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RANGE SIZE AND DENNING BEHAVIOUR OF BROWN KIWI, *APTERYX AUSTRALIS MANTELLI,* IN HAWKE'S BAY, NEW ZEALAND

Summary: Twelve kiwis were radio-tagged and tracked for 12-78 weeks in two sites in Hawke's Bay. Four bonded pairs had ranges of 19.1 to 42.3 ha (estimated by the convex polygon method), which were apparently defended against other kiwis. Two unmated females had ranges of 48.0 and 43.1 ha. Another unmated female occupied a narrow, circular strip, 5.4 km long, covering about 26 ha. The ranges of four kiwis in scrubland and eight in climax beech/podocarp forest were similar in size.

Kiwis roosted on 36% of days in burrows which they excavated themselves. On other days they roosted in natural subterranean tunnels, or in hollows under fallen trees, thick vegetation, or inside logs. Generally they roosted in a different place each day but often returned to sites they had used previously. Members of bonded pairs roosted apart on 92% of days, in different parts of their range.

In terms of current understanding of population genetics, reserves for kiwis in Hawke's Bay probably need to be at least 7500 ha in order to support a genetically enduring population of 250 breeding pairs. None of the existing reserves meet this requirement.

Keywords: Brown kiwi; ratite; *Apteryx auslralis mantelli;* home range; territory; roosting behaviour; roost sites; radio-tracking; reserve design.

Introduction

Kiwis are perhaps the most familiar of New Zealand's birds but, paradoxically, are also among the least well known. In the wild, signs of kiwis such as probe holes, shed feathers and foot prints, are encountered far more often than the birds themselves. Their secretive and nocturnal habits make them difficult to observe. Much of the existing information on diet (Bull, 1959; Watt, 1971; Reid *et al.,* 1982), reproduction (Robson, 1958; Kinsky, 1971; Calder and Rowe, 1977; Calder *et al.,* 1978; Calder, 1979; Reid, 1971a, 1971b, 1972a, 1972b), maturity and longevity (Robson, 1958; Clayton, 1972), and feeding behaviour (Buller, 1888; Wenzel, 1968) has come from studies on freshly dead or captive kiwis.

Published observations on wild birds are exceedingly scarce; indeed Buller's (1888) account of the behaviour of the three kiwi species (brown little spotted, *A. oweni,* and great spotted, *A. haasti)* is still a topical and informative reference. Colbourne and KIeinpaste (1983 and in prep.) recently described the movements and diet of brown kiwis in a pine forest in Northland. Other studies and currently in progress on the little spotted kiwis on Kapiti Island (Jolly, 1985).

Detailed autecological studies are needed so that reserves of appropriate size and quality can be established for kiwis in areas where they are threatened. In Hawke's Bay, North Island brown kiwis are near the southern limit of their range (Bull *et al.,* 1985) and live at low densities compared with those in Northland (pers. obs., J.A. McLennan). Although historical records are few, recent surveys (by J.A. McLennan) indicate that their numbers in 'undisturbed' indigenous habitats are declining. Land clearance has reduced their range substantially in the last 20 years. The current study, of which this paper is the first report, is aimed at determining causes of mortality, requirements of space and habitats, dispersal and settlement of young and reproductive output of brown kiwis in Hawke's Bay. This paper describes range size, dispersion and denning behaviour, and discusses the implications for the design of reserves.

Study Area

The study was undertaken in inland Hawke's Bay, at two sites (Waitere and Haliburtons) near the confluence of the Mohaka and Te Hoe Rivers. The Waitere site *(*176º 44'E, 39º 06'8) comprised 1650 haof regenerating scrub, sandwiched between openfarmland and young plantations of *Pinus radiata*. Theentire area was burnt early this century during an abortive farming attempt, and there have been several smaller fires in parts of the block since then. The present vegetation is a complex mosaic, ranging from

stands of 70-year-old kanuka *(Kunzea,* formerly *Leptospermum, ericoides)* to bracken *(Pteridium aquilinum)* and manuka *(Leptospermum scoparium)* associations less than to years old. The landscape consists of rolling to very steep hills, and narrow valleys with small, deeply entrenched streams. The easier slopes are covered by a thick layer of coarse Taupo pumice, permeated by a network of natural underground tunnels. Shallow Otupae soils and exposed bedrock predominate where gradients exceed 35°. The altitude varies from 290 m to 963 m a.s.l. Frost are common, and there is usually at least one heavy snowfall each winter. Temperatures in summer frequently exceed 28 °C.

Counts and mapping of kiwi calls between August 1982 and March 1984 indicated that Waitere contained about 30 adults, or one per 55 ha.

The study area at Haliburtons (176° 48'E, 39° 06'S) comprised 770 ha, about half of which was mature forest, dominated by tawa *(Beilschmiedia tawa),* podocarps *(Podocarpaceae)* and beech *(Nothofagus* spp.). The other half was young forest, dominated by kanuka, kamahi *(Weinmannia racemosa),* rewarewa *(Knightia excelsa)* and tanekaha *(Phyllocladus trichomanoides).* The area was formerly on the eastern edge of a large tract of forest extending from the Mohaka River to the southern Urewera Range, but recent clearing has left it isolated, bounded by either pasture or young plantations of pine forest. The altitude and climate are similar to those at Waitere, but the terrain is steeper; some valleys have sheer rock walls, 30-80 m high. Possums *(Trichosurus vulpecula)* and red deer *(Cervus elaphus)* have modified the vegetation extensively, and feral pigs *(Sus scrofa)* and goats *(Capra hircus)* are present in low numbers. In January 1985, the study area contained eight adult kiwis (5 females and 3 males) and two chicks which had fledged in December 1984. In the past to years, at least 12 kiwis have been killed in gin traps set for possums at Haliburtons (M. Haliburton, pers. common.), so the density there during the study may have been lower than formerly.

Methods

Capture

The majority of kiwis were caught using Labrador dogs, trained specifically for the task, and muzzled to prevent injury to birds. The dogs were most successful at night, when they could be directed to kiwis which had indicated their whereabouts by calling. A whistle or taped kiwi call was sometimes used to elicit calls, or to bring birds closer. One bird was captured in a pit-fall trap. Following capture, each bird had a radio transmitter attached to its leg, and was then released.

Design of radio transmitter package

The transmitters had either an internal loop aerial or an external whip aerial consisting of 0.7 mm diameter braided stainless steel wire encased in plastic tube. Those with a whip aerial gave a strong signal but were unreliable because the whip generally snapped off where it emerged from the package soon after the transmitter had been fitted. This problem was partly solved by reinforcing the weak point with heat-shrink tubing, and by ensuring that there was at least 2 cm of aerial within the package, so that some signal would still be emitted if the external part broke off. Transmitters with an internal loop aerial gave a weaker but adequate signal and were much more reliable. They could be detected with a three element hand-held Yagi aerial at distances of 50-800 m when kiwis were in daytime shelters, and at 200-2000 m when the birds were active at night. Both types of transmitter were powered with a 750-900 milliamp hour lithium cell battery, giving an average life of 10 to 13 weeks. The battery and transmitter were encased in epoxy resin which also anchored a V-shaped aluminium strip. This strip supported two plastic straps (hospital identification bands) that encircled the kiwis' tibio-tarsus. The straps had a fail safe locking device and were sufficiently soft to prevent injury. They broke naturally after 12-20 weeks in the field, so kiwis were not at risk of being encumbered indefinitely with a package, should either the transmitter or the battery fail. The complete package weighed 30-35 g (less than 2% of body weight) and was approximately 35 x 38 x 20 mm.

Number of birds captured and length of tracking period

At Waitere, five kiwis (2 males and 3 females) were caught and radio-tagged between September 1982 and May 1984 (Fig 1.). No information was obtained from one male, whose transmitter failed immediatey after he was released. The remaining birds were tracked for 11-36 weeks. At Haliburtons eight adults (3 males and 5 females) were caught and radio-tagged between February 1984 and December 1985 (Fig 1.). Three pairs were tracked for 33-78 weeks, and two unmated females for 12-29 weeks. Generally, five or more of the eight kiwis at Haliburtons carried a functioning transmitter between June 1984 and December 1985 (Fig 1.).

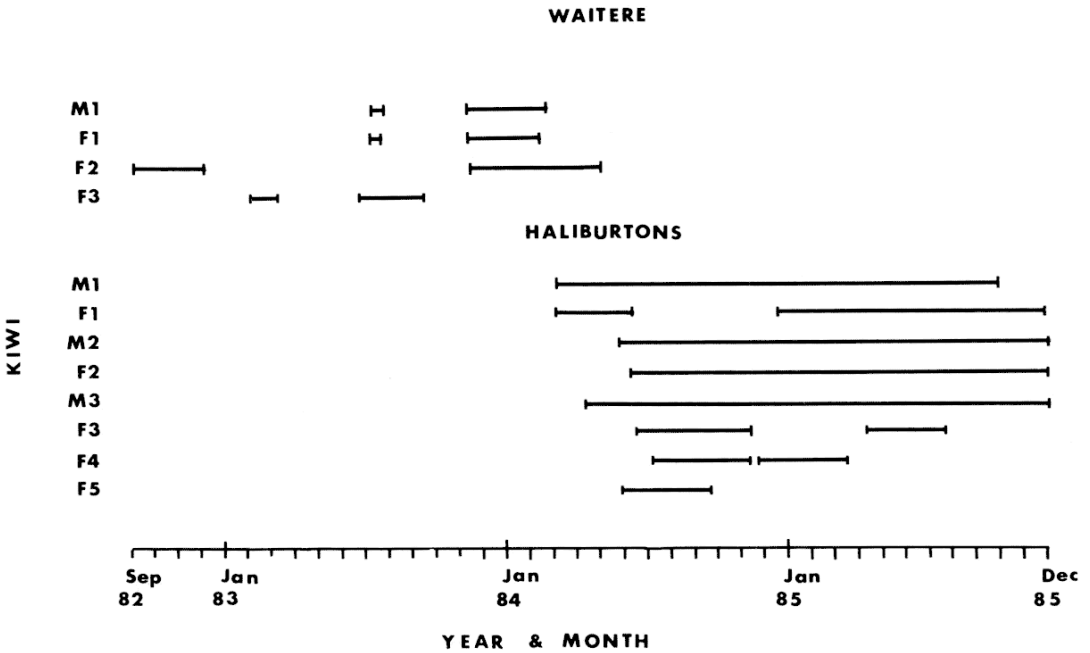

Figure 1: *Date of capture and length of time that each kiwi was radio-tagged at Waitere and Haliburtons. M = male, F = female.*

Frequency of tracking and description of daytime shelters

At Waitere, radio-tagged kiwis were usually located on two consecutive days each week, once during the day and one to three times at night. In some weeks, tracking was undertaken on three or four days. At Haliburtons kiwis were usually located once each day, four times per week, and also once a night, once or twice each week. The locations of kiwis in daytime shelters were determined precisely and later plotted onto a large-scale map. Locations at night were less precise because they depended mainly on triangulation and signal strength for a rough indication of the birds' whereabouts. If, however, a kiwi appeared to be outside its 'normal' range, as indicated by its use of daytime roosts, its precise location was established by following the signal to its source.

The roosts used by kiwis during the day were classified as hollow logs, surface vegetation, natural cavities, and burrows. Whenever a bird was located, the type of shelter it was in, the surrounding vegetation, its precise geographical location (e.g. side of steep bank), and its depth underground were noted. Records were also kept of whether the bird was visible, whether it was alone, and whether it or its mate had been found in that site previously.

Estimation of range size

Many methods are available for estimating the size of an animal's range, and may give similar estimates when applied to the same data. Polygon methods, for example, usually give larger estimates than do grid cell methods (Voigt and Tinline, 1980). For this reason we used three different methods (convex polygon, grid cell, and field worker estimate) to calculate the area of each kiwi's range. If a kiwi had been located fewer than 50 times, or tracked for less than 6 months, only the convex polygon method was used because we did not feel confident enough to use the field worker estimate, and the sample size was too small for the grid cell method.

In the convex polygon method (Southwood, 1966), the home range is defined as the smallest convex polygon enclosing all the points. It is generally considered to give a good indication of the shape of an animal's range (Hough, 1982) but has two disadvantages: the polygon is very sensitive to points on the periphery of a range, and it may include large areas which were never visited, especially when the range is of irregular shape.

Grid methods do not rely on a single contour around extreme points, but sum the frequency of occurrences in each of a number of squares (Adams and Davis, 1967). We used a grid with 20 x 20 m cells, appropriate to the error in plotting fixes. A cell was counted as used if a kiwi was recorded either in it, or in a contiguous cell. After all the fixes had been plotted, islands of used cells were connected to their nearest neighbours on the assumption that the kiwi had moved between them by the shortest route. Cells intersected by this imaginary path were considered used, but their immediate neighbours were not. The home range was estimated as the total area of the used cells.

The third estimate of home range size and shape (field worker estimate) was derived by drawing a boundary line by hand, taking into account radio fixes and additional observations on the locations of faeces, footprints and probe holes. Areas which the birds never used, such as rock walls, were excluded. MacDonald *et al*. (1980) acknowledged that this method of calculating home range left room for 'wishful thinking' by the biologist, but argued that it enabled spatial relationships to be evaluated realistically.

Correction for small sample size

The relationship between cumulative number of locations and range size was established for six kiwis at Haliburtons (Fig 2). Range estimates calculated by the convex polygon method were generally stable after 35-80 radio fixes, when each subsequent set of five locations increased range size by less than *1070*. Grid cell ranges did not stabilise, even after 100-150 locations, and are therefore conservative estimates.

Four of the ranges (three at Waitere and one at Haliburtons) were derived from 24 or fewer locations, insufficient for a stable estimate by the convex polygon method. Their probable total size (corrected area in Table 1) was estimated using the relationships shown in Fig. 2.

Results

Range size of kiwis at Waitere and Ha/iburtons

Convex polygon estimates of the ranges of the 12 radio-tagged kiwis varied from 14.1 ha to 134.4 ha, with an average of 39.5 ha (Table 1). Grid cell

Table 1: *Range size (ha) of kiwis at Waitere and Haliburtons. Estimates of range size calculated by the convex polygon method, grid cell method, and field worker estimate are listed for comparison. The 'corrected area' is an estimate of the range size that would have resulted from the convex polygon method, given a larger number of fixes (Fig.* 3). *The data from bonded males and females were pooled to give the area occupied by each pair.*

Bird	Radio fixes	Weeks tracked	Grid Cell area	Convex polygon area	Corrected area	Field worker area	Pair
			Waitere				
M1	22	15	-	12.6	16.5	-	19.1
F1	16	14	-	10.6	14.1		
F2	52	37	15.9	31.2	-		
F3	24	12	-	36.2	48.0		
			Haliburtons				
M1	139	78	16.8	25.4	-	23.2	42.3
F1	72	50	17.0	41.0	-	30.2	
M2	166	61	15.4	21.6	-	18.9	33.3
F2	124	63	20.0	32.5	-	24.8	
M3	175	69	19.5	38.8	-	36.7	42.0
F3	77	33	19.1	41.1	-	39.4	
F4	50	27	16.9	134.4	-	26.0	
F5	24	12	-	32.6	43.1		

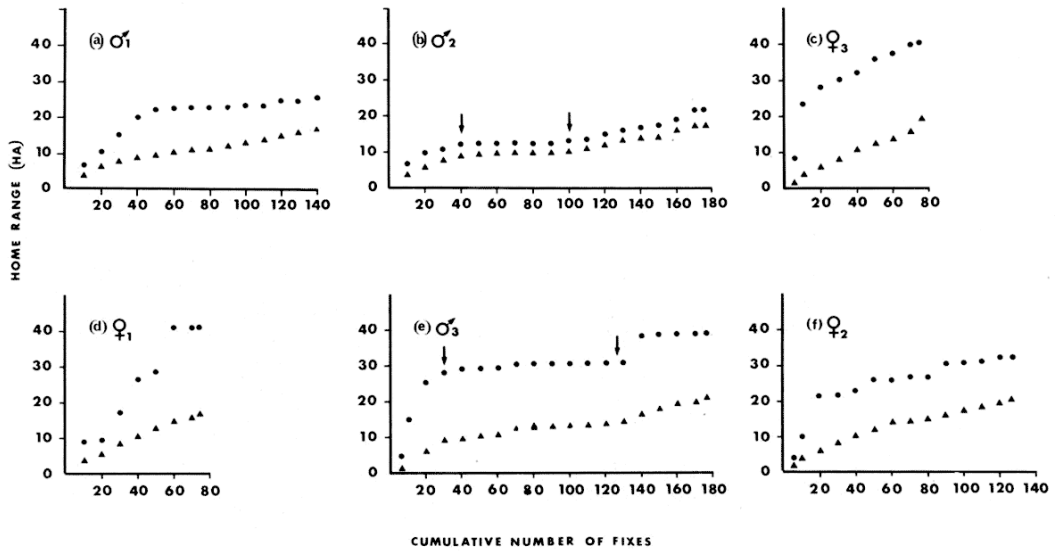

Figure 2: *The relationship between number of locations and estimated home range size for six kiwis at Haliburtons.* ● = *convex polygon estimates,* ▲= *grid cell estimates. The arrows indicate when males began and finished incubation.*

estimates were consistently smaller than those of the convex polygon method, and are undoubtedly conservative. We feel that the field worker estimates are the most accurate; in most instances they were 10-200/0 smaller than the convex polygons, but 20-40% larger than the grid cell estimates (Table I). Our claim is well illustrated by Female four at Haliburtons, who lived entirely within a narrow, circular strip around the ranges of three pairs. Our estimate of her range is 26 ha. The convex polygon estimate (134.4 ha) includes the territories of the other birds (which we know she seldom entered), while the grid cell estimate (16.9 ha) is based on too few locations to be realistic.

Mean range size (based on a combination of field work estimates and corrected polygon estimates) did not differ significantly between Waitere (27.5 ha) and Haliburtons (30.3 ha), but samples are small. The greatest axis of all but one of the ranges was over 500 m, and in three it exceeded one kilometre. The circular route travelled by Female four (unmated) at Haliburtons was 5.4 km. It generally took her 4-7 nights to walk around it. Two other unmated females (Female 3 at Waitere and Female 5 at Haliburtons) had ranges similar in size and shape to those of mated females.

Females tended to have larger ranges than males although the difference was not significant (^{2} = 35.9 and 25.6 ha respectively, df= 7, t= 1.61, p >0.05, Table 1). In bonded pairs, the male lived almost entirely within the range of his mate, but there was usually a portion of her range that he seldom or never used. None of the radio-tagged females at Haliburtons or Waitere had ranges containing more than one male.

Overlap of ranges

The three pairs at Haliburtons had contiguous ranges with one or more mutual boundaries (Fig. 3). These boundaries sometimes, but not always, coincided with firebreaks, roads, ridgetops, streams or changes in vegetation. Paired kiwis seldom entered the ranges of their neighbours. Males were found intruding four times (0.83% of 480 locations) and females four times (1.5% of 273 locations). On two occasions, intruding males were found sheltering in burrows which had been dug and used recently by the residents.

Unmated females entered the ranges of other kiwis significantly more often than did paired females (12% of 74 locations; ^{2}= 18.0, df= I, p<0.00l). Female four at Haliburtons entered the range of every pair at least once, and some ranges several times. Twice she sheltered in burrows that had been excavated and used previously by paired birds. The

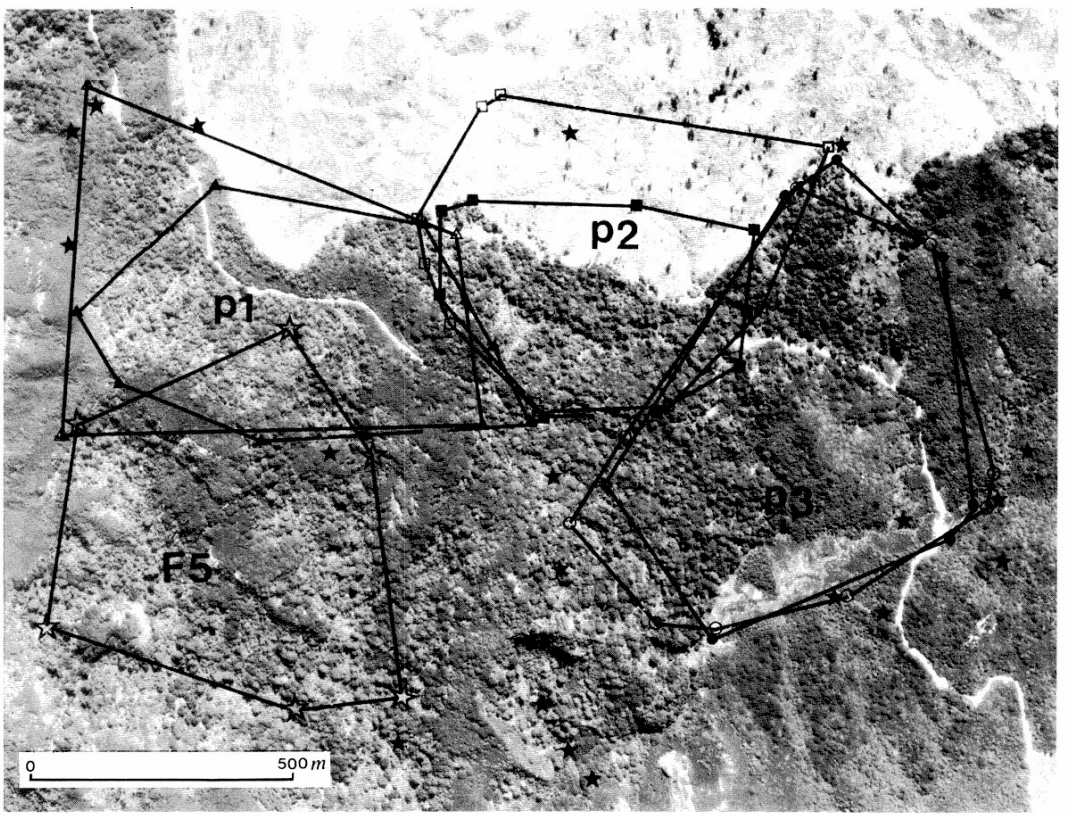

Figure 3: *Spatial distribution of kiwis at Haliburtons. The ranges of the three pairs and Female 5 are labelled. Solid symbols indicate the range of males. open symbols the range of their mates. Solid stars indicate the range of Female 4.*

other unmated female at Haliburtons (Female 5) spent three consecutive nights in the middle of the range of one pair, and sheltered in the same burrow as the resident male on one of the intervening days. She moved out, or was evicted, when the resident female returned from the far side of her range.

Range Use

The birds showed no obvious preferences for a particular terrain or aspect. They utili sed very steep hillsides, with slopes of 50-700, as well as areas with easier gradients. The range of each bird generally included a mixture of landforms, possibly because different types of feeding areas were required in different seasons. Colbourne and Kleinpaste (1983) noticed in Waitangi pine forest that kiwis spent more time feeding in moist, low-lying areas in summer than winter.

The range of one of the pairs at Haliburtons was entirely within beech/podocarp forest, but the ranges of the other two pairs contained a mixture of vegetation. About half of the range of Pair 2 was covered in young *Pinus radiata,* growing amidst charred logs and thinly scattered tree ferns. The female of this pair roosted and fed among the pines significantly more often than did her mate, but both birds had a strong overall preference for the mature bush (Bush vs pine: X^2 = 50.2 (_), 68.5 (_), $p < 0.001$ in both cases; Table 2a). The range of Pair 3 contained four types of vegetation: tall kanuka, kamahi and rewarewa (31.5% by area); young manuka and kanuka interspersed with toetoe

Table 2: *Use of different vegetation types by kiwis at Haliburtons: a) Pair* 2; *b) Pair* 3. *Incubating males were excluded from these analyses. The data for the female of Pair* 2 *include five night fixes which were too inaccurate to use in the estimation of range size.*

a) PAIR 2	Vegetation type	
	Beech/podocarp	*Pinus radiata*
Area (ha)		
No. & % of times female recorded	16.9 105(81%)	15.6 24(19%)
No. & % of times male recorded	89(95%)	5(5%)

b) PAIR 3	Vegetation type			
	Tall kanuka	Young manuka	Hardwood shrubs	Mature bush
Area (ha)	12.9	4.2	1.9	22.0
No. & 070 of times female recorded	16 (22%)	18 (24%)	1 (1%0)	39 (53%)
No. & 070 of times male recorded	22 (27%)	14 (17%)	1 (1%)	46 (55%)

(Cortaderiajulvida; 10.2%); regenerating hardwood shrubs (4.6%); and mature beech/podocarp forest (53.7%). Both sexes were found significantly more often than expected in the manuka/kanuka/toetoe association, and less often than expected in the tall kanuka (X^2= 18.7 (_), 25.8 (_), p<0.001 in both cases; Table 2b)., 68.5

Den Selection

In the half-light of dawn, kiwis ceased activity and selected a den to shelter in during the day. On 64% of 363 occasions at Haliburtons, kiwis denned in natural cavities or hollows under tree roots, fallen branches, thick vegetation, or inside decaying logs (Table 3).Burrows, which the birds excavated themselves, were used on 36% of ocassions. The majority of burrowshad a single well-concealed entrance, approximately 14cm wide by 12 cm high, and a tunnel 1 to 1.5 m long terminating in an enlarged chamber, large enough for two kiwis. Generally the tunnel sloped uphill and had at least one L or U bend, so it was seldom possible to i see the chamber from the entrance. Most chambers were 20-50 cm below the surface.

Table 3: *Dens of kiwis at Waitere and Haliburtons. N = number of observations.*

	N	% of observations in Burrow	Natural cavity	Surface vegetation	Hollow log
Waitere	68	40	31	29	0
Haliburtons	363	36	28	27	9

At Waitere, kiwis denned mainiy in natural underground tunnels, or under bracken, which was much more common than at Haliburtons. However, they also excavated burrows and used them on 40% of occasions (Table 3).

There were some significant differences in the types of dens selected by members of bonded pairs (Table 4). Males used burrows more often than expected, whereas th~ir mates favoured hollows under vegetation (X^2= 15.3, df= 3, p<0.005). Both sexes made similar use of natural cavities and hollow logs.

Table 4: *Selection of dens by members of bonded pairs. N = total number of observations for males (M) and females (F).*

	N	% of observations in Burrow	Natural cavity	Surface vegetation	Hollow log
M1, M2, M3	177	44	28	18	10
Fl,F2, F3	171	29	28	35	8

To some extent the birds were opportunisitic in their selection of dens. At Waitere, for example, kiwis living in areas with dense surface vegetation (bracken) seldom burrowed, unlike those living in open stands of tall kanuka (Table 5). At Haliburtons, fallen logs were more plentiful in cut-over forest than in virgin forest, and the kiwis in each forest type made correspondingly different use of logs as dens (Table 5).

Table 5: *Selection of dens by kiwis in different habitats at a) Haliburtons and b) Waitere. N = number of observations.*

a) HALIBURTONS	N	% of observations in Hollow log	Other shelters
Birds in cutover forest	151	17	83
Birds in virgin forest	197	4	96

b) WAITERE	N	% of observations in Surface vegetation	Other shelters
Birds in bracken	41	44	56
Birds in tall kanuka	27	7	93

Number of dens in ranges

All radio-tagged kiwis used a large number of dens scattered throughout their ranges. Generally they moved to a different one each day, but often returned to dens they had used before. At Haliburtons, for example, a pair with a 33.3 ha range used 32 dens in

23 days: 26 once, 4 twice and 2 five or more times. Dens under vegetation were often used only once, whereas some burrows were used irregularly in most months, probably for many years.

Members of bonded pairs denned together on 8070 of days, increasing to 14% in late May, June and July when breeding started. Females never sheltered with males who were incubating eggs, but one female joined her mate on four consecutive days when he was brooding a chick.

One of the three pairs at Haliburtons changed their dens during the year, using hollow logs significantly more often in winter (28% of days) than summer (2% of days).

Behaviour when denning

We recorded no instances of kiwis changing dens during the day, except when we disturbed them. Kiwis denning under vegetation usually remained still when approached, even when their cover was brushed or parted. However, they often fled if they were touched, and despite their supposed poor sight (Reid and Williams, 1975) could see well enough to run to another shelter without bumping into obstacles.

Birds denning in burrows and natural cavities usually growled and kicked vigorously at an approaching hand. Females, the larger of the sexes, were more vocal and aggressive than males. Predators attempting to enter burrows presumably get a similar reception.

Size of ranges

The ranges of kiwis in Hawke's Bay, however they were estimated, were 3-5 times larger than those in Northland pine forest (Colbourne and Kleinpaste, 1983) and about 10 times larger than those of little spotted kiwi on Kapiti Island (1. Jolly, pers. comm.). Some brown kiwis *(A. a. australis)* in the Murchison mountains in Fiordland move from one catchment to another in winter (A. Garrick, pers. comm.) but it is not known if they are residents or dispersers. Further south, on Stewart Island, C. O'Donnel (pers. comm.) found that brown kiwis occupied overlapping ranges, varying in length from 300 to 530 m. One 10 ha patch of kanuka was used by at least 23 different kiwis.

Differences in the size of kiwi ranges, both within and between regions, probably reflect differences in food supply and intruder pressure. Studies on other bird species have shown that territories are smaller where food is denser or more nutritious (Davies, 1978) or where the costs of defence are high (Davies and Houston, 1984). Although we have no comparative data, both kiwi foods and territorial intrusions were probably more numerous in the pine forest at Waitangi (Colbourne and Kleinpaste, 1983) than in our upland forests of Hawke's Bay. At Waitangi, territory holders had to defend their areas against dispersing juveniles, and mature ex-territory holders, displaced from other parts of the forest by logging. By contrast, we knew of no kiwis at Haliburtons that were unable to find space, although two females there entered the territories of other birds frequently, apparently in an attempt to obtain a mate.

The ranges of the kiwis at Haliburtons might therefore be the optimum size for that habitat. They are unlikely to be larger than the birds need to maximise their fitness, otherwise they would waste energy defending resources surplus to their requirements. None of the ranges, when estimated by the field workers method, included large areas of seemingly suitable habitat which the birds never used. However, as Davies and Houston (1984) point out, it is difficult to test whether a territory contains surplus resources. If territories are defended over many years and their size is adjusted to average resource levels, they may appear to contain an excess of resources over short periods.

We predict that increasing intruder pressure at Haliburtons would cause the established residents to contract their ranges, but at the cost of a reduced breeding success. Severe increases in intruder pressure could lead to a total breakdown of territorial behaviour. This seems to have happened in some forests in Northland (M.A. Potter, pers. obs.) and possibly on Stewart Island (O'Donnel, pers. comm.). Preliminary studies by M.A. Potter on one of these dense, apparently non-territorial populations indicate that clutch size and breeding success is much less than that at Haliburtons (J .A. McLennan, unpublished).

Kiwis seldom took vegetation into a den, and never covered the entrance with leaves and twigs as males did with nesting burrows. Once inside, the birds usually slept standing up, with their bill tucked under a wing. They awoke to defecate, usually moving 10-15 cm to a latrine on one side of the chamber or hollow.

Kiwis seldom left their dens until it was fully dark, 30-90 minutes after sunset. Typically birds emerged quietly but suddenly, and sniffed around the entrance for up to a minute before moving off.

Discussion

Territorial behaviour

The ability of kiwis at Haliburtons to recognise

mutual boundaries and maintain exclusive ranges suggests that they were territorial, but we have little direct evidence that they defended areas by overt aggression or advertisement. We never, for example, observed kiwis fighting or calling repeatedly at each other, as Colbourne and Kleinpaste (1983) did in Waitangi State Forest. Territorial disputes are most likely to be observed when immigrants attempt to settle in areas that are already occupied, or when a resident dies and its neighbours expand their boundaries to take up the vacated space. Neither situation arose during this study, and the range boundaries remained unchanged throughout.

Aggressive responses could, however, be induced at Haliburtons by entering a range and blowing simulated kiwi calls on a whistle. One or both of the residents would then usually reply and begin moving quickly towards the source. Their approach was usually accompanied by the sounds of snapping twigs and heavy footsteps, clearly audible from 50-150 m in still conditions. We suspect that they made this noise deliberately, perhaps to advertise their approach and scare away the intruder.

At Haliburtons, calls by resident birds seldom elicited replies from their neighbours, presumably because residents could distinguish between familar and strange calls. An ability to recognise the songs of neighbours has been demonstrated in many species, among them the great tit, *Parus major* (Krebs, 1971) and the whitethroated sparrow, *Zonotrichia albicolis,* (Falls, 1969). *It* is probably highly developed in long-lived species such as kiwi (Reid and Williams, 1975), which could have the same neighbours for many years.

Unlike most birds, kiwis have a highly developed sense of smell (Reid and Williams, 1975; Wenzel, 1968) and could conceivably use scent to advertise occupancy, as many mammals and some insects apparently do (Wilson, 1975). Both the birds themselves and their faeces have a distinct, pungent smell which lingers in burrows for some days and occasionally weeks after the birds have used them. *It* is noteworthy that when birds intruded into their neighbours' ranges, they often sheltered in burrows that had been used a few days beforehand by the residents. On one occasion an intruding female found a den under a toetoe bush, amidst a thicket of other toetoes, each presumably offering equivalent shelter. The odds of her rmding the site by chance or sight seem exceedingly slim; she probably located it by smell. Dens scattered throughout ranges might therefore act as scent posts, indicating occupied areas.

Size of ranges

The ranges of kiwis in Hawke's Bay, however they were estimated, were 3-5 times larger than those in Northland pine forest (Colbourne and Kleinpaste, 1983) and about 10 times larger than those of little spotted kiwi on Kapiti Island (J. Jolly, pers. comm.). Some brown kiwis (A. *a. australis)* in the Murchison mountains in Fiordland move from one catchment to another in winter (A. Garrick, pers. comm.) but it is not known if they are residents or dispersers. Further south, on Stewart Island, C. O'Donnel (pers. comm.) found that brown kiwis occupied overlapping ranges, varying in length from 300 to 530 m. One 10 ha patch of kanuka was used by at least 23 different kiwis.

Differences in the size of kiwi ranges, both .within and between regions, probably reflect differences in food supply and intruder pressure. Studies on other bird species have shown that territories are smaller where food is denser or more nutritious (Davies, 1978) or where the costs of defence are high (Davies and Houston, 1984). Although we have no comparative data, both kiwi foods and territorial intrusions were probably more numerous in the pine forest at Waitangi (Colbourne and Kleinpaste, 1983) than in our upland forests of Hawke's Bay. At Waitangi, territory holders had to defend their areas against dispersing juveniles, and mature ex-territory holders, displaced from other parts of the forest by logging. By contrast, we knew of no kiwis at Haliburtons that were unable to find space, although two females there entered the territories of other birds frequently, apparently in an attempt to obtain a mate.

The ranges of the kiwis at Haliburtons might therefore be the optimum size for that habitat. They are unlikely to be larger than the birds need to maximise their fitness, otherwise they would waste energy defending resources surplus to their requirements. None of the ranges, when estimated by the fieldworkers method, included large areas of seemingly suitable habitat which the birds never used. However, as Davies and Houston (1984) point out, it is difficult to test whether a territory contains surplus resources. If territories are defended over many years and their size is adjusted to average resource levels, they may appear to contain an excess of resources over short periods.

We predict that increasing intruder pressure at Haliburtons would cause the established residents to contract their ranges, but at the cost of a reduced breeding success. Severe increases in intruder pressure could lead to a total breakdown of territorial behaviour. This seems to have happened in some

forests in Northland (M.A. Potter, pers. obs.) and possibly on Stewart Island (O'Donnel, pers. comm.). Preliminary studies by M.A. Potter on one of these dense, apparently non-territorial populations indicate that clutch size and breeding success is much less than that at Haliburtons (J.A. McLennan, unpublished).

Roosting behaviour

We do not know why males sheltered in burrows significantly more often than did females, nor why adult kiwis, which have apparently evolved in the absence of predation, should bother to burrow at all. Wekas *(Gallirallus australis)* eat the eggs of little spotted kiwis on Kapiti Island (Jolly, 1985) and probably take those of bown kiwis wherever the two species overlap. The nesting burrows of kiwis might therefore have an anti-predator function but, paradoxically, they are generally much shorter than the burrows used as daytime shelters. Indeed, incubating males can often be seen from the burrow entrance, whereas adults in daytime shelters usually cannot. Kiwis may burrow for physiological reasons, such as conserving heat in winter, or moisture in summer. However, the lack of any consistent seasonal changes in the use of den sites suggests that this too is unlikely. The role that burrows may have as possible scent posts for territorial defence is probably secondary, and would not in itself promote burrowing unless burrows are better scent posts than other shelters.

Implications for the design of reserves

The island biogeographic study of East and Williams (1984) indicates that all three species of kiwi have large area requirements. For example, neither Great Barrier (300 km^2) nor D'Urville (163 km2) has brown kiwis, although both islands were connected to the mainland during the last glaciation and are within the species' recent geographical range.

Frankel and Soule (1981) calculated that a population needs to contain 500-1000 breeding individuals if it is to be self supporting over several hundred generations. In smaller populations, increases in genetic variability through natural mutation are insufficient to offset the erosive effects of inbreeding and genetic drift. This suggests that reserves for kiwis in Hawke's Bay need to be at least 7500-15000 ha, if the range characteristics of this study (i.e., 30 ha per pair and little overlap) are typical for the region. In practice reserves will need to be even larger, since in anyone area not all of the habitat will be suitable, the birds will not be evenly distributed, and some territories will be occupied by unmated birds which do not breed. Clearly, reserves of only half this size or less will be needed in Northland, provided it can be demonstrated that kiwis produce sufficient young to replace themselves at densities of one pair per 5-6 ha.

Most of the existing reserves in Hawke's Bay are less than 100 ha, and even the largest (Boundary Stream, 563 ha, and Rakauroa, 567 ha) are probably too small to support 20 pairs (Table 6). Indeed, there are now no patches of indigenous vegetation left anywhere in lowland (< 300 m a.s.l.) Hawke's Bay which approach 7500 ha. Some of the pine forests in lowland areas do meet the criterion for size, but none currently contain kiwis (J .A. Mclennan, unpublished), perhaps because insufficient young are being produced in nearby native forests to colonise them. Exotic forests might, however, be too impermanent for the long-term preservation of kiwis.

The Kaweka (655 km^2) and Kaimanawa (749 km^2) State Forests along the western edge of Hawke's Bay offer the best hope for the preservation of kiwis, provided that the cause of the present apparent decline in numbers in these areas (J .A. McLennan, unpublished data) can be identified and removed. This will require considerably more research.

Table 6: *Size frequency of reserves and forest parks in the Hawke's Bay and Wairoa ecological districts.*

	Reserves			Forest Parks
	0-50	Size (ha)		
Number	31	51-200	201-600	65000-94000
		9	6	3

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