Spatial organization of the North Island Brown Kiwi *Apteryx australis mantelli*: sex, pairing status and territoriality

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In Waitangi State Forest, 51 North Island Brown Kiwi *Apteryx australis mantelli* were tagged with radio transmitters and observed for an average of 2.3 months. All females and the majority of males were paired and maintained territories of 6.7 and 5.5 ha, respectively. Territories overlapped widely between partners but only narrowly with those of paired neighbours. Unpaired males had territories of 12.8 ha and extensively overlapped those of paired males. Territories were maintained by long distance calls and rare aggressive encounters. Males were more territorial than females. Within pairs, males called 1.5 times more often than females and initiated most pair calls. 60% of female calls were responses to their mates. Observers could often induce aggressive behaviour (calling, fast approach) in male kiwi (by playback, for example) but hardly ever in females. Kiwi territoriality cannot be explained by the distribution and availability of food and shelter sites, but seems to serve mainly a reproductive function.

Kiwi are exceptional among birds. They are flightless and purely ground living, they feed on invertebrates and their senses of smell and hearing are highly developed, whereas their eyes are small and functionally less important (Reid & Williams 1975). Apart from the Stewart Island subspecies of the Brown Kiwi *Apteryx australis lawryi*, they are completely nocturnal. Their way of life resembles that of nocturnal, insectivorous mammals.

Observations and reports from the last century (e.g. Buller 1888) indicate that kiwi were abundant and dense during the early times of European settlement in New Zealand. High densities, like that found in Waitangi Forest, North Island, may therefore reflect the situation to which kiwi have been adapted by natural selection. The Waitangi population, the largest known and counted of this subspecies, contained between 800 and 1000 birds at the onset of our study (Kayes & Rasch 1985). Of these birds, 84 had been ringed previously in a capture/recapture study (Colbourne & Kleinpaste 1983, 1984), which enabled us to obtain long-term information on some individuals. Another, even denser population of North Island Brown Kiwi was studied by Potter (1989), and a small and widely-spaced population of eight birds by McLennan *et al.* (1987).

This paper presents results of a 3-year telemetry study on the spacing and social system in a dense population of the North Island Brown Kiwi *Apteryx australis mantelli* at Waitangi Forest.

METHODS

Study area

All data were collected in Waitangi State Forest on the North Island of New Zealand (35°15′S, 174°02′E). About two-thirds of the forest's 2900 ha are planted in intensively managed pines, mainly *Pinus radiata* and *P. elliottii*. The rest consists of patches of native bush, swamps and different seral stages of vegetation. Details about topography, vegetation and management methods at Waitangi forest are given in Colbourne & Kleinpaste (1983).

The study area of approximately 500 ha covered the whole or parts of compartments 6 to 11 (see map in Colbourne and Kleinpaste 1983 for the locations of compartments). Data were mainly collected in a core study area of 90 ha at the southeastern edge of the forest (part of compartment 9). It is hilly with moderate to steep slopes. Large contiguous areas of pines covered 77% of the core study site; on 11% native bush grew in small- and medium-sized patches. Swamps (4%) and shrub-like seral stages (11%) formed long strips along gullies and tracks cutting through the pine plantations.

Study population and general methods

In the three years 1985 to 1987, 19, 29 and 40 individuals were caught and studied, respectively, during the New Zealand winter months (May–October). Details regarding the numbers of birds captured in more than one year are given in Taborsky & Taborsky (1991), including recaptures of kiwi ringed by Colbourne & Kleinpaste (1983).

In 1986 and 1987 almost all adult kiwi which used the core study area regularly were caught and radio tracked for some time, i.e. 18 and 27 birds, for the 2 years, respectively (details in Taborsky & Taborsky 1991). In our core study area the densities were 20 birds and 17 birds per 100 ha for 1986 and 1987, respectively. The average sex ratio was 1.4:1, males to females.

In general the locations of radio-tagged individuals were recorded once every 24-hours or at least every other day. At night when kiwi were active, tracking was done at irregular intervals but mainly in the first two-thirds of the night. A mobile tracking system was used with portable receiver and H-antenna. Usually three to four cross-bearings were taken per fix (loudest signal method, Springer 1979; accurate to an angle of 5°) from different positions as close to the animal as possible without disturbing it. Cross bearings for each location record were taken in quick succession during which period the birds were regarded as stationary. Observer positions and the angles were recorded with help of a dictaphone. Approximately 280 of the locations were additionally checked by approaching the birds carefully and closely until their exact positions could be determined by ear. Elsewhere, we describe the application of correction factors for simultaneously recorded locations (Taborsky & Taborsky 1991). 'Simultaneous' fixes are defined as those taken at intervals of 21–60 min for neighbouring individuals.

Whether a bird was inactive or moving could be estimated from the amplitude changes of the transmitter signals (Kenward 1987). Further information on activity was obtained by noting calls and social interactions. Birds could be watched for no more than a few seconds with a night vision scope or with torches. They were shy and alert to the observer and the heavy undergrowth concealed them perfectly.

In 1987, all calls which could be attributed by telemetry to known individuals and their locations were noted. The time periods required to record locations did not differ between males and females. We calculated relative calling rates for both sexes, i.e. the percentage of locations with calls from the total night locations obtained by telemetry. A rought estimate of absolute calling rates i.e. calls per hour and bird) was obtained by combining information on the number of birds in our study area, measured in 1986 with help of telemetry, and calling frequencies recorded at four listening stations in the same area by Kayes & Rasch (1985). Calls following others immediately and up to one minute later were considered to be reactions to the first call (= 'response calls'). When a call was responded to directly by calls of both members of a neighbouring pair, only the first mate's calls were used in the analysis of vocal reactions to calls.

Data analysis

In most analyses, data from 1986 and 1987 were combined by averaging the data from each year and then calculating the total average for the individual. The distribution of each sample was checked for normality by applying the test ratio of range to standard deviation (Pearson & Stephens 1964). The 10% level was used as a critical measure of the difference from normality. Accordingly, either means and standard deviations or medians and interquartile ranges (iqr) were calculated. If not otherwise mentioned, the non-parametric test statistics follow Siegel (1956) and two-tailed tests were used.

We applied an adaptive kernel method for deriving home range estimates from telemetry and other fixes (Appendix 1). Territory sizes and core areas were estimated from the areas encompassed by the 90% and 50% contour lines, respectively. The critical time interval at which two successive locations were no longer autocorrelated was found to be 2 hours. Therefore, in those statistical analyses which demand independence of sample points, only fixes taken at time intervals of more than 2 hours were used. Appendix 2 describes how this interval was determined, and discusses the problem of cyclic movements.

We checked whether kiwi were more or less often within specific parts of their territories than expected by random spatial distribution. We compared the ratios of territory to core area sizes between observations of 24 territories and expectations derived from simulated sets of locations which were randomly distributed within circles of average territory size. Simulations were run with 100 replicates and their results averaged for each number of locations from 10 to 150, in steps of five. Ratios of each kiwi territory were paired with simulation results of the matching number of locations, and the differences between observed and expected ratios were tested for randomness by the sign test.

We compared the distances between 'simultaneous' fixes (see below) of each territorial kiwi (i.e. 'target birds') and its neighbours with the average distances between the locations of these target birds and all fixes of their respective neighbours (i.e. 53 combinations, night and day data treated separately). If these simultaneous distances were significantly higher or lower than the average distances in the tested pairs of neighbours (Wilcoxon-tests), avoidance or attraction would be suggested between them.

Fixes taken shortly after each other are methodologically biased towards smaller distances because of an observer's walking time between tracking positions. Two birds are more likely to be tracked 'simultaneously', i.e. at small time intervals, when they are close to each other. Therefore, we restricted 'simultaneous' fixes for this analysis to intervals of 21–60 min (see Taborsky & Taborsky 1991 for an evaluation of these intervals and a discussion of its problems).

The distance up to which two individuals may hear each other's noises, even when neither of them is calling, is probably *c.* 50 m. Most of the time active kiwi moved noisily through the dense undergrowth prevailing in our study area. We compared the frequency distribution of inter-neighbour distances (night fixes only) within and below 50 m between fixes taken either at short time intervals of ≤ 15 min (i.e. the biased data set) or at least 2 hours apart (i.e. to the next fix of the neighbour). As fixes taken at intervals of ≤ 15 min are probably biased towards smaller distances (see above), this is a conservative analysis when investigating mutual avoidance between territorial neighbours. For this analysis we pooled the data of all neighbours of a given paired target bird, since the variances between the inter-neighbour distances did not differ (Kruskal-Wallis one-way analyses of variance).

Table 1. *Sizes (medians and interquartile ranges in ha) of 90% (=territory) and 50% (=core area) areas of Brown Kiwi territories and estimates calculated by the minimum convex polygon method (MCP).*

	Males		
	Paired	Unpaired	Females
90% area (ha)	5.5 (3.2–7.4)	12.8 (8.9–19.1)	6.7 (5.5–9.3)
50% area (ha)	1.2 (9.4–1.6)	3.4 (1.2–5.0)	1.3 (0.9–1.8)
MCP (ha)	4.8 (2.8–7.2)	12.1 (4.5–20.3)	6.8 (5.4–7.9)
n individuals	9	5	10

RESULTS

Territory sizes (90% areas), sizes of core areas (50% areas) and sizes of minimum convex polygons (for a better comparison with other home-range studies) are given in Table 1. Territories of pair members were about 6 ha in size and overlapped by about 70% (Fig. 1a). Unpaired males' territories (12.8 ha) were twice as large as those of paired males (5.5 ha). The utilization distribution was multimodal; the core areas were usually not contiguous but broke down into two to four parts. These areas were distributed over the entire ranges, mainly in their centres but partly also close to their margins (Fig. 2). Core areas were smaller than expected from a random distribution of locations within a territory. In 22 out of 24 territories the ratio of 90%: 50% areas (median: 4.7, interquartile range: 4.2–6.3) was higher than for the simulated sets of locations (sign test; $P<0.001$). This demonstrates preferential use of central parts of the territory, as increasing densities of location points result in a decrease of area estimates which are based on the kernel method. The remaining two territories belonged to unpaired males.

Site tenacity

We measured site tenacity by the relationship between the time span of observation and the cumulative size of a home range. In eight of the ten individuals observed for the longest periods of time, the territory sizes did not show a significant increase from the first range estimates ($P>0.1$, linear regression, one-tailed). The median period considered was 52.5 days (iqr = 30.7–66.7 days) and started after obtaining 15 location points.

In August/September 1987 about half of the Waitangi kiwi population of nearly 1000 birds was eradicated by a single dog (Taborsky 1988). In our core study area, two pairs and one paired and one unpaired male were killed. Some of the remaining neighbours expanded their ranges into the vacant areas. If only the periods after the deaths of one or several neighbours are considered, in five of seven birds the cumulative range sizes increased significantly by 15 to 143% ($P<0.05$, linear regression). The study ended before the final outcome of resettlement of these vacant areas could be observed.

Some kiwi occasionally left their territories for short-term excursions intruding far into neighbouring territories. All these fixes were outside the contiguous 90% areas which describe the territories, and their average distance (±s.d.) from the 90% contour lines was 133±43.3 m. The travel distances may have been even greater, as it is unlikely that the locations were recorded at the farthest points of the excursions. In only one of the 13 observed excursions of five males and five females do we know that it was longer than 1 day. This was an unpaired male which stayed for 2 days in a neighbouring territory and then another day in an adjacent unoccupied region.

Two birds, one paired female and one unpaired male, showed a different pattern of wandering, moving far away from their territories. We recorded six excursions of the female with a maximum length of 2.5 km and two excursions of the male with a maximum length of 1.7 km. The durations of four journeys of the female were 1, 1, 9.5 and 11 days, respectively; another journey lasted at least 10 days. In four of these trips the female visited approximately the same area.

Exclusiveness

Figure 1a and b gives the percentages by which territories of paired adult males and females were used by other birds of different social categories for the 90% (territory) and 50% (core area) regions, respectively. Territories of pair partners overlapped to a large extent whereas there was very little overlap with neighbouring pair members. The overlap between paired male neighbours was significantly less than between paired female neighbours $U=10$, $n=9+8$, $P<0.05$, Mann-Whitney *U*-test). About 30% of the area of pair members' territories was used by unpaired territorial males, and about 50% on average by unpaired, non-territorial males, termed floaters (Taborsky & Taborsky 1991). The maximum use of eight males' and seven females' territories by individual floaters was 37, 71, 79, 82, 88, 95, 100, 100% and 25, 75, 78, 88, 90, 98 and 99%, respectively. (Data from six floaters are included; the average overlap value of 50% is comparably low because it contains the portions of all territories a floater uses.) Additionally, most territories were overlapped by several floaters. Therefore, many territories had no exclusive portions at all with regard to use by floaters.

Overlaps of 50% core areas (Fig. 1b) correspond to those of the 90% areas. However, the core areas of unpaired males overlapped to a relatively high extent with those of paired females (median: 17%, range 7.0–34.0%, $n=5$), whereas there is nearly no coincidence with those of paired males (median: 0, range = 0–8.8%, Mann-Whitney *U*-test $U=3$, $n=5$, $P=0.056$.

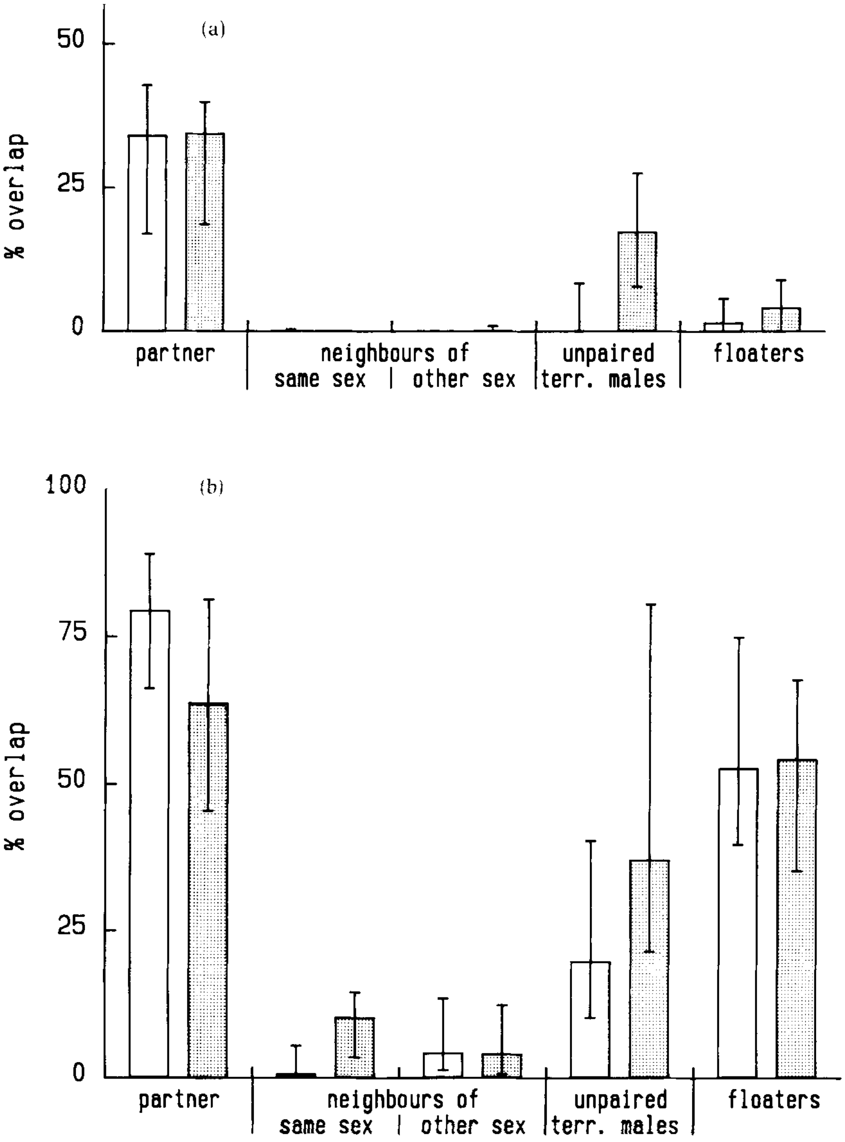

Figure 1. Percentages (medians and interquartile ranges) by which territories of paired males and female Brown Kiwi were overlapped by conspecifics. (a) 90% areas (b) 50% areas. Open histograms, male territories; stippled histograms, female territories.

Social interactions

Calling

The median relative calling rate for territorial males was 23.4% (iqr = 17.5–35.0%, $n = 15$) of all night recordings, and for territorial females it was 13.3%, (iqr = 4.3–16.1%, $n = 9$). The absolute calling rate for males and females was 0.85 times and 0.35 times per hour, respectively, during the first half of the night. Kayes & Rasch (1985) have shown that the calling rates remain constant in the first 6 h after sunset. Rates vary strongly among nights; this variation is influenced by extrinsic factors (e.g. moon phase, Colbourne & Kleinpaste 1984, Kayes & Rasch 1985).

(a) *Response calls.* Male and female calls are often followed by calls (response calls), either from their respective mates (pair calls) or from one or several neighbours and sometimes by both. Usually, the responding kiwi starts calling during or a few seconds after the first kiwi's call. All recorded response calls in which the callers' identities were known were given by and to territorial kiwi. In six cases where the calling individual or pair and the first answering individual were identified, calls from the initiating bird were always given from a distance closer than the average simultaneous distances (sign-test, $P < 0.05$; the respective pairs of distances were 58 + 81, 56 + 139, 28 + 121, 20 + 45, 30 + 153, 65 + 120).

(b) *Calls and response movements.* Calls may be used to mark territory borders. We tested whether kiwi called more often in the periphery of their territories than in their centre by

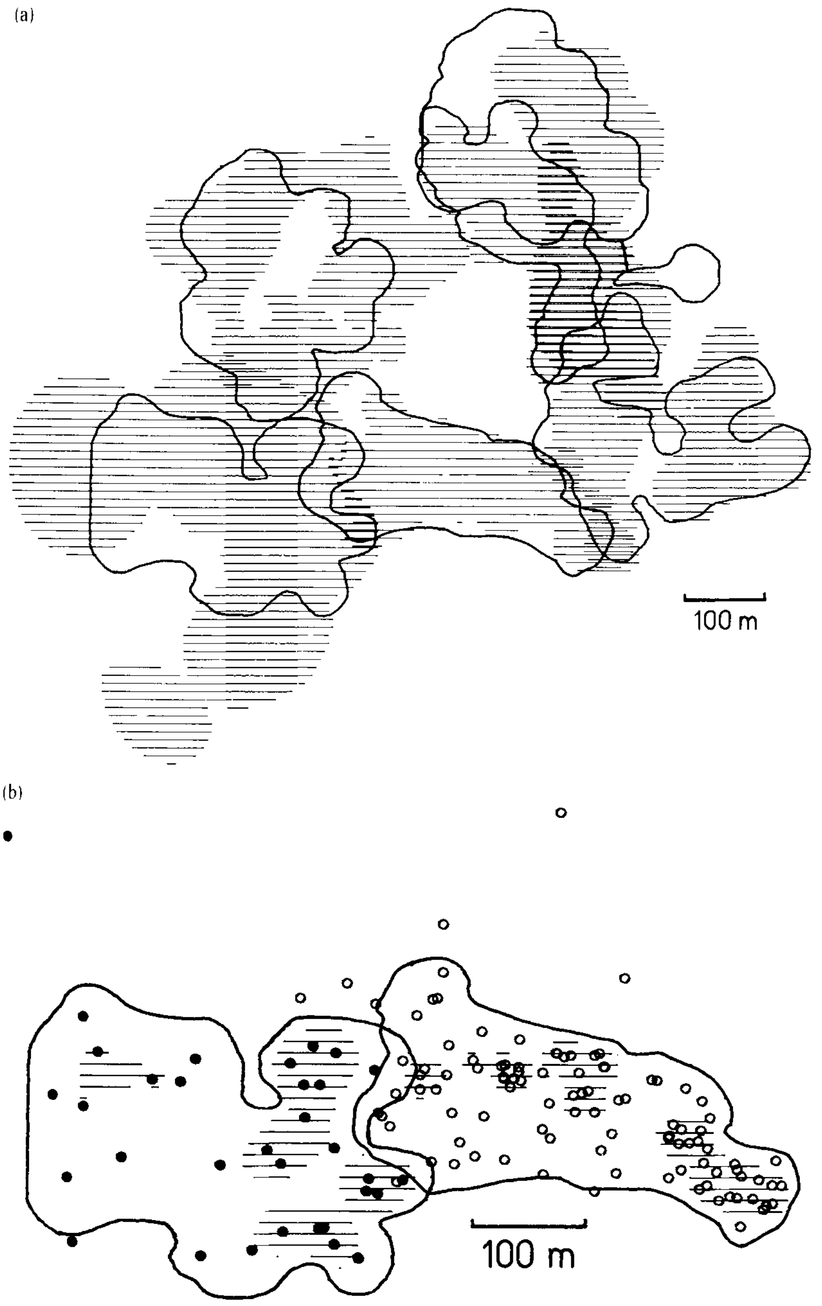

Figure 2. (a) Territories of paired Brown Kiwi in the centre of the study area, calculated by a kernel estimator (see Appendix 1). Enclosed areas, males; hatched areas, females. (b) Territories of two male Brown Kiwi. Enclosed areas, 90% areas (territories); hatched, 50% areas (core areas), ● and ○, radio-fixes of the two males.

separating the territory into three portions: the areas within the 50% (i.e. central), between the 50 and 75%, and outside the 75% (i.e. peripheral) contour lines. We found no significant differences between the spatial distributions of fixes with and without calling over the three portions. This sample comprised ten territorial birds (7 males and 3 females) with sufficient calling records ($\geqslant 12$ per individual; all probabilities above are 0.2, two times three contingency table exact test after Freeman & Halton in Lienert 1986).

To test if calling directly influenced the movements of other birds, we analysed those cases in which the distances were known between a neighbour and a calling bird shortly before and after ($\leqslant 15$ min) the call. Birds hearing calls neither moved towards nor away from callers more often than expected by chance ($P > 0.1$, $n = 13$, sign-test; differences in metres between interindividual distances before and after a call were −131, −69, −50, −43, −38, −28, 0, 0, 0, 0, 10, 75, 94).

Calling pattern of males and females

Intra-pair comparisons showed that males made a signifi-

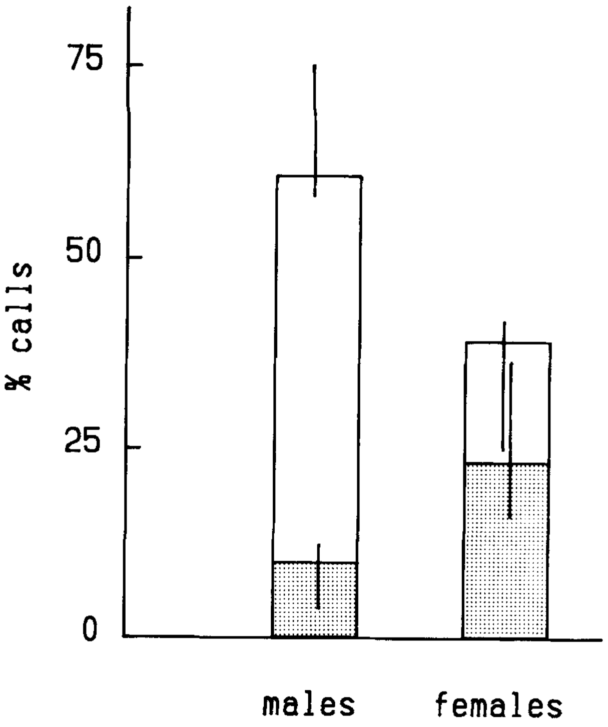

Figure 3. Proportions of calls (medians and interquartile ranges) given by partners in Brown Kiwi pairs (open histograms), including the percentages of response calls to the partner's vocalizations (stippled).

cantly higher percentage of the total calls of a pair than females (Fig. 3, Wilcoxon matched-pairs signed-ranks test, $P<0.01$). Males gave 83.3% (=median, iqr=70.4–100) of all initiated calls of a pair (individual calls alone and first calls of pair calls). Among individual birds, about 60% of female calls and only 16% of male calls were responses to their mates' calls (Fig. 3, Fisher exact test, $P=0.016$). Nearly all female response calls were reactions to their partners (median: 100%, iqr=88.9–100.0), whereas this was only true for 77.8% (=median, iqr=70.8–92.8) of male response calls (Mann-Whitney U-test, $U=4.5$, $n=5+7$, $P<0.05$).

Of the male non-pair response calls ($n=34$), 64.7% were reactions to other males, 20.6% to neighbouring pairs and only 14.7% to singly calling females. (These results are from a data set in which the calling birds were not known individually but the pairing status of callers was estimated by their locations and the distances they were apart.) Of the female non-pair calls, 81.8% were reactions to males and 9.1% each were reactions to female and pair calls, respectively ($n=11$).

The mode of calling differs between males and females. Male calls are a series of clear toned whistles (approximately 10–15), as opposed to the more attenuated series of croaks of the female (Fig. 4). In the hilly and densely forested study area male calls could be heard from distances of 300–500 m, female calls from about 200–300 m. For a range comparison, the maximum diameter of territories was on average 416 ± 119.6 m ($n=15$) and 401 ± 66.7 m ($n=9$) for territorial males and females, respectively, when the maximum distance between locations was taken as a measure.

Aggressive behaviour

We witnessed only one aggressive pursuit during all three study seasons. Two recently widowed females chased each other in the overlapping region of their territories. However, territorial behaviour could frequently be induced artificially. In 36 recorded cases (31 involving a male, five with sex unknown), kiwi reacted to playback or to imitation calls by deliberate approach and/or calling. We noted 21 calling reactions when chasing a kiwi for capture or just noisily walking through its area. Out of the noted 53 cases of artificially induced territoriality only three were by females and 50 by males.

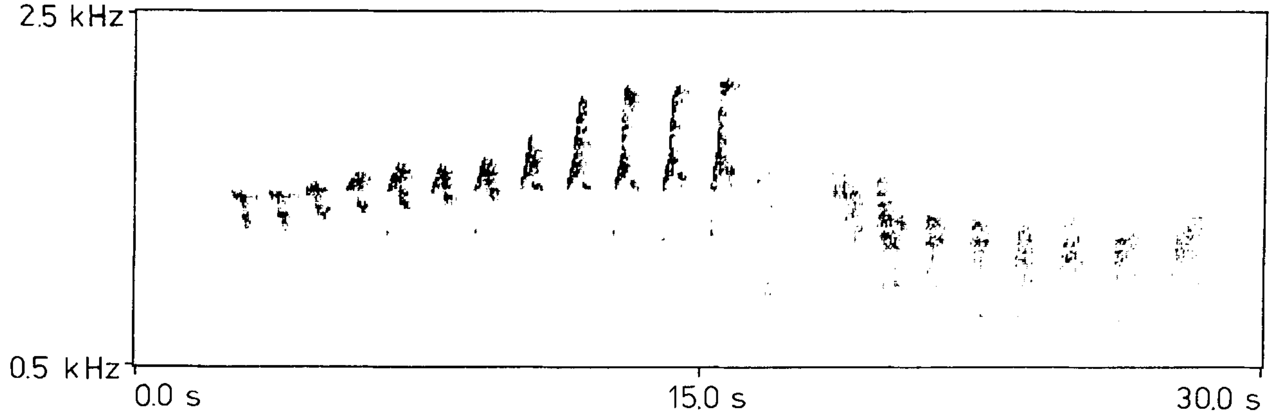

Figure 4. Sonagram of a pair call of Brown Kiwi: Male call (13 elements, of which the last is hardly visible) followed by female response. The male's call includes five clearly expressed harmonic bands and the female's call only one. These are not shown in the sonagram for better resolution of the basal band.

Spacing of neighbours

Only one out of the 53 tested pairs of territorial neighbours showed a significant difference between the distances of 'simultaneous' fixes and their overall average distances. In this case a paired female was usually closer to an unpaired male than expected (but not *vice versa*) in both her day and night locations.

Neighbours never roosted together. When they were tracked within the same 15 min intervals (i.e. almost simultaneously) at night, on only seven occasions were two individuals within 50 m of each other and there was only one direct contact: a probably non-aggressive encounter of a paired and an unpaired male. Additionally, we observed the contest between two females, which we described above, and a contact between a juvenile and an unknown bird. The frequencies of inter-neighbour distances which were greater or smaller than 50 m did not differ whether neighbours were tracked simultaneously (i.e. within 15 min) or more than 2 hours apart (Fisher exact probability tests).

DISCUSSION

Territoriality

Most North Island Brown Kiwi of the Waitangi population held territories (*sensu* Kaufmann 1983) within which core areas were used preferentially. The birds generally stayed within their territories, except for some leaving them occasionally for short-term excursions. This site-fidelity was also found in birds ringed more than 4 years before our study commenced (Taborsky & Taborsky 1991). The ranges remained stable as long as territorial neighbours were not removed. However, when a part of the population was eradicated by a marauding dog, some of the surviving birds started to expand their territories into vacant areas.

Exclusiveness of ranges is highly variable with respect to different social categories of kiwi. The territories of pair partners largely matched, whereas there was very little overlap with the ranges of mated neighbours, and none between their core areas. This largely confirms the results of the ringing study by Colbourne & Kleinpaste (1983) in the same forest and the telemetry study by McLennan *et al.* (1987) of another North Island population. In the latter practically no overlap was found between the ranges of neighbouring pairs, even though they were many times larger than those in Waitangi (see below).

In addition to mated territory owners we found two categories of fully grown unpaired males which showed much larger overlap with other territories. Unpaired territorial males used on average about one third of neighbouring territories; unpaired floating males used on average 50%, and up to 100% of the area within single territories (see Taborsky & Taborsky 1991). Hence, territory owners did not have exclusive but only major use of their ranges. No unpaired males were found by Colbourne & Kleinpaste (1983) and McLennan *et al.* (1987), but five 'straying' females were caught. Of these females, four seemed to be unpaired.

The main mechanisms by which territories are maintained appear to be long-distance calls and rare aggressive encounters. In kiwi, males and females have distinct long-distance calls. They are sometimes directly responded to by calls of the respective mates, or occasionally by territorial neighbours. Male kiwi often reacted to playbacks and imitation whistles by approaching or by calling. This suggests that calling is important for territory maintenance, as has been shown experimentally in other species (Göransson *et al.* 1974, Krebs 1977).

Aggressive encounters occur rarely in kiwi: only five were observed in Waitangi in the course of three studies (Colbourne & Kleinpaste 1983, Kayes & Rasch 1985, and this study), in five study seasons. They were always between members of the same sex. In one case the two contesting females were recently widowed. In all fights, both birds involved called either during or after the interaction. The aggressive encounters were accompanied by growling and hissing. Our observations of apparently aggressive approach reactions to playback, whistling or observer intrusion into the birds' territories confirm observations of McLennan *et al.* (1987). However, the latter did not describe fights and non-pair response calls.

The positions of neighbours which had been tracked in quick succession did not reveal a direct influence of territorial birds on each other's movements. The time frame that had to be used to classify 'simultaneous' fixes may have influenced this result conservatively (see Taborsky & Taborsky 1991). A similar analysis of neighbour's positions taken at shorter intervals ($\leqslant 15$ min) gave exactly the same result, but this cannot be interpreted unequivocally because of a methodological bias towards small distances (see 'Methods').

Although there is some overlap of territories, neighbours rarely stayed within 50 m of each other. At these distances kiwi probably sense each other without calling. However, we could not prove mutual avoidance by investigating frequencies of distances above and below 50 m.

Range size

The territory sizes of paired birds were about 6 ha. Colbourne & Kleinpaste (1983) found a similar range size by applying a 'field worker's estimate' (defined in Potter 1989). Additionally, we found unpaired territorial males holding ranges of about 13 ha. We calculated a density of 18.5 birds per 100 ha which corresponds to one bird per 5.4 ha, despite the fact that two pair members usually shared an area of this size. The apparent discrepancy between these figures is due to the fact that unpaired males hold much larger territories than paired ones, and that in 1987 part of the study area was not claimed by territorial kiwi at all.

The spacing system does not seem to depend strongly on density: McLennan *et al.* (1987) investigated a population in Hawke's Bay with an extremely low density; a total of eight birds lived in an area of 770 ha. The territories were estimated by the 'field worker's estimate' to be about 30 ha in size. Comparing the convex polygon areas, the kiwi ranges in this population were approximately six to eight times larger than those in Waitangi (mean = 39.5 ha, corrected for the number of fixes; compared to 6.8 ha (paired females) and 4.8 ha (paired males) in Waitangi). Nevertheless, both populations consisted primarily of paired kiwi defending territories with little or no overlap.

The spacing system of North Island Brown Kiwi in Paerata differs from that in Waitangi. Potter (1989) described extensive overlap of home ranges, which were seven times the size of the territories of paired kiwi in Waitangi. The Paerata population was even denser than that of Waitangi (80–90 birds in 210 ha), but range sizes equalled those of the birds tracked by McLennan *et al.* in their extremely sparse Hawke's Bay population (mean for convex polygon areas: 40.5 ha, field worker estimate: 30.7 ha). This led to a large overlap of ranges and the birds held no territories at all. Hence, the two populations with the highest kiwi densities known, Waitangi and Paerata, exhibit completely divergent spacing systems.

Difference between sexes

Territorial males called 1.5 times as often as their mates, according to the calling rates per number of night fixes and the intra-pair comparisons. However, for the total population calling ratios of males to females were 2.54 : 1 (Colbourne & Kleinpaste 1984) and 2.73 : 1 (Kayes & Rasch 1985). The deviation of these figures from our intra-pair ratio is caused by the calls of unpaired males: In this study the overall ratio of male to female calls was 2.65 : 1 in 1986 and 2.73 : 1 in 1987, when the call frequencies were weighted for the proportional numbers and the respective calling rates of different male types and of females. These ratios closely match the values found in the two previous vocalization studies.

By far the most calls were initiated by males. Females responded almost exclusively to calls of their partners, whereas nearly a quarter of the male responses recorded in this study followed the vocalizations of neighbours. More than half of these non-pair response calls by males were reactions to other males, which suggests a territorial function.

Females were also territorial. A small proportion of responses were addressed to other females and two of the five aggressive combats observed in Waitangi were between females. Of the total calls of a pair, 17% were initiated by females. Males, however, showed more territorial behaviour than females with respect to calling rates and reactions to playback, imitation whistles and human intrusions into territories. The stronger territoriality of paired males may have led to the smaller overlap between their territories compared to those of paired females (see Fig. 1a).

Function of territories

Food availability does not appear to be the primary cause of territoriality in Brown Kiwi. Unpaired territorial males had ranges twice the size of those of paired males, even though they did not compete for food with partners. The areas used exclusively by two unpaired territorial males, whose neighbouring territories were all known, were small but the access of unpaired territorial males to preferred habitats did not differ from that of paired males. These high quality areas often belonged to several territories concurrently (Taborsky & Taborsky unpubl.) which is contrary to expectation if territories were mainly defended for food. Even with a higher availability of potential food, unpaired territorial males are lighter than paired ones (Taborsky & Taborsky 1991).

The availability of roost or nest sites can also be excluded as a variable causing territoriality in kiwi. In our study area, suitable sites were extremely abundant; nearly all thick ground vegetation or other obstacles were used for roosting. Probably territories mainly serve mate retention. This is suggested by the use of common pair territories, the differential space use of mated and unmated territorial males, the sexual differences in territoriality (see also Taborsky & Taborsky 1991) and by the divergent spacing systems of populations with male and female biased sex ratios (i.e. Waitangi and Paerata).

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APPENDIX 1

Our home range estimate was 'based upon the bivariate probability density function that gives the probability of finding an animal at a particular location on a plane' (Anderson 1982). A specified central percentage region was obtained from the density function (Worton 1987; 'utilization distribution' function, Jennrich & Turner 1969, VanWinkle 1975).

We used a non-parametric kernel estimation method to avoid the restrictions which result from assuming a bivariate normal distribution of locations. Hans Winkler developed a FORTRAN program which uses conical and variable kernels ('adaptive kernel method', Worton 1987, 1989). The appropriate nearest neighbour point determining the bases of kernels depends on the number of sample points (Breimann *et al.* 1977). A calibration function was established to give the ordinal number of neighbour points (non-integers possible; Winkler, Taborsky & Taborsky unpubl.).

Some kiwi left their normal ranges for short-term trips (1–2 days) to areas occupied by other birds. These remote locations may be viewed as outliers or 'sallies' outside the home range (Burt 1943). Regardless of the range method used they would distort the size and shape of the ranges by including large areas which were probably

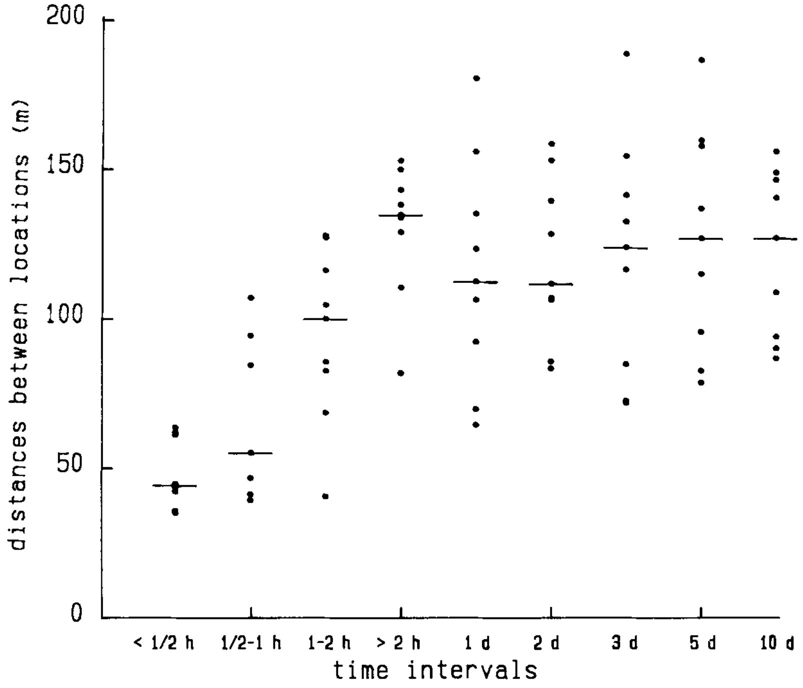

Figure 5. Relationship between time and space intervals of successive fixes of Brown Kiwi (points = medians of individuals; lines = medians of these medians) (see Appendix 2).

never visited by the animal. With our data most outliers would be included in the home range estimates if 95% area were used, which is the percentage region preferred in most studies (see Worton, 1987). Therefore, we used the 90% contour lines ('MAP (0.90) index', Ford & Krumme 1979), which appeared to provide more conservative and better estimates of the real ranges.

We also used 50% contour lines or MAP (0.5), which are a much more robust measure. They encompass the areas of concentrated use in the home ranges, which we call 'core areas'. They are especially useful for comparisons of relative home range sizes between different social classes, as these area estimates are less dependent on the actual position of specific locations than are percentage regions which are close to 100%.

We tested the dependence of range size estimates on the cumulative number of locations (Winkler *et al.* unpubl.). With samples of only five fixes, the area estimates did not differ significantly from the estimates resulting from all points (for 90% areas, $ts = -1.458$, $P > 0.1$, $n = 10$ individuals, paired t-test; for 50% areas, $T = 16$, $P > 0.1$, $n = 10$ individuals, Wilcoxon matched-pairs signed-ranks test). However, we used only samples with more than 15 points to get more conservative estimates of areas.

APPENDIX 2

For most statistical analyses of movements, successive location points must be independent (Swihart & Slade 1985). Therefore, we checked for autocorrelations by relating the time intervals to the distances between two fixes for the spacing data of the nine birds with most fixes. According to Figure 5 the data seem to be independent with intervals of >2 hours. Statistically, we tested for differences between all time intervals classes with the Friedman two-way analysis of variance by ranks using the median distances of individuals. There was no difference between the 1–2 h class and all other classes, whereas the classes of $\leqslant \frac{1}{2}$ h and $\frac{1}{2}$–1 h differed from the >2 h class. Additionally, we compared the data of the two critical classes (1–2 h and >2 h) separately for each individual with Mann-Whitney U-tests. For only one of nine animals did we find a significant difference. With a binomial test, however, the medians of the individuals in the class of >2 h were significantly higher than those of the class from 1–2 h. Therefore, we determined the critical interval to be 2 hours, a conservative measure. With regard to the problem of cyclic movements (Laundre *et al.* 1987), the kiwi observed in this study usually did not use a roosting place for a second time and we did not find other routines or dependencies, long term or short term, in the spacing pattern, even when several locations per night were recorded (B. Taborsky, unpubl. data).