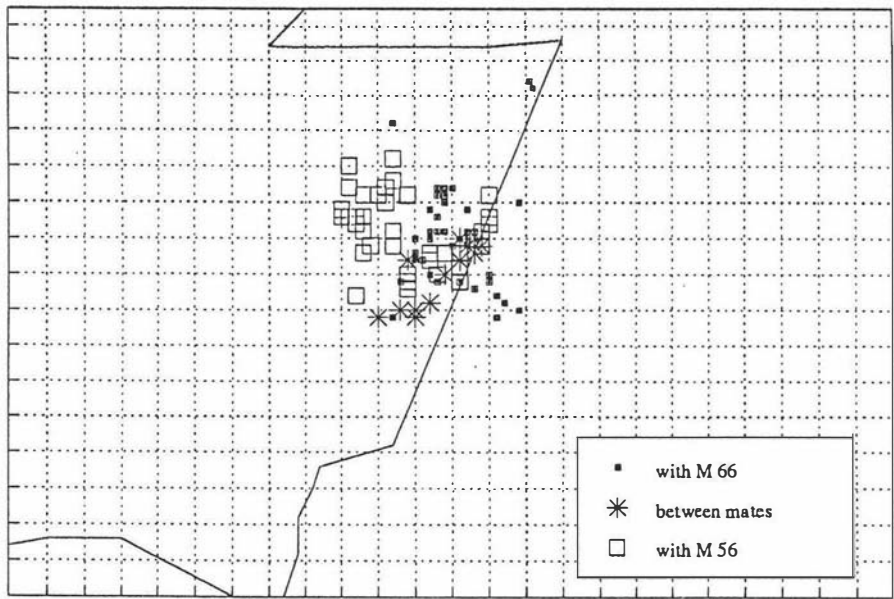
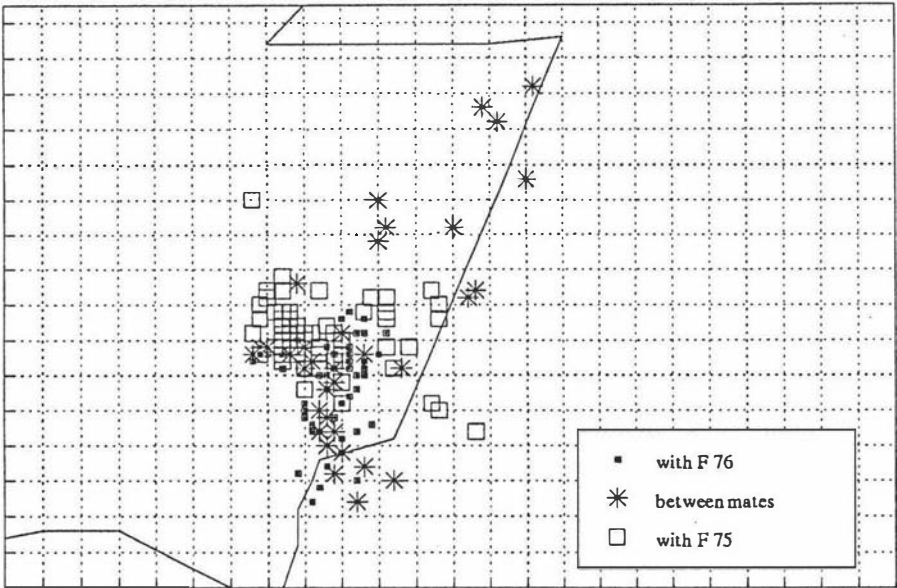


Figure 5.1 continued...

M 67



F 75

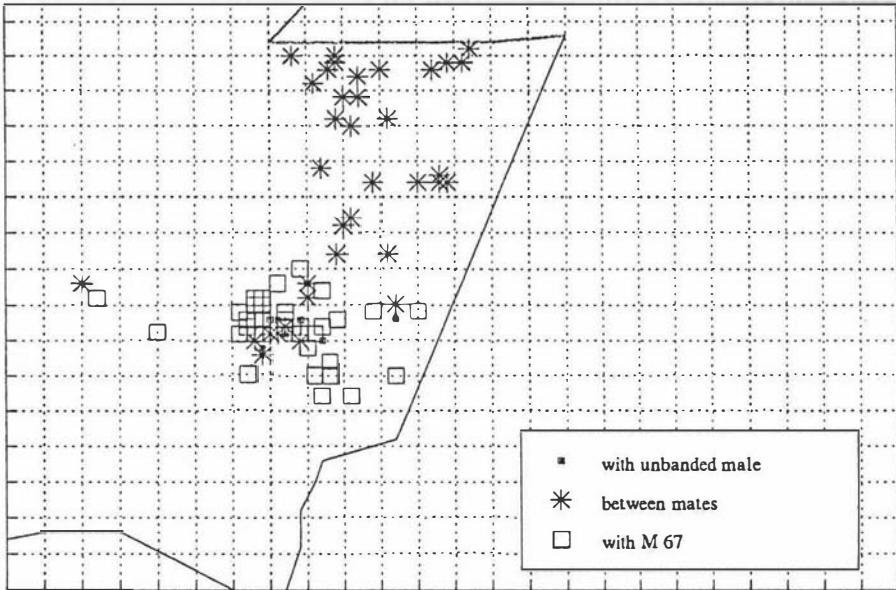


Figure 5.1 continued

(M51), new pair bonds formed between birds that had previously been close neighbours, and following re-pairing, the home ranges of five out of six kiwi (83%) overlapped in large part with their earlier range.

5.4 DISCUSSION

5.4.1 Pair bond stability

Divorce has not previously been recorded among wild kiwi. All earlier studies have pointed to long-lasting, stable pair bonds (Colbourne & Kleinpaste 1983; McLennan 1988; J. Jolly pers. comm.). The 50% per annum divorce rate observed here is not only an extraordinary finding for kiwi, it is also extremely high for any long-lived, non-migratory species (Rowley 1983). In such species, where a high proportion of mates survive between breeding seasons, the reproductive success of each individual is usually predicted to be highest if they re-mate with their previous season's partner (Rowley 1983; Coulson & Thomas 1983; Haig & Oring 1988).

Divorce rates are often highest among young breeding birds, and tend to decrease markedly among older individuals (Coulson & Thomas 1980). However, no method currently exists for aging sexually mature kiwi, so the demography of the Paerata population is unknown. Whatever the proximate cause of the high levels of divorce, it was not obviously related to my presence or interference. In fact, three of the pair-changes occurred during a period when I was absent from the reserve (19 February to 17 April 1987).

5.4.2 Divorce and breeding success

The best predictor of divorce is often reproductive failure in the previous season (Rowley 1983; Coulson & Thomas 1983; Diamond 1987). The divorces observed here did not obviously fit this pattern, but the number of observations are few. Long-term studies of many individually marked birds are needed before the causes, costs, and benefits of divorce to the individual's lifetime reproductive success can be ascertained (e.g. Coulson 1966; Mills 1973; Ollason & Dunnet 1978; Coulson & Thomas 1985; Perrins & McCleery 1985; Harris *et al.* 1987). For the meadow pipit (*Anthus pratensis*) Hötker (1988) determined that lifetime reproduction was more influenced by longevity than by annual reproduction.

5.4.3 Timing of divorce

The divorces observed here occurred predominantly during the first four months of the year. This is the period between breeding seasons, which run from about July to about January (Section 6.3.1). Females were never known to lay eggs for more than one male during a season. This supports the view that kiwi are monogamous, although pair bonds were less perennial in Paerata than in Waitangi State Forest (Colbourne & Kleinpaste 1983) or Hawkes Bay (McLennan 1988).

5.4.4 Sex ratio and mating system

The strongly female-biased sex ratio observed in Paerata does not appear to be unusual among wild kiwi populations. McLennan *et al.* (1987) radio-tracked a small population of kiwi at Halliburtons' in northern Hawkes Bay. This population comprised eight kiwi - three males and five females, or about one male to 1.7 females. Colbourne & Kleinpaste (1983) also reported a female-biased sex ratio in Waitangi State Forest. Of the 84 kiwi caught and banded, 38 were adult females, 22 were confirmed adult males, 10 were juvenile females/unconfirmed males, and 14 were juveniles. The ratio of confirmed males to confirmed females was thus 1 : 1.72. They considered this bias to be a probable consequence of behavioural differences that make males more difficult to catch than females. Their argument, largely supported by my own observations, was that males tend to run faster than females when pursued, and are more likely to "freeze" suddenly or hide under vegetation. Also, males spend considerably less time foraging at night, during their protracted incubation periods, than do females (Section 6.3.4; McLennan *et al.* 1987) and so are less likely to be encountered at night than females. It is not clear whether Colbourne & Kleinpaste's (1983) explanation accounted for all of their observed sex-ratio imbalance in Waitangi State Forest. In Paerata the ratio of males to females caught (11:20) may be partly accounted for by Colbourne & Kleinpaste's (1983) reasoning. However, the observation that all radio-tagged males paired each year while all females did not supports the view that part of the apparent sex-ratio imbalance in Paerata was real. It is unlikely that kiwi have a naturally biased sex ratio in offspring production (Fisher 1930; but see Taylor 1981), so the observed sex-ratio bias probably relates, in part, to differential mortality. The proof and possible reasons for this, however, remain unclear.

Unpaired females in Paerata showed normal seasonal hormonal cycling (Potter & Cockrem unpublished data) suggesting that endocrinologically, at least, they were primed for breeding. The female-biased sex ratio should therefore have had a direct influence on the operational sex ratio (OSR) of this population (Emlen & Oring 1977). The OSR would have been further skewed by the protracted incubation period of males. This imbalance should in theory heighten intrasexual competition among females for access to available males (Emlen & Oring 1977; Colwell & Oring 1988). Emlen & Oring (1977) predict that the degree to which polyandry will develop depends on the intensity of female sexual selection and the environmental potential for females to monopolise males. The relative shortage of males in Paerata and elsewhere may greatly reduce the potential for females to monopolise more than one male, and explain in part the absence of polyandry in this species. If polyandry does exist in kiwi, it is most likely to occur in populations with a male-biased sex ratio.

5.4.5 Home range changes associated with divorce

Mating systems can be sensitive to changes in the local environment, population density (Emlen & Oring 1977), and sex ratio (Oring 1982; Hannon 1983). The most obvious differences between kiwi in Paerata and those in Waitangi State Forest (Colbourne & Kleinpaste 1983) and Hawkes Bay (McLennan *et al.* 1987) relate to population densities and the integrity of home ranges (Chapter 3), so it is likely that the divorce rate among kiwi in Paerata was related to these variables. The driving force for divorce may have been intra-female competition for access to the limited number of males. Freed (1987) has demonstrated that pair bonds in the house wren (*Troglodytes aedon*) may remain stable through limited opportunities for birds to obtain new mates. The extent of home range overlap in Paerata suggests that these kiwi had plenty of opportunities to change partners. However, the advantage to be gained by an individual breaking an established pair bond is unclear, especially when divorce is not obviously associated with nesting failure.

In the vast majority of bird species females, both as juveniles and adults, are more likely to disperse than males (Greenwood 1980, 1983). Most bird species have a resource-defence mating system where males compete for resources in order to attract females. Consequently, it is usually the males that retain the pair's territory after divorce (e.g. Harris *et al.* 1987; Imber 1987). In kiwi, the prediction of which sex would be more inclined to disperse is complicated by their sex-role reversal.

Females are dependent on males for incubation, so males are the potentially limiting sex. This is especially true in situations such as Paerata where the population sex ratio is biased towards females. If males represent a limiting resource then females should disperse and compete for access to males. Males, however, may compete amongst themselves for access to high quality home ranges. As suggested in Section 3.4.2, territory quality may depend in part on access to, and monopolisation of, high quality roost sites. Following divorce both sexes may therefore have reason to move, and both males and females did appear to roam after the breakdown of their pair bond. Despite this, both sexes also showed a high degree of site affinity, and with only one exception (M51) re-paired with birds that had previously been close neighbours. The home ranges of birds after re-pairing therefore tended to overlap to a large extent with their pre-divorce home ranges.

I suggest that the divorce rate in Paerata was high because of a combination of the intense competition that must have existed between females for the limited number of males, and because of increased opportunity to change partners resulting from the high population density and reduced territory integrity.

REPRODUCTIVE BIOLOGY

6.1 INTRODUCTION

The literature on breeding in kiwi has concentrated on their allometrically large and energy rich egg, protracted incubation period, and the large energy reserves of newly hatched chicks (Robson 1958; Kinsky 1971; Reid 1971a,b; 1972a,b; 1977; 1981b; Reid & Williams 1975; Calder 1978, 1979; Calder & Rowe 1977; Calder *et al.* 1978; Rowe 1980; Silyn-Roberts 1982, 1983; Body & Reid 1983). Less is known about kiwi breeding behaviour. For a century the observations made by early naturalists such as Layard (1863) and Buller (1888) provided most of the knowledge of brown kiwi laying and nesting behaviour in the wild. This knowledge was supplemented by other chance observations of nests (e.g. Turbott & Wightman 1955; Sturmer & Grant 1988); by studies of captive birds (Robson 1958; Clayton 1972; Rowe 1974; Goudswaard 1986); and gonadal analyses of recently dead kiwi (Kinsky 1971). These observations and studies indicate that brown kiwi lay in any month of the year, but mainly between July and February (Oliver 1955; Kinsky 1971; Reid & Williams 1975). Reid (1981a) states that free-living kiwi lay 1-2 eggs per year, but kiwi in captivity may lay 4-6 eggs per year. The eggs laid by captive kiwi, however, tend to be smaller than those laid by wild kiwi (Reid 1981a). The incubation period is 74-84 days (Reid & Williams 1975), and may depend on incubation temperature (Rowe 1978).

A recent study by McLennan (1988) provided the first intensive and detailed account of breeding behaviour, fecundity and nesting success in free-living brown kiwi. This study highlighted both the similarities and differences in breeding between wild and captive kiwi. For instance, female kiwi in McLennan's study did not differ from captives in the number of eggs laid each year, nor in the rate at which they laid them. However, the free-living kiwi did have a shorter, more defined breeding season, and spent more time feeding during incubation than captive kiwi.

McLennan's (1988) study was based on a low density, discretely territorial population of brown kiwi (McLennan *et al.* 1987). Paerata Wildlife Management Reserve, in comparison, contains kiwi at about 10 times the density, and territory intrusion is extremely common (Section 3.3.1). Pair bonds within Paerata also tend

to be less stable than in populations studied elsewhere (Chapter 5). An understanding of the natural variation in breeding behaviour and fecundity existing between populations of brown kiwi is important to the wider understanding of this species, and to the development of effective management strategies for each population.

This section describes the breeding behaviour and nesting success of radio-tagged brown kiwi in Paerata Wildlife Management Reserve.

6.2 METHODS

Details of the study site, number of kiwi captured, and tracking techniques are presented in Sections 2.1 and 2.2. Mated pairs were identified as in Section 5.2.2.

6.2.1 Pair monitoring and nest identification

Breeding data were collected over three seasons (1985-1988). Between seasons up to 50% of pairs changed mates (Chapter 5), making it difficult to follow the breeding success of many pairs for more than a single season. Because of this, the breeding attempts of each pair in each season are treated as independent. During the 32-month study data were collected from 18 pairs, comprising 10 males, 12 females, and 14 different combinations of birds.

The frequency with which members of each pair roosted together was closely monitored. This, along with bird weights (Section 6.2.3), gave an indication of when eggs were likely to be laid. Outwardly, not all nest sites appeared obviously different from daytime roosts, so caution was exercised in approaching sites that were considered possible nests. When a possible nest was located I inspected it at night after the occupant had emerged to confirm the presence of an egg. Eggs were not always visible from the entrance and I often had to feel for them. This must have left a scent but I have no evidence to suggest that it caused desertions.

6.2.2 Nest monitoring

I kept my presence around active nests to a minimum to reduce disturbance that might have led to desertion by nesting birds. For this reason most weights and measurements are from abandoned eggs. The presence of a bird on a nest was

confirmed each day by radio telemetry. Emergence and return times of incubating males were determined either by listening for variations in the transmitter signals which indicated whether the birds were moving; by an electronic analoger activated by the breaking of an infra-red light beam; or by small electronic timers (Jenness & Ward 1985) activated by a cotton "trip wire" set across the nest entrance. The latter proved very reliable, portable, and quick to set up while incubating males were absent from their nests at night.

Towards the end of incubation I attempted to check on nests every few nights to determine hatching dates. This was often difficult, however, because incubating males reduced the length of their feeding excursions during this period (Section 6.3.7).

6.2.3 Kiwi weights

Radio-tagged kiwi were recaptured every 4-10 weeks for weighing to enable their body weights to be compared at different stages of the reproductive cycle. The following reproductive stages were used:

Non-breeding - (both males and females) weights from December, January, February or March recorded at least one month after the last egg was laid or nesting completed, but at least four months before the next egg was laid or incubation started. This corresponds with the period of least overt pair bonding behaviour, such as the frequency with which pairs roost together (Section 6.3.1).

Pre-laying - (both males and females) the period up to 16 weeks prior to the female of a pair laying. For males this category was divided into four periods: 16-12, 12-8, 8-4, and 4-2 weeks prior to their mate laying. For females pre-laying was divided into six periods: 16-12, 12-8, 8-4, 4-2 and 2-0 weeks before laying their first egg, and 2-0 weeks before laying their second egg.

Laying - (males only) the period two weeks either side of the date when their mate laid her first egg.

Post-laying - (females only) the one-week period immediately after laying either: i) their first egg of the season; or ii) their second egg.

Incubation and brooding - (males only) this was divided into two periods: early incubation (2-8 weeks into incubation); and late incubation and brooding (>8 weeks into incubation or brooding a chick). Males were not removed from nests for weighing in case this caused them to desert. Weight changes during incubation were therefore only determined for males which had already deserted their nest or, on rare occasions, for incubating males that were caught while off the nest at night.

6.2.4 Statistical analyses

The time intervals between multiple eggs laid in a single nest and those laid in different nests were compared using the Mann-Whitney U_s test (Sokal & Rohlf 1981). One-way analyses of variance followed by the Student-Newman-Keuls test were used to compare nest attendance patterns; emergence and foraging times of incubating and non-incubating birds; and seasonal and reproductive stage changes in body weight. First and second-egg female weight data were combined for analysis because of the small sample size. Seasonal changes in body-weights were further analysed using a polynomial test for trends (SPSS Inc. 1983). This analysis partitioned the between-group sums of squares into linear and quadratic trend components.

6.3 RESULTS

6.3.1 Breeding season

During the study 18 pairs laid 27 eggs between them. The laying dates of 26 of these were known approximately (Figure 6.1). Eggs were laid over eight months of the year, from July to February. The first egg of each season was laid between July and November. If a second egg was laid in the first clutch this occurred between August and December. Second-clutch eggs were laid between October and February. One of these second-clutch eggs was laid by a female whose mate had already successfully hatched her first egg. The other second-clutch eggs were all laid after an earlier nest failed or was deserted, and hence were replacement clutches. Egg laying was only one indicator of breeding seasonality in kiwi. Three months prior to the first eggs being laid there was a marked increase in the frequency with which pairs roosted together (Figure 6.2). In March pairs spent less

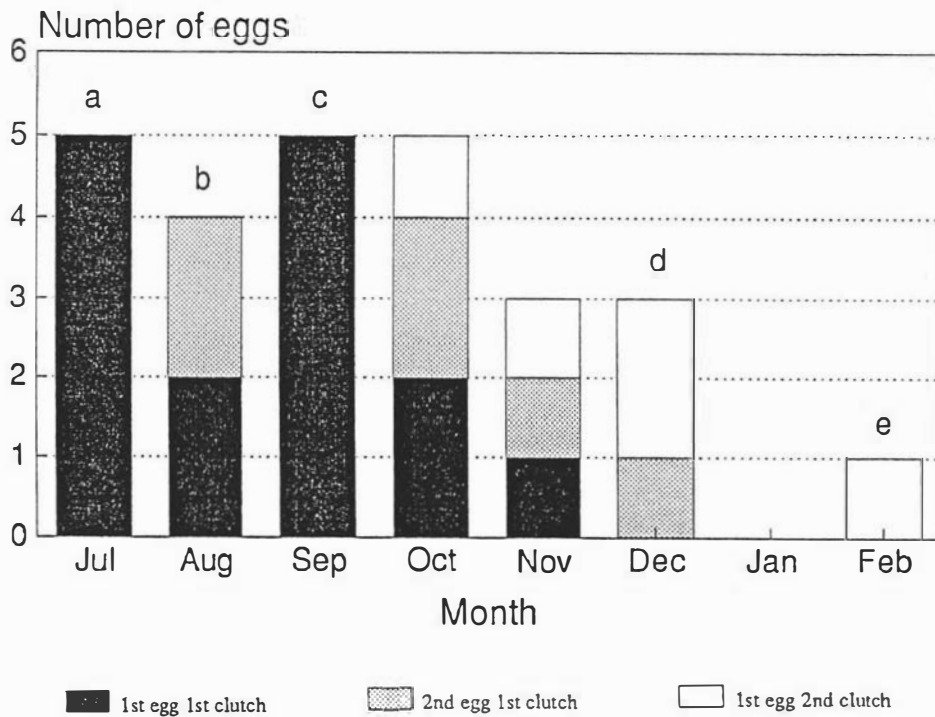
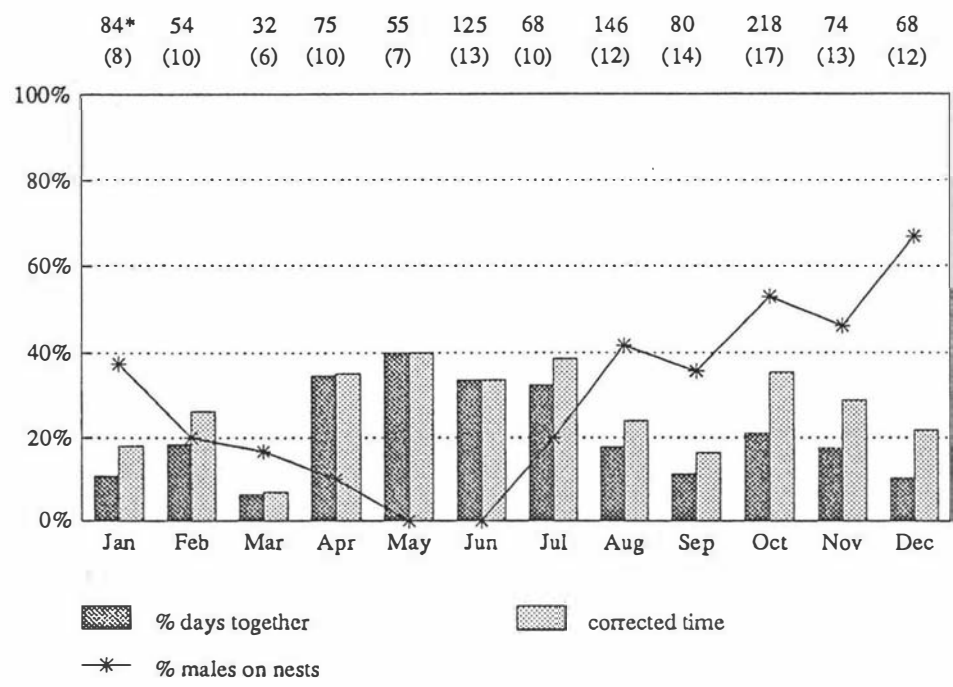


FIGURE 6.1: Time and pattern of egg laying by 18 pairs of kiwi in Paerata, 1985-1988. a) One 1st clutch egg in the July total may have been laid in the first 2 days of August; b) one 2nd egg 1st clutch in the August total may have been laid in the first 2 days of September; c) one 1st clutch egg in the September total may have been laid on the first day of October; d) one 2nd clutch egg in the December total may have been laid during the last 2 days of November, and another 2nd clutch egg may have been laid during the first 4 days of January; e) this egg may have been laid on the last day of January.



*No. observations
(No. pairs)

FIGURE 6.2: The monthly frequencies with which pairs roosted together and the proportion of males incubating for at least part of each month. See text for details about ‘corrected time’ together.

than 7% of days together. This increased sharply in April and peaked at 40% of days in May. Males were found incubating in all months except May and June. The proportion of radio-tagged males incubating reached a peak of 67% ($n = 12$) in December (Figure 6.2). Incubating males are effectively unavailable to roost with their mate, so Figure 6.2 also shows a corrected frequency of roosting together based on observations for those pairs in which the male was not already actively engaged in incubating. Pairs roosted together most frequently between April and July. This peak precedes by three months the peak in egg laying (July - October; Figure 6.1).

6.3.2 Nest sites

Twenty nests were located. Of these 18 (90%) were in burrows, one (5%) was in a hollow in the base of a tree stump, and one (5%) was in a large (3 x 3 m) clump of toetoe.

The burrows ranged from 45-125 cm in length (mean \pm SE = 71 ± 5 cm) and 10-23 cm in diameter (mean \pm SE = 14 ± 1 cm; $n = 18$). Eggs were visible from the entrance of 11 of the 18 burrows. In the other seven the eggs were hidden around bends and curves.

Nest burrows tended to be considerably shorter than those used as daytime shelters (Section 3.3.2). Twelve of the nests were located in thick bush, seven in open bush, and one nest burrow was in a 3-m wide grass verge on the side of an unsealed road, about 300 m from the nearest patch of bush larger than 1 ha in size. Eleven of the burrows ran in horizontally from their entrance, five sloped downwards, and two sloped up. One of the latter sloped so steeply (approximately 20°) that it may in part have been responsible for the death of the chick on hatching. The chick was found about 2 m from the nest the day after it hatched, and appeared to have rolled out of the nest and down a nearby bank.

None of the burrows used as nests showed any sign of recent excavation. Several of the nest burrows were used as daytime roosts before eggs were laid. One was used by two males. The male which subsequently nested in the burrow was recorded there on four days during the three months prior to eggs being laid. The other bird, a neighbouring male, used the burrow as a roost on a single occasion 60 days before the first egg was laid, but just three days after the resident male had used the roost. One pair spent 10 days together in a burrow before the egg was laid. Another pair alternated in their use of a burrow several times during the 12 days prior to egg laying. One nest, in a 1-m long burrow, was used intensively by both

TABLE 6.1 Time and pattern of laying in Paerata kiwi during three breeding seasons. M = male; F = female; NC = not calculated.

Pair (M/F)	Season	Clutch number	Egg number	Laying date	Interval between eggs (days)
51/53	1985-86	1	1	? found 20/9/85	-
55/52	1985-86	1	1	30/9/85	-
56/58	1985-86			? did not breed, or had an early nest failure	
	1986-87	1	1	14/8/86	
		2	1	23/10/86	70
57/62	1985-86	1	1	28/9/85	
		2	1	30/1 to 12/2/86	124-137
61?/59	1985-86	?	1	28/9 to 1/10/85	-
61/59	1986-87	1	1	1 to 3/7/86	
		2	1	18/11/86	130-132
51/65	1986-87	1	1	20/10/86	
		1	2	? after 23/11/86	≥34
	1987-88	1	1	? mid-July 1987	
		2	1	28/11 to 15/12/87	135-152
66/68	1986-87	1	1	16/10/86	
		1	2	? December	NC
67/76	1986-87	1	1	17 to 21/11/86	-
70/64	1986-87	1	1	8/7/86	
		1	2	? before 2/9/86	<56
	1987-88	1	1	4/9/87	
		1	2	? before 19/10/87	<44
71/72	1986/87	1	1	11/7/86	-
	1987-88	1	1	5/9/87	
		1	2	? before 8/10/87	<32
74/73	1986-87	1	1	5 to 10/8/87	
		1	2	29/8/87	19-24
56/68	1987-88	1	1	? before 2/8/87	
		2	1	12/12/87	>132
67/75	1987-88			F did not lay - M pirated another nest; see text	

members of a pair during the five weeks before egg laying. The egg was broken and the nest deserted within two weeks of the egg being laid. Two months later both birds started using the burrow again on a regular basis as a daytime roost. They continued to use the burrow as a roost on and off during the next year.

Replacement or second clutches were always laid in a different nest from the first. None of the four nest sites found in 1985-86, or the 10 found in 1986-87, were reused in the following one or two years. However, three of the 20 nests found during the study contained old fragments of egg shell indicating previous nesting attempts at those sites. Nest burrows may therefore be reused over a long time frame.

6.3.3 Laying

Twenty-seven eggs were laid during the study. Twenty-six eggs were laid in 20 nests and one egg was not located. Fourteen nests contained one egg and six contained two eggs. Eight nests failed or were deserted within four weeks of the first egg being laid. Of those nests surviving more than four weeks, seven contained single egg clutches and five contained two-egg clutches.

Breeding females never laid more than two eggs in a season. Of the 18 breeding attempts recorded, 11 females laid two eggs, four laid one egg, one female laid an egg that may have been either a first or second clutch egg, and two pairs apparently failed to lay at all in one season (Table 6.1).

The time interval between eggs laid in a single nest was consistently and significantly shorter (Mann-Whitney $U_s [5,4] = 20$; $P = 0.02$), and up to 8 times less, than the interval between eggs laid in different sites (Table 6.2). This difference was consistent regardless of the success of the first clutch, or the stage at which it failed.

TABLE 6.2 Time intervals between eggs laid in a single nest compared with the time interval between eggs laid in different nests. M = male; F = female.

Eggs laid in same nest			Eggs laid in different nests		
Pair (M/F)	Season	Interval (days)	Pair (M/F)	Season	Interval (days)
70/64	1986-87	<56	57/62	1985-86	124-137
74/73	1986-87	19-24	56/58	1986-87	70
70/67	1987-88	<44	61/59	1986-87	130-132
71/72	1987-88	<32	51/65	1987-88	135-152
			56/68	1987-88	>132

Nine eggs measured between 120-132 mm long by 77-83 mm wide. On average (\pm SE) these eggs measured 125.9 ± 1.5 mm by 80.7 ± 0.6 mm. The fresh weights of five eggs were 425, 430, 450, 490 and 510 g, over 20 g heavier, on average, than those laid in Hawkes Bay (McLennan 1988), and nearly 100 g heavier than those laid in captivity (Reid 1981a).

6.3.4 Incubation

On at least six occasions females spent the first one or two days on the nest after laying their first egg. One female also spent a day on her nest after laying the second egg of her two-egg clutch. Her mate roosted elsewhere that day. Otherwise, females were never again observed on nests during the day. All males started incubating within two to three days of the first egg being laid. Once started, most males incubated every day until either the egg hatched or was abandoned. However, three males took 2-10 days off incubating during the first two weeks after the egg was laid. Two of these males then settled into incubating every day, while the third deserted.

Incubating and brooding males left their nests every night (100% of 81 observations) except during the 1-2 days immediately before the chick hatched (Section 6.3.7). Incubating males emerged between 1 hour 20 minutes and 5 hours 10 minutes after sunset ($n = 37$; mean \pm SE = 208 ± 7 min.). Once the egg hatched they emerged significantly earlier in the night ($n = 7$; mean \pm SE = 111 ± 23 min.; $F_{[1,42]} = 23.8$; $P < 0.001$). However, both incubating and brooding males emerged significantly later at night than non-incubating kiwi ($n = 20$; mean \pm SE = 45 ± 6 min.; $F_{[1,62]} = 113.4$; $P < 0.001$)

Incubating males spent an average of 217 ± 22 min. (SE) ($n = 13$; range = 60 - 375 min.) off their nests each night. This was less than half the active period of non-incubating kiwi during the breeding months (July - February) (510 ± 22 min.; $n = 9$; $F_{[1,20]} = 83.6$; $P < 0.001$).

One egg took 85 days to hatch. In another nest the first egg was laid on 16 October and a second, discovered on 4 January, had not been present in November, so must have been laid in December. One egg hatched on 16 January and the second egg was subsequently abandoned. If it had been the second egg that hatched the incubation period would have been less than 48 days. If it was the first egg that hatched then the incubation period was 92 days.

In a third nest the first egg was laid on 20 October. A second egg was laid in the nest sometime during November. The female (F65) that laid the first egg gained a little weight between 22 October and 23 November, so if she laid the second egg this must have been after 23 November. A single egg hatched on 6 February. The other egg was cracked and discarded. If it had been the first egg that hatched, the incubation period was 109 days. If the second egg was laid by F65 (i.e. after 23 November), and this was the egg that hatched, then the incubation period was less than 75 days. However, I cannot rule out the possibility that the second egg had been laid by a different (unknown) female.

6.3.5 Nest takeover

One nest was attended by two males during the 1987-1988 breeding season. The female of an established pair (M70/F64) laid her first egg in a burrow on 4 September. Her mate started incubating within two days, and the female laid a second egg in the nest sometime before 19 October.

In mid-October a neighbouring male (M67) was noticed spending a considerable amount of time, both day and night, within 100 m of M70's nest, and was recorded as close as 40 m from it. On 22 October (48 days into incubation) M70 deserted the eggs, and was not again recorded near the nest. Two days later M67 was first recorded on the nest. Male 67 incubated the eggs until 17 December, when I confirmed that one of the eggs had hatched. The other egg disappeared in mid-November. A small blood sample was taken from the chick. This blood sample was compared by DNA fingerprinting analysis (Burke & Bruford 1987) with samples taken from F64 and M70, and from M67 and his mate F75. This analysis confirmed that F64 and M70 were the true parents of the hatched chick (A. Cooper unpublished data).

6.3.6 Body weight changes with season and reproductive stage

Season

Females

Breeding females tended to show seasonally cyclic changes in body weight that peaked in winter at the onset of breeding (Figure 6.3). Individual variation in

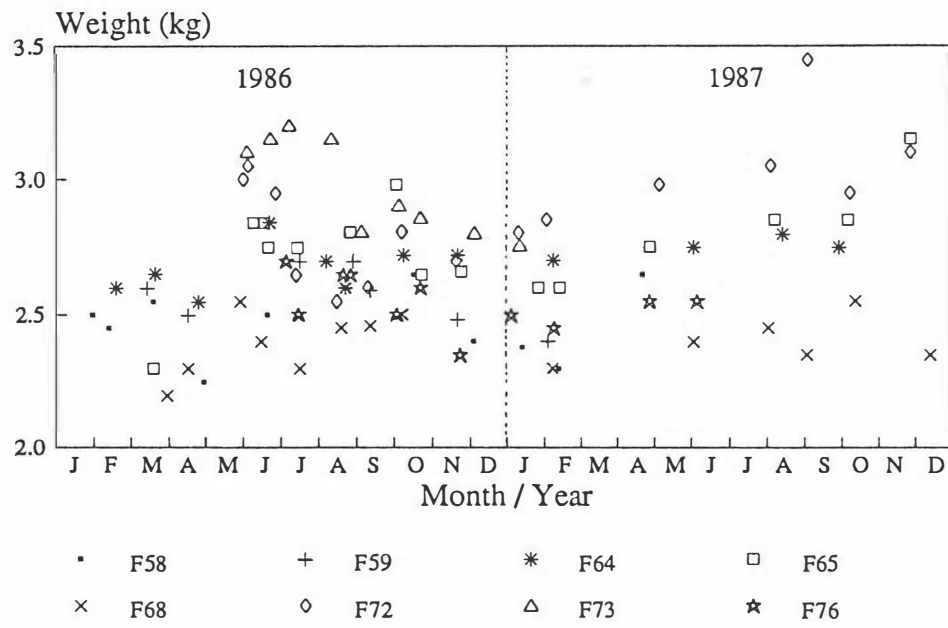


FIGURE 6.3: Seasonal changes in weight of breeding female kiwi at Paerata during 1986 and 1987.

basal body weight and time of egg-laying meant, however, that neither the monthly variation in weight ($F_{[11,99]} = 0.65$; $P > 0.05$) nor the apparent seasonal trend (linear component $F_{[1,99]} = 1.98$; $P = 0.16$; quadratic component $F_{[1,99]} = 3.11$; $P = 0.08$) were significant. Non-breeding females showed less seasonal variation in weight than breeding females (Figure 6.4).

Males

Males were more uniform in their seasonal body-weight changes than females, showing both significant monthly variation in weight ($F_{[11,75]} = 4.46$; $P < 0.0001$) and a significant annual trend with weights peaking in winter at the onset of breeding (linear component $F_{[1,75]} = 9.63$; $P = 0.003$; quadratic component $F_{[1,75]} = 7.16$; $P = 0.009$) (Figure 6.5).

Reproductive stage

Females

Females showed significant changes in body weight over the various reproductive stages ($F_{[6,39]} = 2.57$; $P = 0.03$) (Figure 6.6). There was a steady increase in body weight over the four months before laying, and on average females gained about 400 g over this period ($P < 0.05$).

A more detailed breakdown of the changes in body weight during the reproductive cycle was possible from sequential weighings of individual birds. Females that were weighed less than four weeks before laying, and again within one week after laying on average lost 250 g, or 6-11% (mean = 9%), of peak body weight for each egg they laid (range = 200-330 g; $n = 9$). When females laid a two-egg clutch this weight loss tended to be cumulative. For example, one female laid two eggs between 19 and 24 days apart, and lost 400 g. Another laid two eggs in less than 32 days and lost 500 g in weight. The interval between eggs laid in separate clutches was considerably longer than the interval between eggs laid in the same clutch (Table 6.2). This enabled some females that laid two one-egg clutches to regain much of their weight loss between eggs. One female gained 300 g in the four months between her first and second egg, returning to her peak pre-laying weight of 3150 g. Another female gained 400 g in the four weeks immediately before laying.

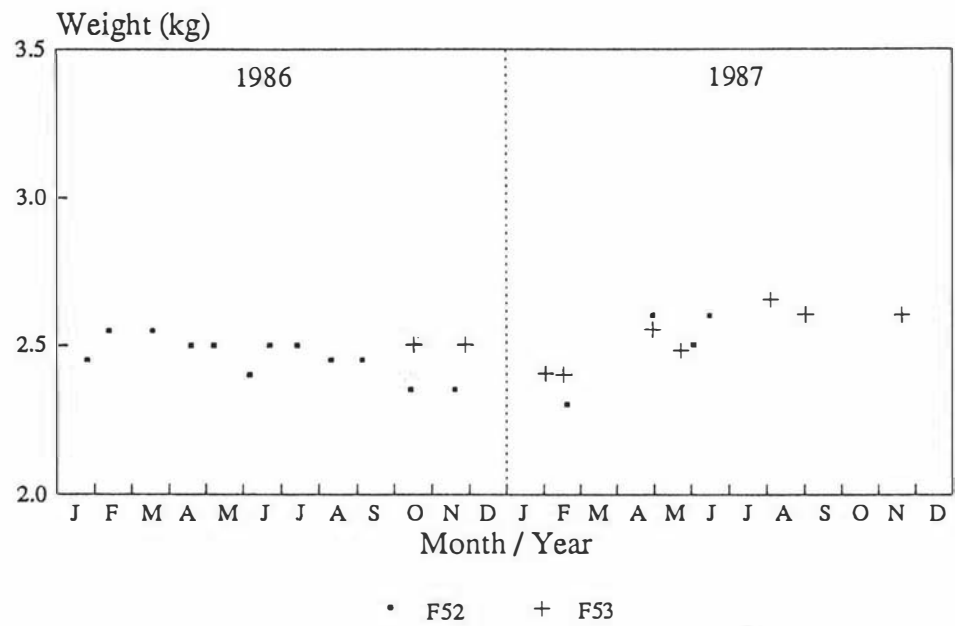


FIGURE 6.4: Seasonal changes in weight of non-breeding female kiwi at Paerata during 1986 and 1987.

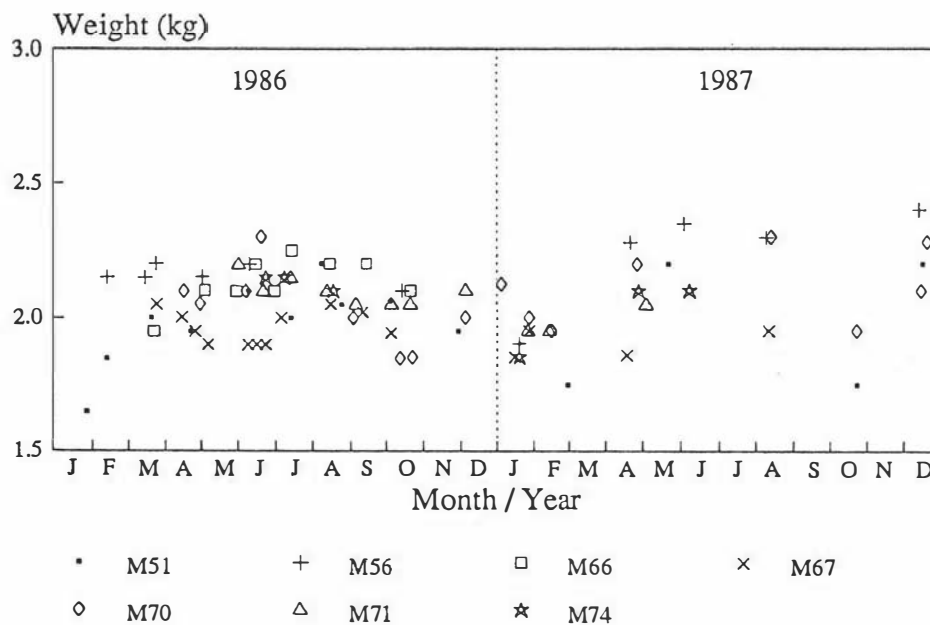


FIGURE 6.5: Seasonal changes in weight of male kiwi at Paerata during 1986 and 1987.

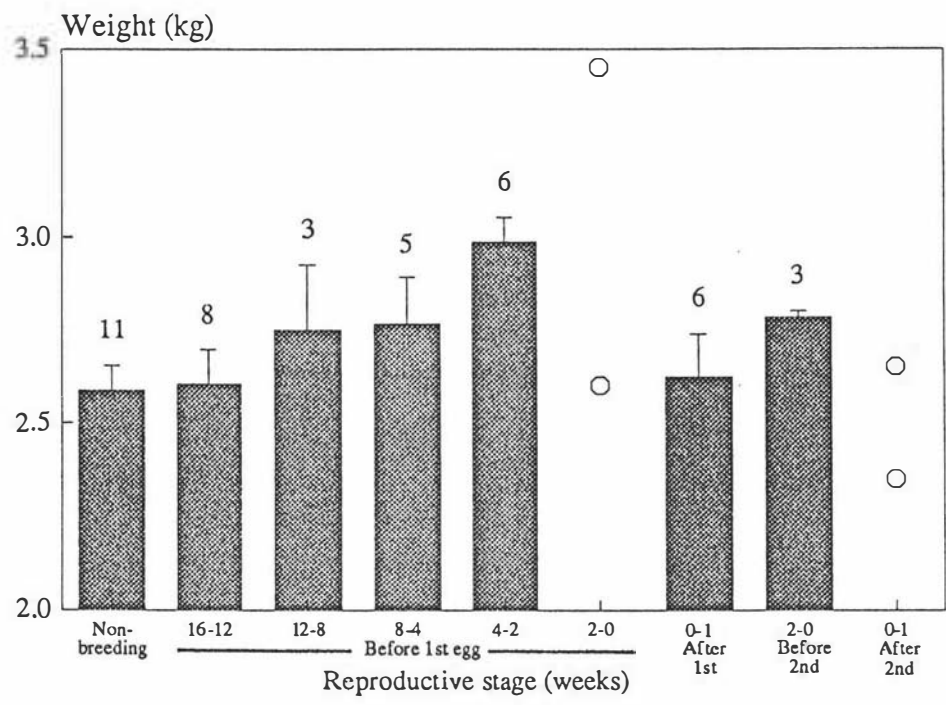


FIGURE 6.6: Weights of female kiwi (mean \pm SE) at Paerata at different stages in the breeding cycle. Numbers above the standard error bars indicate sample size. Individual data points are plotted for samples of two or less.

Males

Male body weight varied significantly during the reproductive cycle ($F_{[7,27]} = 7.72$; $P < 0.0001$) (Figure 6.7). Males were on average about 200 g heavier at the time their mates laid than during the non-breeding period ($P < 0.05$). Males in the late stages of incubation or brooding were lighter than at any other time (all $P < 0.05$), and were on average 420 g lighter than at the time of laying.

Individual males that were weighed both before and after incubating full-term (85-121 days) on average lost 380 g (range = 300-450 g; $n = 4$), or 14-20% (mean = 17%) of peak body weight. One male lost 350 g (15% of peak body weight) after incubating for just 47 days. As with females, some males were able to regain some of their lost weight between clutches. One male, for example, weighed only 1750 g after successfully hatching a chick from his first clutch. Eight weeks after the chick fledged his mate laid again. During this period he regained 450 g, bringing him back to his peak pre-breeding weight of 2200 g.

6.3.7 Hatching and chick behaviour

One male did not leave his nest for two nights while the chick was hatching. Another left his nest for 2 hours 30 minutes the night his chick hatched, but not until 0300 h (6 h 20 min. after sunset). Two other males did not change their pattern of incubation prior to the chick hatching. One chick left its nest for the first time when five days old, another when six or seven days old. Two females made frequent night-time visits to their nests during the week before, and two weeks after the eggs hatched. They were never found roosting in the nesting burrows during this period as McLennan (1988) observed in Hawkes Bay.

One chick between 10 and 14 days old was fitted with a radio transmitter for four days. On the first night after this the chick walked about 50 m from the nest, and the female spent half an hour within 20 m of the chick. On the second night the male, female and chick spent over 1 hour within 10-20 m of each other, about 25 m from the nest. On the third night the chick moved up to 90 m away from the nest, while the male fed 60-90 m away, and female 230 m away. The chick travelled 300 m from the nest on the fourth night, and the male spent most of this time over 400 m from the chick. The chick did not return to the nest that night, but roosted 160 m from there under a clump of dead blackberry. The female roosted 60 m, and the male 300 m from the chick on the day of fledging.

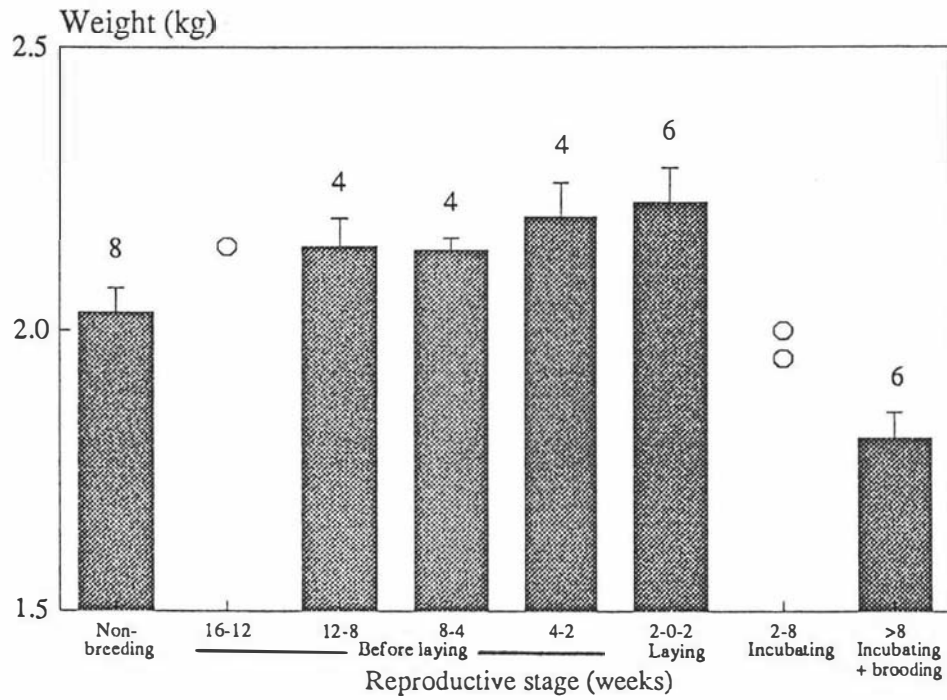


FIGURE 6.7: Weights of male kiwi (mean \pm SE) at Paerata at different stages in the breeding cycle. Numbers above the standard error bars indicate sample size. Individual data points are plotted for samples of two or less.

Three chicks left their nests for good, or fledged, when between 15-20 days old. The age of two others was not known. Two to four days before fledging four chicks weighed 225, 240, 240 and 250 g. One chick was weighed four times over a 10-day period (Table 6.3). This chick remained consistently heavier than captive reared chicks of similar age (Reid 1972a).

TABLE 6.3 Weight changes in a brown kiwi chick during the first twelve days after hatching.

Chick age (days)	2	4	10	12
Chick weight (g)	285	265	245	250

6.3.8 Breeding success

Of the 26 eggs laid and located only six (23%) hatched (Table 6.4). Sixteen eggs (62%) were deserted at various stages of incubation. Five (19%) were abandoned after being incubated nearly full term, apparently because the eggs became cracked or started to decay. Eleven others (43%) were deserted within six weeks of being laid. I probably caused the desertion of three nests (3 eggs) when I caught the males to change their transmitters. One of these nests was under a large clump of toetoe, one in the base of a tree stump, and the third in a 1.2 m long burrow. In all three cases the egg had only recently been laid, and in the last mentioned case the female was roosting with her mate.

Two other eggs failed to hatch because the male (M71) died about six to eight weeks into incubation. I found the male dead on his nest after returning from a four-week absence from the reserve. The male showed no skin or bone damage, so his death appeared not to have been predator-related.

No positive evidence was obtained that eggs in attended nests were preyed upon. However, two eggs (8%), both from double egg clutches, vanished without trace. A possum was found in another nest, containing two eggs, four weeks after it was abandoned. The possum denned in the nest on the following three days. It was not there on the fourth day, and the contents of both eggs were found to have been eaten. In both cases a hole 5-6 cm wide had been chewed through the side of the shell. The eggs in two nests were smashed into small ($<1\text{ cm}^2$) fragments before being abandoned. McLennan (1988) described a similar occurrence in Hawkes Bay, and he considered that the male may have been responsible. The smashing of the Paerata eggs was probably also the work of kiwi, but I would not rule out the possibility that kiwi other than the incubating males may have been involved.

TABLE 6.4 Breeding success of pairs of kiwi in Paerata Wildlife Management Reserve.

Pair (M/F)	Season	Clutch number	No. eggs	Fate
51/53	1985-86	1	1	Deserted 20/10/85, egg rotten
55/52	1985-86	1	1	Hatched, fledged by 24/1/86
56/58	1986-87	1	1	Deserted day of laying
		2	1	Hatched 15/1/87, found dead outside nest next day
57/62	1985-86	1	1	Egg smashed, nest deserted after 18 days incubation
		2	1	Egg smashed, nest deserted after 61-73 days incubation
61/59	1986-87	1	1	Nest deserted after 13-35 days incubation
		2	1	Nest deserted after at least 18 days incubation
51/65	1986-87	1	2	One hatched 6/2/87, other egg cracked and rotten
	1987-88	1	1	Hatched, fledged 24/10/87
		2	1	Nest deserted within 1 week of laying
66/68	1986-87	1	2	One hatched 16/1/87, fledged 3/2/87. Other egg abandoned
67/76	1986-87	1	1	Deserted within 4 weeks of laying
70/64	1986-87	1	2	One egg vanished about mid-term, other egg abandoned 94 days into incubation
	1987-88	1	2	M70 deserted nest on 22/10/87. M67 took over incubation 24/10/87 (see text). One egg hatched, fledged 17/12/87. Other egg vanished mid-term
71/72	1986/87	1	1	Deserted during first week of incubation
	1987-88	1	2	M71 found dead on nest 18/11/87
74/73	1986-87	1	2	Deserted after second egg laid
56/68	1987-88	1	1	Deserted 4-6 weeks into incubation
		2	1	Deserted first day of incubation
67/75	1987-88			M pirated another nest; see 70/64 above

One of the six chicks that hatched died shortly afterwards when it fell from its nest (Section 6.3.2). The other five survived to fledge, making the fledging success for the 26 eggs 19%. The average production per pair was only 0.3 chicks/year.

6.4 DISCUSSION

6.4.1 Variations in breeding behaviour between populations of brown kiwi

Females

Brown kiwi in Paerata show a similar seasonality in egg laying to those in Hawkes Bay (McLennan 1988), and both wild populations have a shorter, more distinct breeding season than those in captivity (Robson 1958; Goudswaard 1986). However, the annual egg production of Paerata kiwi of 1.5 eggs/pair was less than half that of kiwi in Hawkes Bay, which laid 3.5 eggs/pair/year (McLennan 1988), and only one-quarter that of some kiwi in captivity (Reid 1981a). The low number of eggs laid by females in Paerata was reflected also in their average clutch size. Most completed clutches in Hawkes Bay contain two eggs (McLennan 1988), while Paerata kiwi frequently laid single egg clutches, and some Paerata kiwi did not breed every year. It is unlikely that these differences are primarily genetically determined. Brown kiwi in captivity may lay up to six eggs/year (Reid 1981a), and many of these birds originated from Northland. In fact, many were salvaged from the local Tangiteroria district (Otorohanga Kiwi House, pers. comm.).

Clutch size is determined by a complex web of interrelating ecological and demographic factors, including food and mineral supply, weather, intra- and interspecific competition, nest predation, population age structure, and adult condition (Winkler & Walters 1983). Some of these factors are likely to be less important than others in explaining variations in clutch size in brown kiwi. The kiwi's nocturnal behaviour and unusual feeding habits, for instance, probably mean kiwi are subject to minimal interspecific resource competition. Perrins (1977) showed that if clutch size is large and predation pressure sufficiently high, then birds will be selected to limit their clutch size. Prior to the introduction of mammalian predators the weka (*Gallirallus australis*) was probably the only heterospecific predator kiwi had to contend with. While formerly widespread in the North Island (Bull *et al.* 1985), the weka is not currently extant in either the Paerata or Hawkes

Bay sites, and egg predation by mammalian predators was low in both locations. Even in captivity where kiwi are protected from predators clutches rarely exceed two eggs, so the observed variations in clutch size are unlikely to have been predator-related.

Weather differences between Northland and Hawkes Bay may influence clutch size to a limited degree. Kiwi breed in winter, and Northland averages slightly warmer winter temperatures than north-western Hawkes Bay (Tomlinson 1976). Otherwise their climates are not greatly dissimilar.

Age too may influence kiwi clutch size. Clutch size may increase from one to two eggs as females get older (Goudswaard 1986). This might account for some of the variation between Paerata and Hawkes Bay if Paerata females were predominantly young birds. Unfortunately the population age structures of kiwi in Hawkes Bay and Paerata are not known. This is unlikely to account, however, for no Paerata females laying more than two eggs per year.

What effects are adult condition and food and mineral supply likely to have had on clutch sizes in Paerata and Hawkes Bay? In the absence of any major pathological factor, adult condition and food and mineral supply are likely to be interrelated. Both may be affected by density-related intraspecific resource competition. Paerata females were more variable in their peak pre-laying weights (range 2600 - 3450 g) than Hawkes Bay females, although the sample size for Hawkes Bay was very small (three females over two seasons; McLennan 1988). The pre-laying weights of females in Hawkes Bay fell about the middle of the range of pre-laying weights in Paerata (i.e., about 3000 g), so in this respect these two populations did not differ significantly.

Hawkes Bay females regained little weight between successive eggs, but the intervals between eggs were short. When Paerata kiwi laid two eggs in the same clutch they, like the Hawkes Bay kiwi, regained little or no weight between eggs. However, when laying intervals were longer (eg. between clutches), Paerata kiwi often managed to regain some of their lost weight. The average 250 g weight loss for each egg laid by Paerata kiwi was about 70 g greater than the loss sustained by Hawkes Bay kiwi. Paerata eggs tended to be slightly heavier than Hawkes Bay eggs, but this does not account for all of the weight-loss difference. McLennan (1988) calculated that Hawkes Bay kiwi may obtain about 40% of the material for each egg from stored reserves. Repeating the calculation for Paerata kiwi suggests that these birds may have obtained about 54% of the material for their eggs from body reserves. This may indicate a difference in food resource availability between

these populations that could help explain the observed differences in clutch size. Alternatively, it may simply reflect differences in how soon before and after laying kiwi were caught and weighed.

Seasonal weight changes within a bird may give a rough indication of energy reserves in the form of stored lipids. They give no indication, however, of mineral reserves. If nutrient demands can not be met by re-metabolising body stores, they must be assimilated directly from food consumption (Drobney 1980). One element that is in high demand during the later stage of egg production is calcium. Although the kiwi eggshell is thinner than the allometry of other birds' eggs would predict (Silyn-Roberts 1982, 1983), it still represents about one-sixth of the calcium body store (Calder & Rowe 1977). Unlike most birds, kiwi have solid bones (Reid & Rowe 1978), lacking the soft inner medullary bone that other birds can rapidly metabolise as a store of calcium for use in egg production (Hurwitz 1978). Consequently Reid & Rowe (1978) speculated that female kiwi depend heavily on a dietary source of calcium over a short period of calcification. Hughes & Wood-Gush (1971) noted that chickens regulate their calcium intake in relation to demands for egg formation, and suggest that the selection of calcium by laying hens represents a "specific appetite". Existing knowledge of the natural diet of brown kiwi (Gurr 1952, Bull 1959; Watt 1971; Reid *et al.* 1982; Kleinpaste & Colbourne 1983; Colbourne & Powlesland 1988) gives no indication of seasonal changes in dietary selectivity in response to changing mineral and nutrient demands. However, it is possible that the number of eggs kiwi lay each season is affected by calcium availability.

There is one further factor that may help explain clutch size variations between Paerata and Hawkes Bay. Nest failure in both locations resulted in a change of nest site. Early nest failure had little or no effect on the time interval between eggs in Hawkes Bay (McLennan 1988). In Paerata, however, a change in nest site was consistently associated with a longer laying interval than existed between eggs laid at one site (Table 6.2). Conceivably all nests deserted at the one-egg stage were destined to be single-egg clutches. It is also possible, however, that the early loss/desertion of an egg may have inhibited the immediate laying of a second.

Why Paerata kiwi lay so many one-egg clutches and so few eggs per year remains unclear, but it is likely to be a response to a range of interacting factors.

Males

Incubating males in Paerata emerged, on average, 1 hour 45 minutes later (in terms of sunset time), and spent 1 hour 20 minutes less time feeding each night than males in Hawkes Bay (McLennan 1988). Over an 85-day incubation period this represents nearly five days more in nest attendance. This could be expected to show in terms of the number of days Paerata eggs take to hatch. Unfortunately, the small sample sizes and limited accuracy with which hatch dates were known in both populations prohibits confirmation of this.

Why did this substantial difference in nest attendance exist between these populations? Many birds show an inverse relationship between the time they spend incubating and the ambient air temperature (Drent 1975). This does not explain the difference here because Northland tends to have the warmer temperatures during winter and spring when kiwi breed (Tomlinson 1976). This suggests, if anything, that Northland kiwi should spend less time on their nests than Hawkes Bay kiwi.

Food availability also fails to readily explain the observed differences in incubation pattern between these populations. If Paerata kiwi spent less time foraging during incubation than males in Hawkes Bay because food was more abundant, they may have been expected to show similar, or less, weight loss during incubation than Hawkes Bay kiwi. Instead, Paerata males that incubated full term (85-121 days) lost about 1.8 times more weight than Hawkes Bay males (Paerata mean = 380 g; Hawkes Bay mean = 210 g (McLennan 1988)).

In both populations some eggs disappeared midway through incubation and others were smashed. McLennan (1988) considered that males may smash their own eggs. In the communally laying ostrich (*Struthio camelus*) the major hen recognises her own eggs and will selectively discard the eggs of the other hens from the nest (Bertram 1979). The high density of kiwi and extensive overlap of territories in Paerata (Chapter 3) increases the possibility that kiwi other than the incubating male might find nests and smash or remove eggs that were not their own. If this does occur, then the differences in incubation patterns between Hawkes Bay and Paerata may reflect differences in the requirement for nest guarding against conspecifics resulting from differences in population densities and social structures. This possibility needs further investigation.

Why did male 67 take over male 70's nest and incubate the eggs himself? If he was a young bird this conceivably could have been a case of "helper at the nest" (Emlen 1984). Male 67's age was not known, but his body measurements did not

alter noticeably over the two years he was radio-tracked (Appendix). Helper breeding systems typically lead to increased production and/or survival of young by the breeding pair(s) (Emlen 1984). This was not the case here as the father of the eggs (M70) did not revisit the nest after his desertion, and he and his mate did not re-nest that season. Helping at the nest could also have increased M70's productivity if the continuing demands of incubating those eggs threatened his survival. However, both M70's weight (1950 g) and condition at the time of his desertion were normal for that stage of incubation.

Male 67 had not bred successfully the previous season (1986-87) and he divorced and re-paired before the 1987-88 breeding season (Section 5.3). His new mate remained light and apparently did not lay that season. Male 70's nest was within M67's normal home range, so the nest takeover may simply have been a case of M67 mistaking the eggs for ones laid by his own mate. This raises questions about how nest sites are chosen, and how the female communicates the whereabouts of a newly laid egg to her mate. This information can be conveyed some days or even weeks after an egg is laid. McLennan (1988), for example, reported a male abandoning an old nest that contained a decaying egg, and moving to new nest site containing an egg that had been laid by his mate 19 days earlier.

Chicks

Kiwi chicks were entirely nocturnal in Paerata, as they are in Hawkes Bay (McLennan 1988). Chicks in captivity, in contrast, are often active during the day (Robson 1958; Reid & Williams 1975; Goudswaard 1986). The one chick I weighed repeatedly over the 12 days following hatching did not lose as much weight during this period as most chicks in captivity (Reid 1972a). This supports McLennan's (1988) suggestion that the extended hours of activity of captive reared chicks may be hunger-related. A similar argument has recently been used to explain diurnal foraging by adult brown kiwi on Stewart Island (Colbourne & Powlesland 1988).

Females in both Hawkes Bay and Paerata visit nests near the time of hatching and soon after. However, once the chicks have fledged neither parent appears to have anything further to do with them, although no fledged chicks have been radio-tracked for extended periods.

6.4.2 Productivity, predation and population management

Remarkably few brown kiwi eggs are eaten by predators. None of the attended eggs observed in this study were definitely taken by predators, and only 5% of attended eggs were eaten in Hawkes Bay (McLennan 1988). In comparison, Moors' (1983) study of 13 other species of bird (8 native and 5 introduced) in lowland bush showed an average loss of 39% of eggs to introduced mammalian predators. Jolly (1985a) found that weka ate up to two-thirds of eggs laid each season by the little spotted kiwi on Kapiti Island, so brown kiwi egg losses may be greater where their range overlaps with the weka..

The annual fledging rate of 0.3 chicks/pair compares with 0.5 chicks/pair/year in Hawkes Bay (McLennan 1988). If kiwi live to 20 years (Reid & Williams 1975), and breed from about their third year in the wild (captive kiwi can breed at two years of age (Goudswaard 1986)) then at 0.3 chicks/pair/year a pair could fledge about five chicks in their lifetime. Both chick and adult mortality would have to be very low for this production rate to be sufficient to maintain current population densities. No studies have yet been undertaken to investigate chick survival, but during their first year they must be highly vulnerable to predation. Until kiwi reach sexual maturity (about 2 years old) they are within the size of prey commonly taken by feral cats (Fitzgerald & Karl 1979), and are probably readily taken by mustelids. Paerata Reserve, and the surrounding farmland, had a high feral cat population (pers. obs.), and I caught one within 2 m of an unattended nest containing a young chick. During the study I saw seven ferrets in the reserve or on adjacent farmland, and managed to catch and kill four of these. Local farmers, some of whom had been in the district for over 30 years, reported ferrets to be recent colonists within the region. This opinion was supported by several Department of Conservation staff in Whangarei, and is grave news for Northland wildlife.

Although adult kiwi may be large and strong enough to fight off attacks by cats or mustelids, they too are not immune to predation. The recent devastating effect of one ravaging dog on the Waitangi kiwi population bears testament to this (Taborsky 1988a,b; Diamond 1989).

If we are to ensure the continuing survival of brown kiwi on the mainland we need to know more about chick survival, and the way predator pressure influences this. If predation of chicks is high there will be a need for ongoing predator monitoring and control in remaining kiwi populations.

ENDOCRINOLOGY

7.1 INTRODUCTION

Sex-role reversal, where the male is predominantly or solely responsible for incubation and brood care, occurs in less than one percent of bird species (Oring 1982). New Zealand's three species of kiwi are members of this group. Male and female great spotted kiwi sometimes share incubation (J. McLennan pers. comm.), but male little spotted and brown kiwi perform all of this task (J. Jolly pers. comm.; McLennan 1988). Kiwi eggs are allometrically large and energy rich (Reid 1971a,b; Calder 1978, 1979; Calder *et al.* 1978), and the incubation period (74-84 days in the brown kiwi (Reid & Williams 1975)) is exceeded only by the large albatrosses (Lack 1968; Rahn & Ah 1974; Calder *et al.* 1978). The atypical reproductive and behavioural characteristics of the kiwi provide an opportunity to investigate the endocrine regulation of sexually dimorphic breeding behaviours.

Little is known about the endocrine control of behaviour in sex-role reversed species. Most of this knowledge comes from recent studies of just two species: the spotted sandpiper (*Actitis macularia*) (Rissman & Wingfield 1984; Fivizzani & Oring 1986; Oring *et al.* 1986a,b), and Wilson's phalarope (*Phalaropus tricolor*) (Fivizzani *et al.* 1986; Oring *et al.* 1988). These studies indicate that the sex-role reversal shown in these two species is not based upon a reversal of the typical male/female plasma levels of androgens and estrogens. In both species androgen levels were 6- to 8-fold greater in pre-incubating males than in females, and females had higher levels of estrogens than males. However, reversal of the typical sex roles is not totally unrelated to hormonal changes. In both the spotted sandpiper (Oring *et al.* 1986b) and Wilson's phalarope (Oring *et al.* 1988) males tend to have higher plasma prolactin levels than females throughout the breeding season, and this difference was significant during incubation in the sandpiper, and during laying in the phalarope.

Rissman & Wingfield (1984) also found male sandpiper to have high levels of estradiol (values for estradiol given in this paper should read ng/ml, not pg/ml - see Fivizzani *et al.* 1986) that they thought might facilitate development of incubation behaviour and formation of the brood patch. However, nothing unusual was discovered about estradiol levels in Wilson's phalarope (Fivizzani *et al.* 1986).

There is a need to investigate the system of endocrine control of behaviour in other sex-role reversed species. In this chapter I describe annual and reproductive stage variation in plasma testosterone, progesterone and estradiol-17 β levels in a free-living population of radio-tagged North Island brown kiwi.

7.2 METHODS

Details of the study site, number of kiwi captured, and tracking techniques are presented in Sections 2.1 and 2.2.

7.2.1 Field sample collection

Radio-tagged kiwi were caught every 4-10 weeks where possible for weighing and blood sampling. Blood (0.6-2.0 ml) was drawn into a pre-heparinised syringe from a tarsometatarsal vein. The time from capture of a bird to the completion of blood collection ranged from 5 to 30 minutes. Samples (n=181) were collected opportunistically between 1000 and 0200 hours. After collection, samples were placed on ice and transported to the field base for centrifugation. Plasma was drawn off after centrifugation and stored in liquid nitrogen (-196°C) for later transport to Ecology Division, D.S.I.R., Lower Hutt. There the samples were transferred to an ultra-cold deep freeze (-80°C) where they were stored until analysis.

Serial blood samples were obtained from most birds to determine the changes in hormone levels at different stages of the reproductive cycle. The following categories were used:

Non-breeding - (both males and females) samples from December, January, February or March taken at least one month after the last egg was laid or nesting completed, but at least four months before the next egg was laid or incubation started. This corresponds with the period of least overt pair bonding behaviour, such as the frequency with which pairs roost together (Section 6.3.1).

Pre-laying - (both males and females) the period up to 16 weeks prior to the female of a pair laying. As time intervals between eggs were often long (Section 6.3.3), and sample sizes were small, data from first and second eggs were combined. For males this category was divided into four periods: 16-12, 12-8, 8-4 and 4-0 weeks prior to

their mate laying. For females pre-laying was divided into five periods: 16-12, 12-8, 8-4, 4-2 and 2-0 weeks before egg laying.

Incubation - (males only) actively incubating, or less than 24 hours after deserting a nest. These two groups were combined as they did not differ significantly from each other in their plasma levels of testosterone ($F_{[1,6]} < 0.01$; $P > 0.05$), progesterone ($F_{[1,6]} = 0.03$; $P > 0.05$) or estradiol ($F_{[1,6]} = 0.47$; $P > 0.05$). All but one of the males in this category were sampled during the first two weeks of incubation.

Brooding - (males only) males attending chicks.

Post-laying - (females only) samples collected less than two weeks after an egg was laid.

7.2.2 Statistical analyses

Bartlett's test (Sokal & Rohlf 1981) was used to test the normality of the data. When necessary hormone values were subject to \log_{10} -transformation to satisfy the assumptions required for parametric statistics. Month and reproductive stage data were analysed by one-way analysis of variance followed by Student-Newman-Keuls test to determine differences between hormone concentrations at specific stages of the annual and breeding cycles. Relationships between hormones were investigated with Pearson's correlation analysis.

7.2.3 Hormone analyses

All radioimmunoassays were performed by, or under the supervision of, Dr John Cockrem (Ecology Division, D.S.I.R., Lower Hutt). The assay methods were as follows (J. Cockrem pers. comm.). Plasma levels of testosterone, progesterone and estradiol were measured by direct radioimmunoassay. Duplicate 10 μ l aliquots of each sample were used for each hormone assay, with levels of steroid determined from standard curves prepared in steroid-free chicken plasma. All assays were performed in 6 x 50 mm polystyrene test tubes (Luckhams, Burgess Hill, U.K.).

Testosterone

Testosterone was measured using a kit from Farnos Diagnostica (Turku, Finland). The antiserum is specific for testosterone. Cross-reactivities with other steroids include 5α -dihydrotestosterone (10%), 5β -dihydrotestosterone (15%), 5α -androstene- 3β - 17β -diol (5.0%), and epitestosterone, androstenedione and estradiol (all <1.0%). The assay procedure was modified from the kit protocol and was as follows. Antiserum (40 μ l) was added to 10 μ l sample and incubated for 1 h at room temperature. Iodinated testosterone (40 μ l) was then added and the mixture incubated for 2 h. A second antibody solution (100 μ l) was added and incubated for 20 minutes. PEG (200 μ l; 10% in saline) was added immediately prior to centrifugation (2500 g, 15 minutes, 4°C). The supernatant was removed by aspiration, and the radioactivity in the precipitate counted in an LKB gamma counter (LKB, Bromma, Sweden). The unknown concentrations were determined from the standard curve which was fitted using a spline function.

Displacement curves for increasing amounts of kiwi plasma and of the testosterone standard were compared following logit-log transformation and found to be parallel. Testosterone (1.25-25.0 pg/tube) was added to kiwi plasma and was quantitatively recovered. The correlation coefficient between the amounts added and those assayed was 0.99. The limit of sensitivity of the assay (testosterone concentration two standard deviations below maximum binding) was 0.06 ng/ml.

Progesterone

Progesterone was measured using a kit from Farnos Diagnostica (Turku, Finland). Cross-reactivities of the antiserum with other steroids include 17β -hydroxyprogesterone (75%), 5α -dihydroprogesterone (8.8%), 5β -dihydroprogesterone (7.1%), 17α -hydroxyprogesterone, corticosterone, testosterone and estradiol (all <1.0%). The assay procedure was modified from the kit protocol and was as follows. Antiserum (10 μ l) and iodinated estradiol (10 μ l) were added to 10 μ l sample and incubated for 1 h at room temperature. Cold PEG (200 μ l) was then added and the tubes centrifuged (2500 g, 15 minutes, 4°C). The supernatant was removed by aspiration, and the radioactivity in the precipitate counted in an LKB gamma counter (LKB, Bromma, Sweden). The unknown concentrations were determined from the standard curve which was fitted using a spline function.

Displacement curves for increasing amounts of kiwi plasma and of the progesterone standard were compared following logit-log transformation and found

to be parallel. Progesterone (3.1-50.0 pg/tube) was added to kiwi plasma and was quantitatively recovered. The correlation coefficient between the amounts added and those assayed was 0.99. The limit of sensitivity of the assay (progesterone concentration two standard deviations below maximum binding) was 6 pg/ml.

Estradiol

Estradiol was measured using a kit from Diagnostic Products Corporation (Los Angeles). The antiserum is highly specific for estradiol. Cross reactivities with other steroids include estrone (1.3%), estriol (0.24%), and testosterone, progesterone, corticosterone and androstenedione (all <0.004%). The assay procedure was modified from the kit protocol and was as follows. Antiserum (10 μ l) was added to 10 μ l sample and incubated for 2 h at room temperature. Iodinated estradiol (10 μ l) was then added, followed by a 1 h incubation prior to adding 100 μ l cold precipitating solution (goat anti-rabbit gamma globulin and dilute PEG in saline). After 10 minutes the tubes were centrifuged (2500 g, 15 minutes, 4°C), the supernatant removed by aspiration, and the radioactivity in the precipitate counted in an LKB gamma counter (LKB, Bromma, Sweden). The unknown concentrations were determined from the standard curve which was fitted using a spline function.

Displacement curves for increasing amounts of kiwi plasma and of the estradiol standard were compared following logit-log transformation and found to be parallel. Estradiol (0.3-5.0 pg/tube) was added to kiwi plasma and was quantitatively recovered. The correlation coefficient between the amounts added and those assayed was 0.99. The limit of sensitivity (estradiol concentration two standard deviations below maximum binding) was 6 pg/ml.

7.3 RESULTS

7.3.1 Annual cycles of gonadal steroids

Testosterone

Male blood plasma testosterone levels varied significantly between months ($F_{[11,51]} = 4.56$; $P < 0.001$) (Figure 7.1). Testosterone levels increased dramatically between April and May ($P < 0.05$), remained high through until August, and then

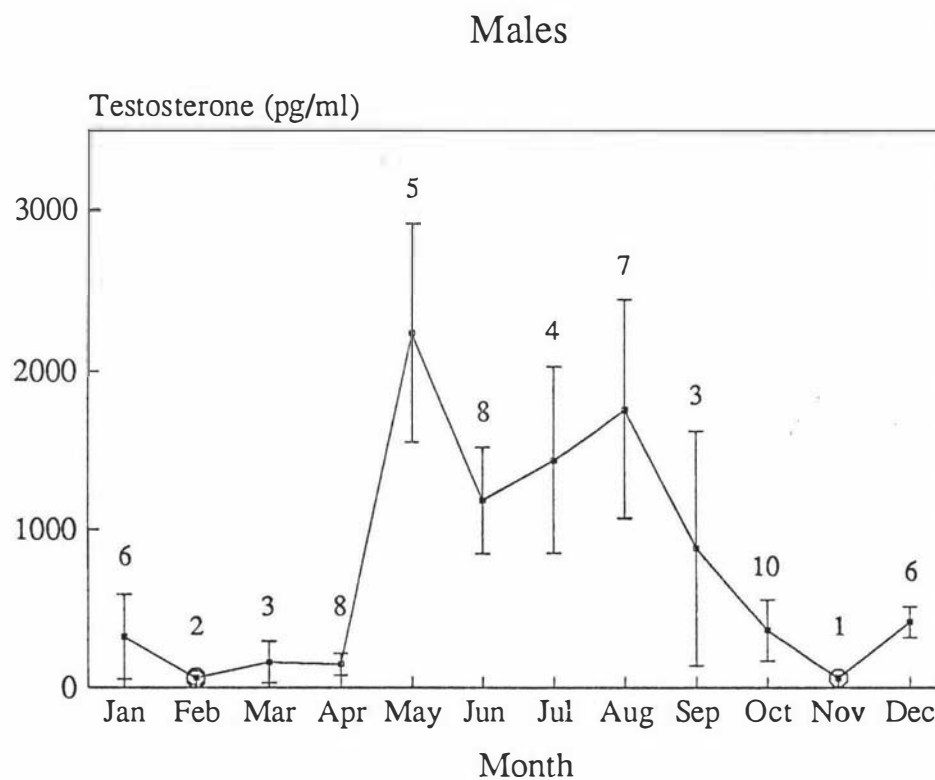


FIGURE 7.1: Plasma levels of testosterone (mean \pm SE) in male brown kiwi by month. Numbers above standard error bars indicate sample size. Individual data points are plotted for samples of two or less.

declined during September and October ($P < 0.05$). Testosterone concentrations then remained low until the following May.

Females, in contrast to males, showed no significant variation between months in testosterone ($F_{[11,95]} = 1.15$; $P > 0.05$), and tended to remain near or below the lower limit of assay sensitivity (60 pg/ml).

Progesterone

Neither males ($F_{[11,51]} = 0.75$; $P > 0.05$) nor females ($F_{[11,106]} = 1.38$; $P > 0.05$) showed significant monthly variations in plasma progesterone levels (Figure 7.2). In March females tended to have higher plasma concentrations than males, but the difference was not significant ($F_{[1,5]} = 2.99$; $P > 0.05$). In all the other months males tended to have higher levels of progesterone than females, and in May ($F_{[1,9]} = 8.25$; $P < 0.025$) and October ($F_{[1,23]} = 7.03$; $P < 0.025$) males had significantly higher levels.

Estradiol

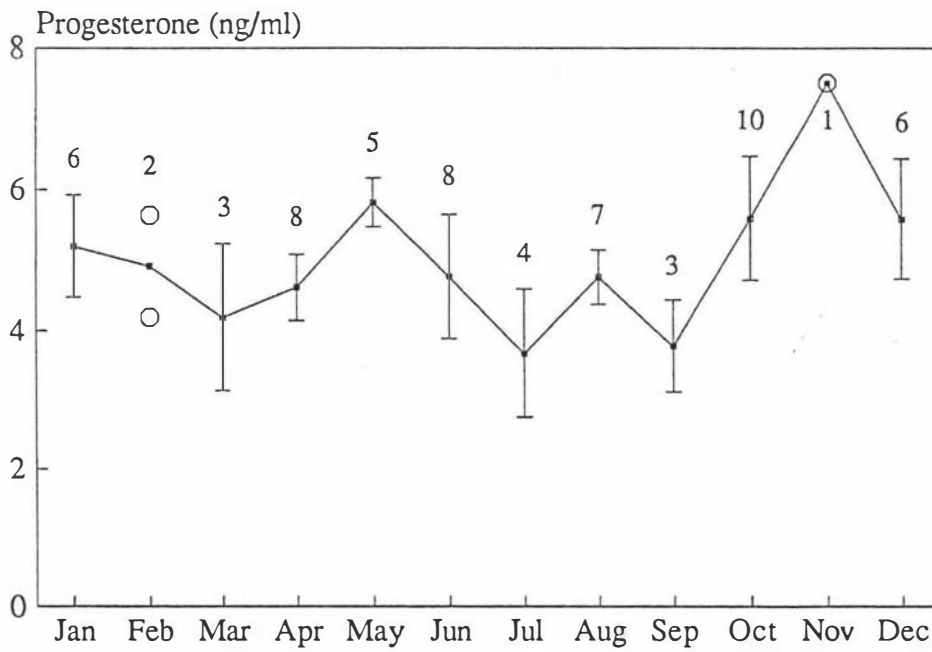
Circulating levels of estradiol varied significantly between months in both males ($F_{[11,51]} = 7.62$; $P < 0.001$) and females ($F_{[11,106]} = 28.5$; $P < 0.001$) (Figure 7.3). Estradiol levels increased dramatically between March and April in both male and female kiwi (both $P < 0.05$), rising from below minimum detectable levels in both sexes (< 6 pg/ml) in March, to average over 1600 pg/ml in males and over 2600 pg/ml in females in April. In males, estradiol remained high through until August and then declined significantly during September and October ($P < 0.05$). From the peak in April, estradiol in females declined steadily through May and June, and dropped significantly in July ($P < 0.05$). A short sharp rise in estradiol occurred in August, and dropped again in September ($P < 0.05$). Plasma levels of estradiol in females then continued to decline to low levels in January, February and March ($P < 0.05$). Males showed a rise in estradiol in August similar to that shown by females, but in this case the difference was not significant.

Male and female kiwi did not differ significantly in their monthly plasma concentrations of estradiol, except in April, when females had higher levels than males ($F_{[1,13]} = 6.15$; $P < 0.05$), and July, when males had higher levels than females ($F_{[1,8]} = 5.96$; $P < 0.05$).

Although testosterone and estradiol followed similar annual trends, the monthly plasma concentrations of these two hormones were not significantly

FIGURE 7.2: Plasma levels of progesterone (mean \pm SE) in male and female brown kiwi by month. Numbers above standard error bars indicate sample size. Individual data points are plotted for samples of two or less.

Males



Females

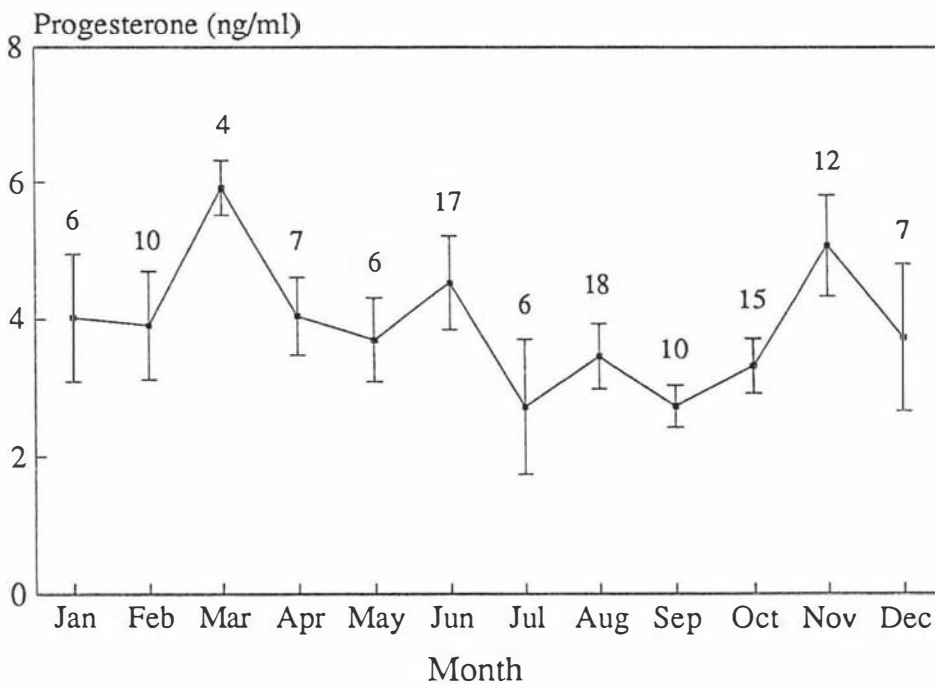
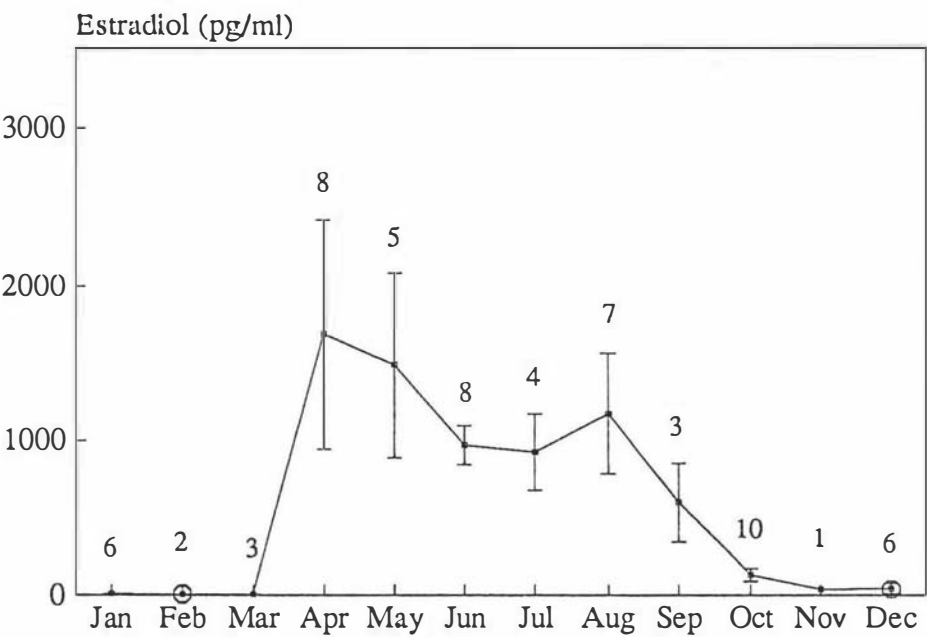
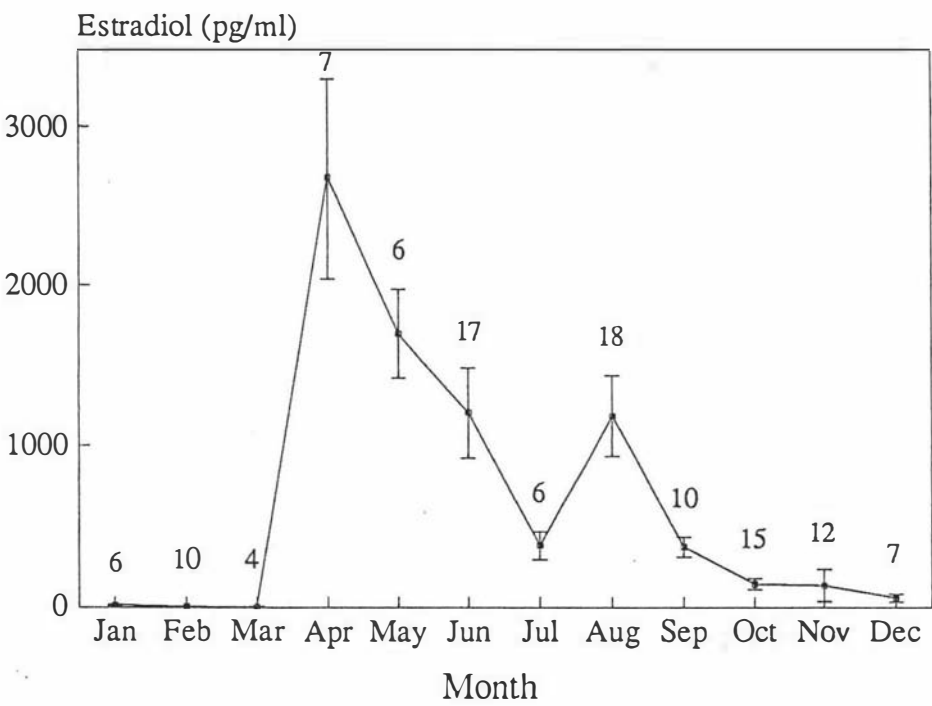


FIGURE 7.3: Plasma levels of estradiol (mean \pm SE) in male and female brown kiwi by month. Numbers above standard error bars indicate sample size. Individual data points are plotted for samples of two or less.

Males



Females



correlated in either males ($n=63$; $r=0.041$; $P>0.05$) or females ($n=107$; $r=-0.175$; $P>0.05$).

7.3.2 Hormonal cycles and breeding

Testosterone

Changes in testosterone levels during different stages of the reproductive cycle are shown in Figure 7.4. Plasma testosterone concentrations differed significantly between stages in both males ($F_{[6,26]} = 5.48$; $P<0.001$) and females ($F_{[6,28]} = 3.08$; $P=0.019$). In males, testosterone peaked between 12 to 4 weeks, and possibly up to 16 weeks before eggs were laid. Levels during this period were significantly higher than in non-breeding males, brooding males, or in males during the four weeks prior to egg laying (all $P<0.05$). Although testosterone levels tended to be higher during the 12-4 weeks before egg laying than in incubating males, the difference was not significant. Non-breeding and brooding males, and males less than four weeks before their mate laid an egg, did not differ significantly in their testosterone levels. However, incubating males had higher concentrations of testosterone ($P<0.05$) than brooding males.

In females, testosterone peaked 4-2 weeks before egg laying, when plasma testosterone concentrations were significantly higher than in non-breeding and post-laying females, and in females 16-4 weeks before laying (all $P<0.05$).

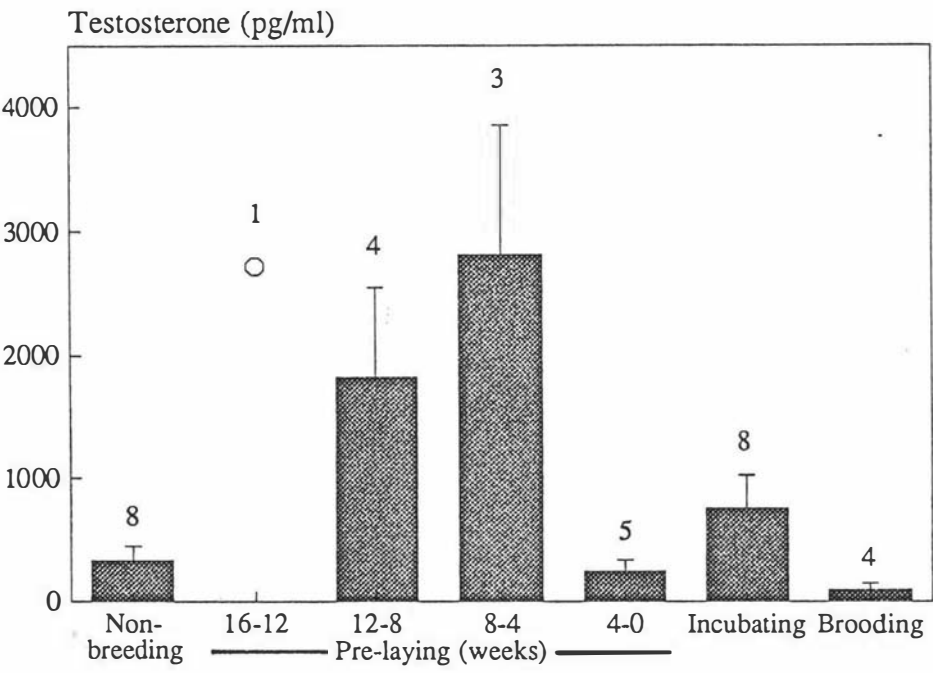
Brooding males and non-breeding females did not differ significantly in their levels of testosterone ($F_{[1,10]} = 2.44$; $P>0.05$), but both non-breeding males ($F_{[1,14]} = 5.93$; $P<0.05$) and males during the four weeks prior to egg laying ($F_{[1,11]} = 8.44$; $P<0.025$) had higher testosterone levels than non-breeding females. Even peak testosterone levels in females 4-2 weeks before laying did not significantly exceed minimum (brooding) levels in the males ($F_{[1,5]} = 2.66$; $P>0.05$). Peak testosterone levels were over an order of magnitude greater in males than those in females.

Progesterone

Neither male ($F_{[6,26]} = 2.04$; $P>0.05$) nor female ($F_{[6,35]} = 0.68$; $P>0.05$) kiwi showed significant variations in progesterone between different reproductive stages (Figure 7.5). Nor did males and females differ significantly in their

FIGURE 7.4: Plasma levels of testosterone (mean \pm SE) at different stages of the breeding cycle in male and female brown kiwi. Numbers above standard error bars indicate sample size. Individual data points are plotted for samples of two or less.

Males



Females

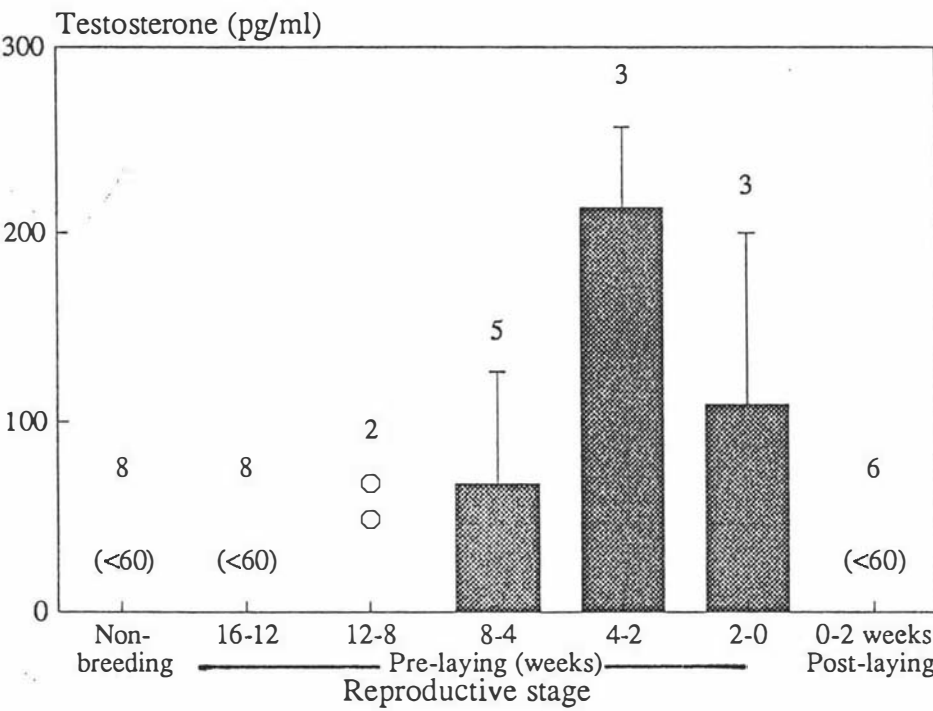
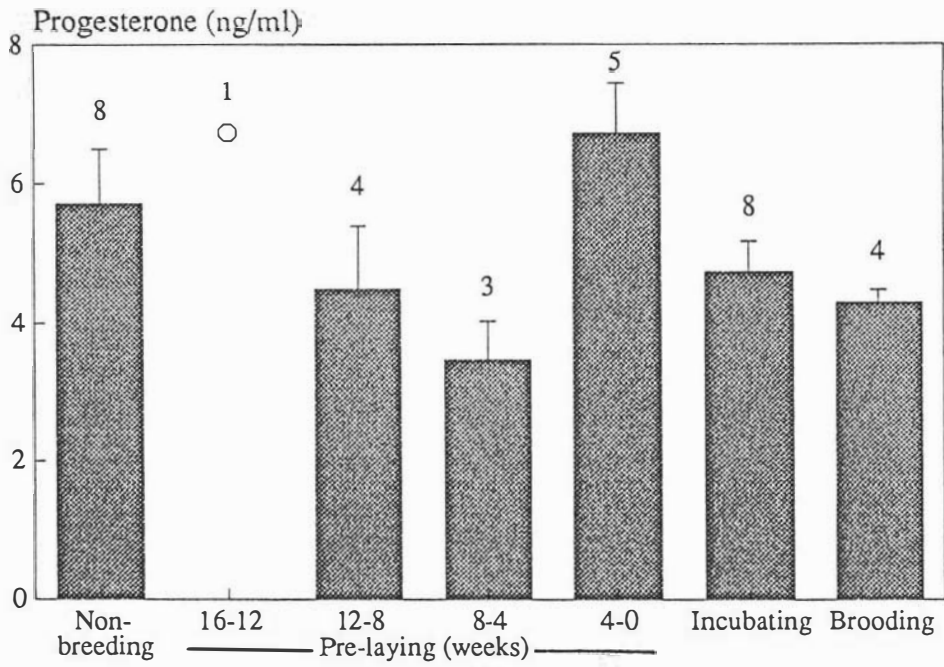
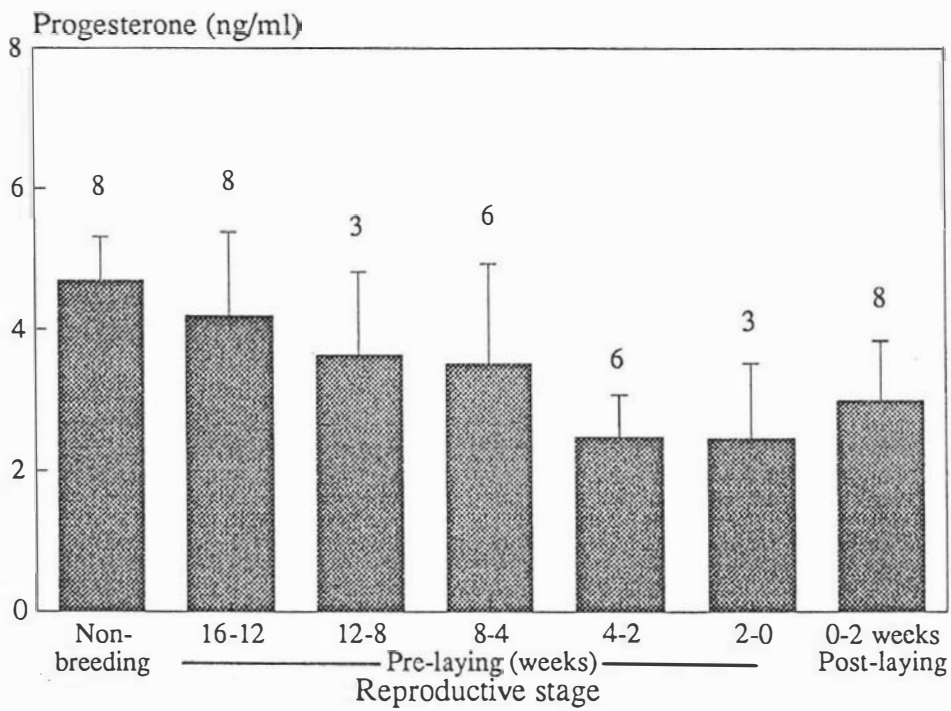


FIGURE 7.5: Plasma levels of progesterone (mean \pm SE) at different stages of the breeding cycle in male and female brown kiwi. Numbers above standard error bars indicate sample size. Individual data points are plotted for samples of two or less.

Males



Females



progesterone levels during comparable reproductive stages, except during the four weeks prior to egg laying, when males had significantly higher levels of progesterone than females ($F_{[1,12]} = 24.47$; $P < 0.001$).

Estradiol

Plasma concentrations of estradiol varied significantly with respect to reproductive stage in both males ($F_{[6,26]} = 7.43$; $P < 0.001$) and females ($F_{[6,35]} = 14.51$; $P < 0.001$) (Figure 7.6). Estradiol levels were significantly higher in incubating males, and in males during the 12 weeks prior to egg laying, than in non-breeding males (all $P < 0.05$), but did not differ significantly between non-breeding and brooding males. Breeding females, from 16 weeks before egg laying until two weeks after egg laying, had significantly higher plasma concentrations of estradiol than non-breeding females (all $P < 0.05$), but the apparent differences between pre-laying and laying stages were not significant. The apparent trend is that estradiol peaked twice - first 16-12, and second 4-2 weeks prior to egg laying, with levels declining during the two weeks before laying.

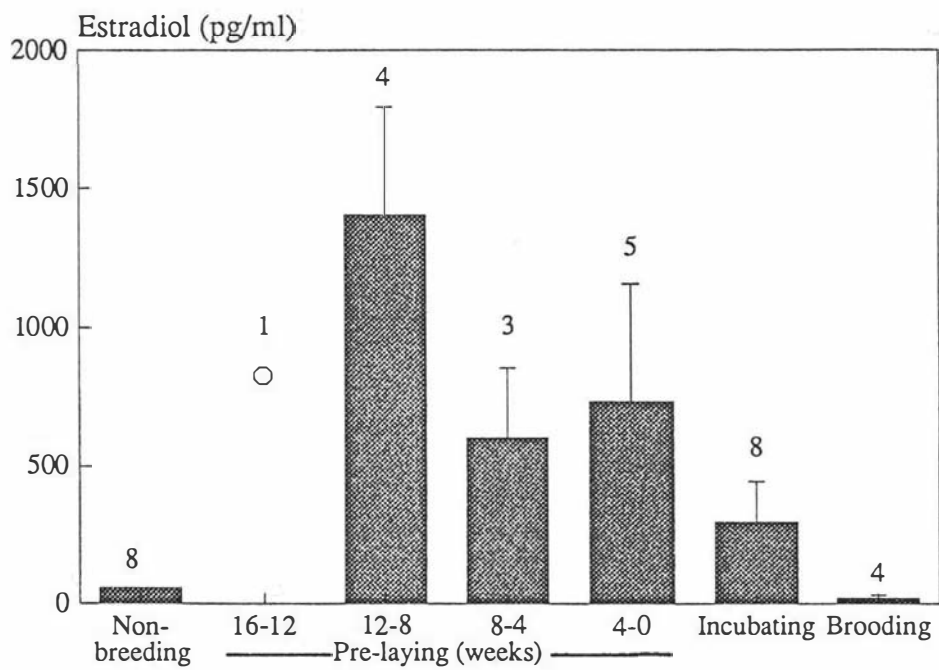
Males and females did not differ significantly from each other during any reproductive stage prior to egg laying, although males tended to have higher estradiol levels than females 12-8 weeks before laying.

7.4 DISCUSSION

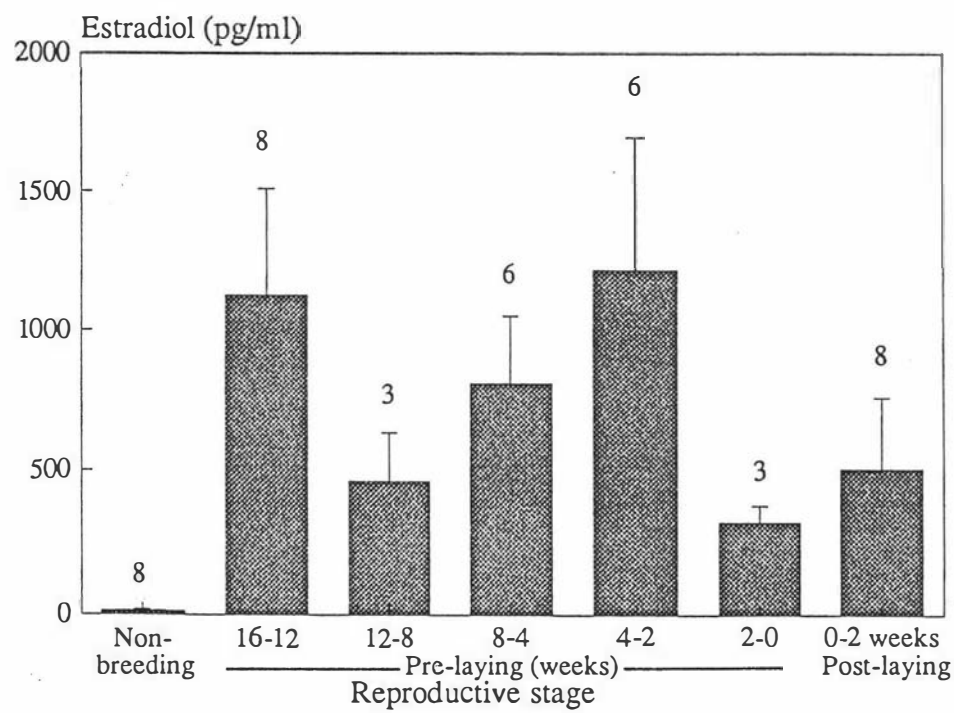
The results of this study add important new details to current knowledge of the endocrine regulation of avian sex-role reversal. Previous studies in this field have concentrated on just two species, the spotted sandpiper (Rissman & Wingfield 1984; Fivizzani & Oring 1986; Oring *et al.* 1986a,b) and Wilson's phalarope (Fivizzani *et al.* 1986; Oring *et al.* 1988). As in these species, sex-role reversal in the kiwi is ^{not} accompanied by a reversal of the normal male/female levels of androgen. However, male kiwi tended to maintain higher plasma concentrations of progesterone than females through most of the year, and the annual profile of plasma estradiol levels were remarkably similar in males and females.

FIGURE 7.6: Plasma levels of estradiol (mean \pm SE) at different stages of the breeding cycle in male and female brown kiwi. Numbers above standard error bars indicate sample size. Individual data points are plotted for samples of two or less.

Males



Females



7.4.1 Testosterone

Males

Male brown kiwi showed a dramatic increase in plasma testosterone levels between April and May. At mid to high latitudes the annual photocycle provides many species with accurate predictive information for the initiation of both gonadal growth and gonadal hormone secretion (for reviews see: Assenmacher & Jallageas 1980; Farner & Gwinner 1980; Wingfield & Farner 1980; Wingfield 1983). In Northland day length decreases (night length increases) by over an hour each month between 1 February (day length = 13 hr 52 min.) and 1 May (day length = 10 hr 40 min.) (N.Z. Meteorological Service data), so a first hypothesis would be that this may trigger the production of testosterone in males, and estradiol in both male and female brown kiwi (see discussion on estradiol).

Testosterone has been widely linked to male aggression, territorial defence, singing and courtship (Lofts & Murton 1973; Temple 1974; Arnold 1975; Searcy & Wingfield 1980; Harding 1981; Balthazart 1983; Dawson 1983; Ramenofsky 1984; Wingfield 1984b; Wingfield *et al.* 1987; Rehder *et al.* 1988). Kiwi are exclusively territorial in low density populations (McLennan *et al.* 1987), but territory integrity may be compromised in high density populations like Paerata (Chapter 3). Possibly both sexes contribute to territory defence, but their relative contributions are unknown. Reid & Williams (1975) considered the female the more aggressive sex, but males tend to be more vocal (Colbourne & Kleinpaste 1984). Monthly call rates were not systematically monitored in Paerata, but Colbourne & Kleinpaste (1984) reported calling rates in Waitangi State Forest to be seasonally cyclic. They recorded fewest calls per hour in January, a sharp rise in the calling rate between March and April, and peak monthly calling rates in June and July. Testosterone levels in brown kiwi in Paerata increased sharply between April and May, and remained high through to September, so this rise may reflect calling behaviour. Many spring breeding species show a vernal increase in testosterone that corresponds with territory establishment (Wingfield & Farner 1978a,b; Wingfield & Farner 1980; Silverin & Wingfield 1982; Wingfield 1984a). Kiwi start breeding in winter and their testosterone levels increase in autumn. In some populations kiwi retain the same mate and territory for several years (Colbourne & Kleinpaste 1983; McLennan *et al.* 1987; McLennan 1988). In comparison, Paerata brown kiwi frequently changed mates and territories between years (Chapters 3 and 5). These

divorces and territory changes usually occurred between January and April, one to four months before the May increase in plasma testosterone levels. High levels of testosterone can also be associated with increased mate guarding by paired males (Moore 1984; Ball & Wingfield 1987). Again, however, brown kiwi testosterone levels lagged behind the sharp April increase in the frequency with which bonded pairs roosted together (Figure 6.2; Section 6.3.1).

Peak testosterone levels occurred in male brown kiwi 16-4 weeks before their mates laid, and dropped sharply four weeks before laying. Incubating males tended to have lower plasma testosterone concentrations than males 16-4 weeks before their mates laid but the difference was not significant, possibly because of the small sample size. In most species testosterone levels drop with the onset of incubation irrespective of whether the male incubates (e.g. Wingfield & Farner 1978a,b; 1979; Silverin & Wingfield 1982; Wingfield *et al.* 1982; Rissman & Wingfield 1984; Fivizzani *et al.* 1986; Fivizzani & Oring 1986; Hector *et al.* 1986a,b). Plasma androgens apparently remain high only in nest parasite species such as the brown-headed cowbirds (Dufty & Wingfield 1986a). Indeed, high testosterone values may be incompatible with parental care in birds (Silverin 1980; Wingfield 1983; Hegner & Wingfield 1987). The relatively high testosterone levels in incubating male brown kiwi may not represent an unbiased sample, as three of the eight males were sampled up to 24 hours after they had deserted their nest, and all but one of the remaining males were sampled during the first two weeks of incubation. Testosterone levels in incubating Wilson's phalarope may resurge in less than one hour following egg loss (Oring *et al.* 1988), and testosterone levels decrease as incubation progresses (Fivizzani *et al.* 1986). However, Wilson's phalarope show a further sharp decline associated with hatching similar to that shown by brown kiwi. Oring *et al.* (1988) interpreted this as indicating that while testosterone declines during incubation to a level minimising sexual receptivity and allowing incubation, it may continue to function in maintaining a basal level of receptivity that allows sexual resurgence following clutch loss. More extensive sampling of incubating brown kiwi is required to determine whether a similar situation exists in this species.

Females

Testosterone levels in females also may rise during aggression in territory defence (Wingfield & Farner 1978a,b; Dufty & Wingfield 1986b). The relative aggressiveness and contribution to territorial defence of male and female kiwi is not

known, but female kiwi did not show significant annual increases in their testosterone levels. However, female aggression is not always associated with testosterone levels. Neither female spotted sandpiper (Rissman & Wingfield 1984; Fivizzani *et al.* 1986) nor female Wilson's phalarope (Fivizzani *et al.* 1986) show elevated androgen levels during periods of intense female aggression associated with mate acquisition. In these species female aggression may be due to changes in the receptivity of neural centres to moderate levels of androgen and estrogen (Fivizzani *et al.* 1986; Fivizzani & Oring 1986). The lack of a significant annual cycle of plasma testosterone in female brown kiwi does not, therefore, rule out the possibility that female kiwi contribute to territory defence.

The highest levels of testosterone in females occurred 4-2 weeks before egg laying. Testosterone is synergistic with estradiol and progesterone in the stimulation of enzymes involved in calcium mobilisation (DeLuca 1974; Tanaka *et al.* 1978), and in female mallards (*Anas platyrhynchos*) peak testosterone levels correspond precisely with the period of egg laying (Donham 1979). However, this explanation does not fit well with female kiwi, as their testosterone levels peaked 4-2 weeks before the shell would have been laid down. A more likely explanation of this peak may be that testosterone is involved in the stimulation of protein synthesis in the liver (Yu & Marquardt 1973a,b) and albumin secretion by the oviduct (Yu & Marquardt 1973c,d).

7.4.2 Progesterone

Neither male nor female brown kiwi showed significant monthly variations in plasma progesterone levels, nor did progesterone levels vary significantly between reproductive stages. However, in all months except March males tended to have higher plasma progesterone concentrations than females, and males had significantly higher levels than females during the four weeks prior to egg laying. Consistently higher progesterone levels in males compared with females has not previously been recorded. However, both incubating and brooding male spotted sandpipers have higher progesterone levels than equivalent status females (Fivizzani & Oring 1986), and prolactin levels in both the spotted sandpiper (Oring *et al.* 1986b) and Wilson's phalarope (Oring *et al.* 1988) tend to be higher in the males than in the females throughout the breeding season.

Males

The role of progesterone in the integration of the reproductive cycle of male birds is far from clear (Ball & Wingfield 1987). Silver *et al.* (1974) were unable to detect significant changes in plasma progesterone that correlated with the onset of incubation in captive male ring doves (*Streptopelia risoria*). Few studies have been made of progesterone in free-living male birds. In the collared dove (*S. decaocto*) (Péczely & Pethes 1979), the rook (*Corvus frugilegus*) (Péczely & Pethes 1982), the western gull (*Larus occidentalis*) (Wingfield *et al.* 1982) and the European starling (*Sturnus vulgaris*) (Ball & Wingfield 1987) there are no dramatic changes in progesterone levels with the onset and progression of breeding. Male black-browed (*Diomedea melanophris*) and grey-headed (*D. chrysostoma*) albatrosses (Hector *et al.* 1986b) show rises in progesterone just after the first copulation, a decline at laying, stable levels throughout incubation, and a sharp decline during the brood and guard period. In some species such as the wandering albatross (*D. exulans*) progesterone remains below minimum detectable levels for most of the year (Hector *et al.* 1986a). Male spotted sandpiper show no significant seasonal difference in progesterone (Fivizzani & Oring 1986), but they do show a correlation between progesterone levels and the exact number of days of incubation in the male, with concentrations being greater later in the season. Too few samples were obtained from different stages of incubation in the brown kiwi to determine whether such a trend exists in this species.

Females

In females progesterone is essential for the control of ovulation, although high levels generally occur for only a few hours prior to follicle rupture (see Sharp 1980 for review). In ring doves, Silver (1978) considered that progesterone produced a change from courtship behaviour to incubation. This may also be the case in European starlings where progesterone is at its highest level in females during laying, and decreases during incubation (Dawson 1983). However, the pattern is variable between species, and can not always be attributed to any particular reproductive event (see Donham 1979; Hector *et al.* 1986a,b).

Female brown kiwi are similar to female spotted sandpiper in not showing significant seasonal changes in progesterone (Fivizzani & Oring 1986).

7.4.3 Estradiol

The secretory profile of estradiol in the brown kiwi is particularly unusual, both in the extraordinarily high concentrations obtained in the males, and in the close similarity of the annual cycle in males and females. Both sexes showed an enormous increase in plasma estradiol levels in autumn, with levels rising from near minimum detectable levels in March, to average over 1600 pg/ml in males and 2600 pg/ml in females just one month later. As with testosterone in male brown kiwi, this sharp rise may be triggered by decreasing day length.

Males

In most avian species studied to date, estradiol levels are 2-4 times higher in females than in males (Fivizzani *et al.* 1986; review in Farner & Wingfield 1980). This pattern is not altered in the sex-role reversed Wilson's phalarope (Fivizzani *et al.* 1986). However, male spotted sandpiper have high estradiol levels that reach concentrations similar to those in non-laying females (Rissman & Wingfield 1984), and considerably higher than estradiol levels reported in monogamous males that share incubation with females (Wingfield *et al.* 1982). The estradiol levels observed here in incubating brown kiwi males are very similar to those reported in nesting spotted sandpiper (Rissman & Wingfield 1984). However, the plasma concentrations of estradiol in male brown kiwi 12-8 weeks before their mate laid were, on average, twice the peak estradiol levels observed in non-nesting male spotted sandpiper. Rissman & Wingfield (1984) considered that the high estradiol concentrations in male sandpiper might facilitate development of incubation behaviour and formation of the brood patch in these birds, as it does in females of other species (e.g. Hutchinson *et al.* 1967; Jones 1969; Silver 1978; Kern 1979; Dawson 1983). In some species brood patch development can be induced in both sexes with a combination of prolactin and estradiol (Bailey 1952; Selander & Kuich 1963). Manipulative experiments are required to confirm the role of estradiol in male brown kiwi.

Females

In females, estradiol is thought to be important in the development of the reproductive tract and in egg formation, possibly synergistic with testosterone (Yu

& Marquardt 1973a,b,c). Maximum estradiol levels have also been found to coincide with courtship and nest building in several species (Korenbrodt *et al.* 1974; Wingfield & Farner 1978a,b; Silver 1978; Dawson 1983).

In female brown kiwi estradiol levels were low in non-breeding birds, and high during the 16 weeks prior to egg laying. In captivity males tend to prepare the nest (Goudswaard 1986), although in the wild females tend to be more often found in burrows showing signs of recent excavation (pers. obs.). The relationship between nest building and estradiol levels in female brown kiwi is further obscured by the fact that they tended to nest in burrows that were excavated some years earlier (McLennan 1988; Chapter 6). Although not significant, estradiol levels in female brown kiwi tended to decline about the time of egg laying. This suggests that the primary roles of estradiol in female brown kiwi may be related to courtship or egg formation.

The endocrine regulation of sex-role reversal in the brown kiwi is similar to that in spotted sandpiper and Wilson's phalarope in not being accompanied by a reversal of androgen levels in males and females. Progesterone and estradiol cycles in brown kiwi are most similar to those in spotted sandpiper. The high levels of estradiol found in both these species are particularly intriguing, and indicate that there is much we do not currently understand about the endocrine control of sex-role reversal. The kiwi's peculiar behavioural and endocrinological characteristics make this a valuable species for future research.

GENERAL SUMMARY AND MANAGEMENT RECOMMENDATIONS

8.1 INTRODUCTION

The aim of this study was to describe environmental and physiological requirements for reproduction in the North Island brown kiwi to aid the design of effective conservation strategies for this species. To achieve this I investigated brown kiwi habitat use, spacing behaviour, pair bonding, breeding biology, and reproductive endocrinology. This chapter is presented in three sections. The first summarises the major findings of the study (Section 8.2). Second, the management implications of these findings are discussed and recommendations on the management of kiwi and their reserves are made (Section 8.3). Finally, some of the major deficiencies in current knowledge of brown kiwi are identified (Section 8.4).

8.2 GENERAL SUMMARY

Study site and general methods

1. The study was undertaken between September 1985 and April 1988 in Paerata Wildlife Management Reserve, Tangiteroria, Northland. The 210 ha reserve was calculated to contain 80-90 kiwi, or about one kiwi per 2.5 ha. This was comparable with the density of kiwi in Waitangi State Forest (Colbourne & Kleinpaste 1983), but about 10 times greater than that found in Hawkes Bay (McLennan *et al.* 1987). Thirty-two kiwi were caught and banded. Of these twenty-six (10 males and 16 females) were fitted with radio transmitters, and tracked for up to 116 weeks. A total of 3543 location records were collected, comprising 2096 daytime and 1447 night-time fixes. Radio-tagged kiwi were recaptured every 4-10 weeks for weighing and blood sampling.

Spacing behaviour and habitat use

2. Home range sizes were determined by four methods: convex polygon; outer boundary of chronologically linked observations (OBCLO); grid cell; and field worker. The average range sizes determined by the four methods were 40.5; 22.4; 15.8 and 30.7 ha respectively. Male and female brown kiwi did not differ significantly from each other in range size.
3. All range estimate methods were sensitive to the number of fixes. Therefore intra- and inter-population range size comparisons should only be made on set numbers of observations per individual collected by a uniform tracking procedure. Compared in this manner the range sizes of kiwi in Paerata were remarkably similar to those of Hawkes Bay kiwi, despite the 10-fold difference in population density between these sites.
4. The high density of kiwi in Paerata was maintained at the expense of territory integrity, and home ranges overlapped extensively. One 1-ha grid square within Paerata was used by at least 13 different kiwi.
5. The type of roosts Paerata kiwi used was influenced significantly by the presence of their mate. When roosting with a mate sites offering the greatest shelter and security were preferred. These were also the roosts for which there appeared to be greatest competition. The extent of competition for some roosts suggests that quality roosts may have been at a premium at Paerata.
6. Kiwi spent disproportionately long periods of time in open bush and near bush edges when foraging at night. Open bush tended to be used less in summer than in other seasons, although the kiwi were individually variable. How the night-time use of habitat related to food availability was not determined.

Dispersal between bush remnants

7. Eighty-three percent of the kiwi made use of bush outside the reserve, and all bush remnants isolated by less than 100 m of pasture were used by kiwi.
8. The maximum distance Paerata kiwi were ever observed to walk between bush remnants was 330 m, although more distant remnants were present.

Only a single pair of kiwi ever made an excursion of this distance. This suggests that 330 m may be close to the upper limit of how far kiwi will commute between bush remnants over open country. Longer migrations (of up to 1.2 km from the reserve) were made by kiwi using small bush remnants as a series of "stepping stones".

Pair bonding

9. Paerata kiwi were sequentially monogamous and had an annual divorce rate of around 50%. This contrasts with the long-lasting stable pair bonds observed in other kiwi populations.
10. Most divorces occurred between January and April. This corresponds to the non-breeding period. Divorce was not, however, obviously related to the previous year's breeding success of each pair, but there are few data.
11. In many cases (66%) divorce was followed by extreme home range movements of the affected kiwi. The propensity to move was not associated more with one sex than the other. With one exception, however, new pair bonds formed between birds that had previously been close neighbours. Following re-pairing the home range of these kiwi usually (83%) overlapped in large part with their earlier ranges.
12. Paerata contained an unbalanced sex ratio, with females outnumbering males by about 1.3 - 1.4 to 1. All males paired and attempted to breed each year, but some females did not.

Reproductive biology

13. The frequency with which pairs roosted together increased sharply two to four months before laying, peaking at 40% of days in May.
14. Eggs were laid over eight months of the year from July to February. Females laid their first egg between July and November. If a second egg was laid in the first clutch this occurred between August and December. Second clutch eggs were laid between October and February regardless of whether the first clutch contained one or two eggs.

15. Twenty nests were located. All but two of these were in burrows. None of the nest burrows showed signs of recent excavation. Replacement and second clutch eggs were always laid in a different site to the first. Old fragments of egg shell in some nests indicated that nest sites may be reused over a long time frame.
16. The time interval between eggs laid in a single nest was consistently and significantly shorter than the interval between eggs laid in different nests regardless of the success of the first nest, or of the stage at which it failed.
17. Paerata kiwi averaged just 1.5 eggs/pair/year - less than half the 3.5 eggs/pair/year laid by kiwi in Hawkes Bay (McLennan 1988). Furthermore, Paerata females never laid more than two eggs each in a season.
18. The average fresh weight of five Paerata kiwi eggs was 461 g. This is over 20 g heavier than eggs laid in Hawkes Bay (McLennan 1988), and nearly 100 g heavier than those laid in captivity (Reid 1981a).
19. Males did all the incubating, and were found on nests in all months except May and June. Females never attended males on the nest during the day except prior to, and for one to two days after laying. However, some females visited their nests at night, especially during the week before and two weeks after the eggs hatched.
20. Incubating males emerged every night to feed except when chicks were hatching. Paerata males emerged about 1 h 45 min later (in terms of sunset time) and spent 1 h 20 min less time off their nest each night than incubating males in Hawkes Bay (McLennan 1988). Males that incubated full term in Paerata lost about 1.8 times more weight than male kiwi in Hawkes Bay.
21. The fledging rate in Paerata was just 0.3 chicks/pair/year. This compares with 0.5 chicks/pair/year in Hawkes Bay (McLennan 1988).
22. Kiwi chicks (and adults) in Paerata were entirely nocturnal, as they are in Hawkes Bay.

Endocrinology

23. Sex-role reversal in brown kiwi was not accompanied by a reversal of the typical male/female plasma androgen levels, consistent with findings in other sex-role reversed species. Despite this, male kiwi tended to maintain higher plasma concentrations of progesterone than females through most of the year, and their annual profile of plasma estradiol was remarkably similar to that in female kiwi.
24. Testosterone levels increased dramatically between April and May in male kiwi and remained high through to September. This corresponds with the annual onset of breeding, and with the months of greatest calling activity (Colbourne & Kleinpaste 1984). Testosterone peaked in males 16-4 weeks before their mates laid, and dropped sharply during the four weeks before laying. This drop in testosterone near the onset of incubation is consistent with the pattern observed in other avian species. Females showed no significant annual change in testosterone levels. They did, however, show an increase in testosterone 4-2 weeks before laying.
25. Plasma progesterone levels did not vary significantly between months or reproductive stages in either sex. Intriguingly, progesterone levels were almost always higher in males than in females.
26. The secretory profile of estradiol was also unusual, with levels reaching extraordinarily high concentrations in males. Both sexes showed an enormous increase in plasma estradiol levels in autumn which may be triggered by decreasing day-length. When examined by reproductive stage, estradiol levels were highest in males during the 12 weeks prior to egg laying, and during incubation. This suggests that estradiol may facilitate the development of incubation behaviour and incubation patch formation in these birds. In females, estradiol levels were highest during the 16 weeks prior to egg laying, and may play a role in courtship behaviour and egg formation.
27. The peculiar behavioural and endocrinological characteristics of the brown kiwi make it a valuable species for further investigation.

8.3 MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

8.3.1 Introduction

The kiwi is New Zealand's most widely known bird, yet it has been the subject of remarkably little management-oriented research. This may reflect a degree of complacency over their well-being. The brown kiwi remains widespread even though 17 of New Zealand's 46 endemic species of land and freshwater birds have become endangered or extinct since the arrival of humans and mammalian predators (Mills & Williams 1979). In itself this does not indicate that brown kiwi continue to thrive. Anecdotal evidence, historical records and recent surveys in part of their range suggest that the North Island brown kiwi are in decline, even in some large reasonably unmodified forests (McLennan 1988). Concerns such as this were expressed at the 1986 Kiwi Research and Conservation Workshop (Powlesland 1988), and a list of research deficiencies were identified. The data presented in this thesis help address some of the issues raised at the workshop. In this section I discuss the implications of my findings for kiwi reserve design, and population and habitat management. Management recommendations are summarised in Section 8.3.5.

8.3.2 Reserve design

Reserves need to be designed to reduce the risk of local extinction of kiwi to an acceptably low level. Ideally, populations should be large enough to have a high probability of long-term survival - preferably measured in thousands rather than hundreds of years. If reserves are to be designed to achieve this, we require information on what constitutes a minimum viable population (MVP) for kiwi, and the area requirements of such a population. In this section I discuss the size requirements for kiwi reserves, and methods of improving and enhancing existing kiwi habitat.

Reserve size

Estimating MVP's is complex, and there is no "magic number" (Gilpin & Soulé 1986; Soulé & Simberloff 1986). As a general guideline, Frankel & Soulé

(1981) suggested that most vertebrate populations need to contain 500-1000 breeding individuals to have long-term viability. McLennan *et al.* (1987) used this estimate to calculate the habitat size requirements for brown kiwi in Hawkes Bay. They calculated that reserves in that part of the North Island need to be between 7500-15000 ha each to contain MVP's. This estimate was based on an exclusive area requirement of 30 ha per pair. Kiwi in Paerata also roam over 30 ha ranges. Home range overlap enabled these brown kiwi to obtain densities up to 10 times greater than those observed in Hawkes Bay (Chapter 3). Population densities similar to those in Paerata occur elsewhere in Northland (eg. Waitangi State Forest (Colbourne & Kleinpaste 1983) and Waipoua State Forest (Colbourne *In* Powlesland 1988, p. 16)). Therefore reserves of 750-1500 ha may be sufficiently large in this part of the country to contain MVP's of kiwi.

Variation in kiwi density and spacing behaviour in different locations means that reserve size requirements will vary across their range. A better understanding is needed of the factors determining kiwi population densities and spacing behaviour.

Corridors and "stepping stones"

While 83% of Paerata kiwi used bush remnants outside the reserve only 30% of kiwi crossed more than 120 m of grassland. No bush remnants separated by more than 330 m of open land were ever used by these kiwi (Section 4.3.2). This suggests that migration and hence gene flow is likely^{to} be low between islands of bush separated by much more than 300 m. Some Paerata kiwi travelled over much greater distances than this (up to 1.2 km) outside the reserve by using bush remnants as "stepping stones". The opportunity therefore exists to link separated areas of kiwi habitat with strategically placed bush "stepping stones".

Buffer zones and reserve enhancement

Kiwi can use marginal habitat surrounding reserves (Section 3.3.3; Chapter 4). The bush remnants around the southern end of Paerata contributed over 20 ha of useful habitat to the 210 ha reserve. Kiwi reserves should therefore incorporate buffer zones in their design. These zones need not be within the reserve, but could be maintained on adjacent land through cooperation with neighbouring landowners. Strategically placed pockets of bush can also encourage kiwi to migrate between separated areas of habitat.

A potential problem in using bush corridors and "stepping stones" in kiwi reserve design is the risk of exposing kiwi to increased predation. For this reason bush corridors and "stepping stones" should be kept as large as possible.

8.3.3 Reserve management

Good reserve design will lessen but rarely eliminate the need for management (Gilbert 1980). Management of a species can operate indirectly by manipulation of the habitat and environment, or directly by manipulation of the population. Population management is discussed in the next section (8.3.4), while this section concentrates on the management of the local environment. In particular, the effects cattle have on the quality of kiwi habitat and the effects of mammalian predators on kiwi survival and recruitment are discussed.

Cattle in reserves

The land now comprising Paerata has been grazed almost continuously by cattle during the past 40-50 years. During my study the reserve was grazed in two blocks. The larger 161 ha block was stocked with 90 head of cattle, while the smaller 40 ha block contained 25 cattle. Does the high density of kiwi in Paerata indicate that grazing and kiwi are compatible? Certainly some local landowners have argued this. An opposing view has been that wildlife reserves should be totally closed to cattle.

The solution to this problem was not a primary aim of this study, yet the issue is an important one. Kiwi are able to make use of a wide range of habitat types. Kiwi have made use of modified habitats such as exotic plantations (e.g. Waitangi State Forest) and pasture (e.g. Paerata) but in these situations they have also had access to substantial areas of native bush, scrub, or swamp refuges. These refuges are an important element in kiwi habitat that must be protected. Kiwi may be adversely affected where herbivores such as goats, possums or cattle remove the dense vegetation that can serve as daytime refuges for them. In addition to removing potential roost sites by grazing and trampling, overgrazing can reduce regeneration and threaten the long term integrity of the forest. Kiwi are extremely sensitive around their nests, and it was impossible to know whether disturbance by cattle contributed to the high rate of nest desertion observed in Paerata. Cattle may destroy shallow burrows and possibly crush kiwi inside. No kiwi were known to

have died this way during my study, but one nest and the egg it contained were found crushed by cattle one week after the incubating male had abandoned the site.

In contrast, there were two ways in which cattle may have been beneficial in Paerata. First, Paerata kiwi spent disproportionately long periods in open bush and near bush edges and less time in thick bush when foraging at night than expected from the relative abundance of these habitat types (Section 3.3.3). If this reflected food abundance then grazing may have improved this resource within the reserve. Second, Paerata contained substantial areas of grassland. The immediate removal of cattle would probably result in the grass growing long and rank inhibiting forest regeneration. More research is needed to determine the beneficial and deleterious effects of cattle and grazing on kiwi and reserves.

Predators

Few kiwi eggs appear to be lost to predators, except perhaps where the kiwi's range overlaps with that of the weka (Section 6.4.2). None of the attended eggs observed here, and only 5% of those in Hawkes Bay (McLennan 1988), were definitely taken by predators. Adult kiwi are large and aggressive, and can probably defend themselves and their nests against most of the introduced predators. A notable exception is the dog. In 1987 a single dog destroyed as many as 500 kiwi in Waitangi State Forest in little more than six weeks (Taborsky 1988a,b; Diamond 1989). It was chance that Taborsky's study, involving telemetry, was in progress at the time and recorded the incident. The similar destruction of other kiwi populations have no doubt gone unnoticed. Dogs pose a major threat to kiwi, and kiwi reserves should be strictly closed to them.

Juvenile kiwi are probably most at risk from introduced predators. Like adults they are vulnerable to dogs. In addition to this, until they reach sexual maturity (about 2 years old) they are within the size of prey commonly taken by feral cats (Fitzgerald & Karl 1979), and are also probably taken by mustelids. The annual fledging rate is extremely low in both Paerata (0.3 chicks/pair/year) (Section 6.3.8) and Hawkes Bay (0.5 chicks/pair/year) (McLennan 1988). Therefore even low rates of predation among juvenile kiwi are likely to have devastating effects on recruitment. Adults may live for 20 years or more, so there could be a considerable time-lag before the loss of recruitment became obvious.

Regular (at least annual) predator monitoring and control programmes need to be instigated in prime kiwi habitats and once every two to four years populations should be surveyed to provide an indication of population trends.

8.3.4 Population management

In this section the types of monitoring programmes needed are discussed and ways of managing small and isolated populations are suggested.

Population monitoring

One of the recommendations of the 1986 Kiwi Research and Conservation Workshop (Powlesland 1988) was to establish a banding programme at 10 sites so that information on the longevity, density and genetics of these populations could be obtained. The workshop also strongly supported the establishment of a "kiwi call scheme" to collect nationwide data on kiwi distribution and abundance. Good progress is being made with the collection of call rate data from around the country (R. Colbourne, pers. comm.), but more effort is required to ensure that key populations are surveyed regularly. Currently, Waitangi State Forest is the only forest to have been subject to systematic and repeated vocalisation (Corbett *et al.* 1979; Colbourne & Kleinpaste 1984; Rasch & Kayes 1985), and banding (Colbourne & Kleinpaste 1983, 1984; Taborsky 1988a,b) surveys. Many more populations must be similarly monitored if population trends are to be determined.

Population manipulation

Most remaining populations of brown kiwi are probably below minimum viable population size. The fragmented nature of many of the remaining kiwi populations and their habitat means that effective management of these small populations will be of vital importance to the conservation of this species. Encouragingly, recent studies on the risks of extinction (Pimm *et al.* 1988; Lewin 1989) indicate that the conservation value of small isolated sub-populations may previously have been underestimated. Some of the management options for isolated populations of the North Island brown kiwi are considered below.

First, populations of kiwi need to be identified on a region by region basis and the status of their habitat determined and secured. In some cases several small areas of habitat will be able to be linked with bush corridors and "stepping stones" (Section 8.3.3). Genetic studies are needed to determine the degree of homozygosity within these populations. In the absence of natural or effective

artificial corridors, management must deal with local extinctions and deficits in gene flow by transferring individuals (Soulé & Simberloff 1986).

Efforts should continue to be made to recover and relocate kiwi wherever they are threatened with land clearance. Captured birds should be used to restock protected reserves, or to establish artificial gene flow between isolated populations. Kiwi can respond well to relocation if handled correctly (M.A. Potter, unpublished data).

8.3.5 Summary of Management Recommendations

1. Kiwi reserves need to be large if they are to contain populations with long-term viability (500-1000 individuals). Just how large may vary between 750-15000 ha in different regions.
2. Smaller populations are also of conservation value and should not be neglected.
3. Bush corridors and "stepping stones" should be used to reconnect separated islands of habitat. "Stepping stones" should be separated by no more than 300 m of open ground to have a high probability of being used by kiwi, and should be as large as possible to minimise the rise of predation to kiwi using them.
4. In the absence of natural or effective artificial corridors, managers must deal with local extinctions and with deficits in gene flow by transferring individuals and by founding new populations.
5. Local landowners should be encouraged to plant and maintain bush remnants on land adjacent to kiwi reserves to supplement the habitat available to these kiwi.
6. Cattle should, for the moment, be maintained in low regulated numbers in Paerata. More research into the effects of cattle on kiwi and their habitat is needed before this management system is replicated elsewhere.
7. Kiwi reserves must be strictly closed to dogs. Both landowners and the general public must be made aware of the dangers dogs pose to kiwi populations.

8. Regular (at least annual) predator monitoring and control programmes must be instigated in prime kiwi refuges.
9. Key populations should be identified and surveyed regularly (every two to four years) to give an indication of population trends.
10. Kiwi recovery operations should continue to be undertaken wherever kiwi are threatened by land clearance. Captured birds should be used to: i) (re)establish populations in protected habitats; and ii) instigate a programme of artificial migration between isolated populations of kiwi to maintain gene flow.
11. A coordinated effort is needed between managers, researchers, landowners and interested volunteers if kiwi are to survive in remaining remnants of habitat.

8.4 FUTURE RESEARCH

Kiwi research has reached an exciting stage. Radio-telemetric technology has removed some of the major problems associated with studying these shy nocturnal bush-dwelling birds, and sufficient basic research has been undertaken to pose a new generation of questions. Some of the major issues that I believe need to be addressed are summarised below.

1. What are the factors regulating population density across the brown kiwi's range? Are the 10-fold population density differences between Northland and Hawkes Bay genetically determined, or do they reflect differences in habitat quality, habitat size, food availability, social organisation or predation pressure?
2. What are the mechanisms regulating spacing behaviour and territoriality in kiwi?
3. Are cattle beneficial, neutral or detrimental to kiwi and their reserves? Paerata contains fences that would allow the reserve to be divided into grazed

and ungrazed sections for direct comparison of the effects of these two management strategies.

4. What factors determine the fecundity of kiwi in different populations? Why do Paerata kiwi average just 1.5 eggs/pair/year when Hawkes Bay kiwi average 3.5 eggs/pair/year (McLennan 1988)?
5. What happens to chicks after they leave the nest? Nothing is currently known about chick and juvenile behaviour, dispersal or survivorship in the wild.
6. What are the factors regulating pair bond durability? Divorce in Paerata was not obviously related to breeding success but the sample size was small. What are the divorce rates in other populations of brown kiwi?
7. The endocrine regulation of breeding in kiwi offers a fascinating and wide-open field. For instance, why do male kiwi have such high plasma levels of estradiol? How does estradiol affect breeding behaviour and parental care in these birds? What activates the reproductive system in Autumn? How do other hormones integrate with the steroid hormones and compare with the pattern in other species?

Kiwis' unique allometry, behaviour and physiology make them of enormous potential value to the development of a wider understanding of avian breeding, behaviour and endocrine systems. Yet kiwi numbers are declining and their long-term survival prospects are marginal. The major thrust of future research must be management-oriented, and there must be a concerted effort to put management recommendations into practice.

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APPENDIX

KIWI BODY MEASUREMENTS

Summary of the body measurements of kiwi caught in Paerata Wildlife Management Reserve. The kiwi number (eg. 51) refers to the last two digits of its New Zealand Banding Scheme leg band. The prefix to these bands was "R 350". M = male; F = female; J = Juvenile; TMT = tarsometatarsus; L = left foot; R = right foot (all measurements in millimetres).

Kiwi	Date	Beak length	TMT			Middle toe	
			length	breadth	width	(L)	(R)
M51	26-1-86	99	88	14	11	46	
	11-2-86	98					
	9-6-86	97					
	25-5-87	98	89	17	12		
F52	24-1-86	142	99	16	11	55	
	11-2-86	142					
	30-4-87	141					
	2-6-87	141	96	16	11.5		
F53	10-10-85	133					
F54	6-10-85	128					
M55	17-3-86	105	86	14	11	51	51
	21-4-86	105					
M56	13-11-85	105.5	88	14.3	10.8	52	52
	6-12-85	105					
	11-2-86	105.5	93	14.5	11.5	52	52
	3-6-87	105					
	29-3-88	105					
M57	14-11-85	102	93	16	11	55	55
F58	1-10-85	141	95	16	13	51	52
	13-11-85	139					
	11-2-86	140					
	15-10-85	140					
F59	18-10-85	144	98	16	13	52	52
	14-3-86	144.5					
	16-4-86	144					
F60	28-9-85	129					
M61	14-10-85	104	92	13	11	49	48
	24-11-85	104					
	1-6-86	103.5					

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APPENDIX CONTINUED...

Kiwi	Date	Beak length	TMT			Middle toe	
			length	breadth	width	(L)	(R)
F62	14-11-85	128	120	16	13	60	61
F63	23-1-86	139	100	17	12	54	
F64	17-2-86	133	96	15.5	12.5	54	
	3-6-87	132	98.5	15.5	12		
	28-9-87	131.5		16	11		60
F65	19-3-86	120	95	16	11.5	55	56
	9-6-86	120					
	28-4-87	119					
	7-10-87	120	97	19	16	55	
M66	22-3-86	96	89	13.5	11	50	50
	30-5-86	96					
M67	24-3-86	97	89	15	10	54	53
	11-8-87	96					
	1-3-88	97	86	15.5	11	56	
	4-4-88	97.5	89	14.5	11	52	
F68	30-3-86	121	92	15	11	57	55
	29-5-86	121					
	3-6-87	122	89	15	11		
J69	31-3-86	74	74	11	9	48	47
M70	16-4-86	103	86	14	11	53	52
	27-4-87	103					
	3-6-87	102					
	13-8-87	102					
	22-10-87	102	86	15	13	53	
	5-4-88	103	85	15	11.5		51
M71	1-6-86	101.5	88	14	11	48	46
F72	1-6-86	132	98	17	12.5	66	61
	6-5-87	132	100	18.5	13		
	8-10-87	131.5	99	17	13	58	
	1-3-88	132	96	17.5	13.5		
	4-4-88	132	97	17	14	60	60
F73	4-6-86	146	103	16.5	12	58	58
	10-1-87	145	102	17	12	59	59
M74	23-6-86	102	88	14	11	51	53
	28-4-87	102					
	6-6-87	102	87	15	12	52	50
	1-4-88	103	87	15	12	48	

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APPENDIX CONTINUED...

Kiwi	Date	Beak length	TMT			Middle toe	
			length	breadth	width	(L)	(R)
F75	27-6-86	135		14.5	11	58	58
	6-12-86	135.5					
	2-3-88	135.5	92	16	12	59	
F76	5-7-87	123	95	15	12	55	57
	28-4-87	124					
	6-6-87	123	95	16	12	55	55
M77	21-10-86	98	82	12.5	10.5	47	47
F78	26-4-87	131	100	18.5	14	60	
	31-3-88	131	94	18	14	56	
F79	28-5-87	136.4	96	16	12	53	
F80	15-6-87	136.5	100	16	11	63	
F82	3-8-87	129	87	17.5	13	21*	53
	29-2-88	130	95	17.5	14		54
F83	15-8-87	134	98	16.5	13	58	58

* Toe amputated - only stump left.