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Social Organization of North Island Brown Kiwi: Long-term Pairs and Three Types of Male Spacing Behaviour

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Abstract

We observed 51 kiwi by radiotracking for an average period of 2.3 months each, in Waitangi State Forest, New Zealand. Spacing data for more than one reproductive season are available from 27 individuals, with intervals of up to six years for some of them. Females have a high potential for polyandry, especially in the Waitangi population with a male-biased sex ratio of 1.4 : 1. However, behavioural evidence suggests a monogamous mating system with long-term pair bonds. Pair members tend to stay close to each other and nearly all observed social interactions were between them. We show that there are three types of male spacing behaviour, which are related to the pairing status. A surplus of fully grown males (22.1 % in 1986, 37.3 % in 1987) remained unpaired. About half of these bachelor males maintained territories, which were twice the size of paired males' territories. This probably serves to recruit mates. The other half of unpaired males used huge home ranges of six times the size of paired males' territories, overlapping several territories of conspecifics. We have no evidence that these floaters take part in reproduction.

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Introduction

Kiwi are exceptional among birds in various aspects. They are flightless and nocturnal, and use mainly their well developed senses of smell and hearing for orientation. At night they feed on soil invertebrates, during daytime they rest in shelters. North Island brown kiwi males are about 20 % lighter than females and do all the broodcare (Colbourne & Kleinpaste 1983, own data [see below]; McLennan 1988). Therefore, one might expect that females are more aggressive than males, as in the phalaropes for example (Oring 1982). However, kiwi males are much more territorial than females (Taborsky & Taborsky 1992).

Previous field studies have shown that brown kiwi hold territories in which they feed, roost and reproduce and it has been suggested that they live in monogamous pairs (Colbourne & Kleinpaste 1983; McLennan et al. 1987;

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MCLENNAN 1988). TABORSKY & TABORSKY (1992) showed that pair members hold territories which match largely and that both sexes show territorial behaviour. Territories of paired and unpaired birds fit the definition of KAUFMANN (1983), which demands that individuals or members of a group (pair) have *priority of access* to a fixed portion of their range, but allows *some* access of other individuals as well.

Kiwi have an extraordinary pattern of parental investment. Females produce one of the largest and the most energy rich eggs among birds compared to body weight (REID 1971a, b; CALDER 1979). North Island brown kiwi males alone incubate the eggs, for the longest incubation period known among birds (almost 3 months, REID & WILLIAMS 1975; CALDER 1978). This would allow females to leave the territory and/or mate with other males while their partner is bound to the nest. Additionally, females are able to lay more than two eggs (i.e. one clutch; MCLENNAN 1988; own obs.), therefore their potential for polyandry is high. The male biased sex ratio of 1.4 to 1 found in Waitangi (see below) would again raise the polyandry potential.

Two other field studies (COLBOURNE & KLEINPASTE 1983; MCLENNAN et al. 1987) gave no hint that kiwi might be polyandrous. However, the methods applied in the first study (capture-recapture data) differed greatly from ours, as did the population size (a total of 8 birds) and habitat in the latter.

This is one of two papers reporting data on the spacing and social systems of North Island brown kiwi (*Apteryx australis mantelli*), collected with the help of radio telemetry in the Waitangi State Forest, Northland, New Zealand. We describe three categories of adult males: *paired territorial males, unpaired territorial males* and *floating males,* which use space differently. We also show that females live with their mates monogamously in long-term stable pairs. The other paper (TABORSKY & TABORSKY 1992) deals with kiwi territories, their maintenance and function, and with relationships between neighbours, and it compares the spacing system of kiwi with that of other palaeognaths.

Methods

Study Area

All data were collected in Waitangi State Forest (2900 ha) on the North Island of New Zealand (35°15'S, 174°02'E). Details of the forest, study area (500 ha) and population size are given in TABORSKY & TABORSKY (1992) and in COLBOURNE & KLEINPASTE (1983, 1984). Data were collected mainly in a core study area of 90 ha at the south-eastern edge of the forest.

Study Population and General Methods

The kiwi population of Waitangi has been studied since 1978 (CORBETT et al. 1979). In 1981 and 1982, 84 kiwi were banded by COLBOURNE & KLEINPASTE in an area including our main study site. Our study was performed during the New Zealand winter months (May—Oct.) in the years 1985 to 1987. We caught the birds by hand when they were active at night, some of them at day-time using a trained kiwi dog. Checks on the abundance of birds were occasionally done with help of playback of calls or with call imitations produced with help of a dog whistle. In the three study seasons, 19, 29 and 40 birds were caught, respectively. From the total of 66 captured individuals, 10 were recaptures of the birds banded in 1981/82. Additionally, one previously banded kiwi was found dead. 18 birds were captured in two of the three study seasons, two birds in all three of them. Altogether, data from 27 individuals are available from more than one year on spacing, morphological measures and, in most of those cases, on the social status of the bird.

The birds were marked with metal serial bands at the tarsometatarsus. Self-adhesive reflective tape was attached to the bands to allow the kiwi to be individually recognized by colour code in torchlight (COLBOURNE & KLEINPASTE 1983). All kiwi were weighed at each capture with an electronic balance accurate to the nearest gram and the bill length was taken with calipers to the nearest 0.1 mm as a measure of body size. The overall condition of captured birds was assessed and they were checked for parasites, wounds and signs of moult. In nearly all cases the birds could clearly be assigned to the age categories "juvenile" or "adult" by their body sizes, weights, and colour and state of leg scales and claws. The beak length was sexually dimorphic with no overlap between fully grown females (longer) and males. In most cases the sex was also checked by noting the distinctive calls given by males and females (see sonagramm in TABORSKY & TABORSKY 1992).

The average weight of the transmitters was 26 g with an antenna of 7—9 cm length. They were attached to the tibiotarsus above the tarsometatarsal joint with flexible plastic bands as used for marking human subjects in hospitals (MCLENNAN et al. 1987). We improved these bands with textile tape, and they tore and fell off with the transmitter after 4 to 6 weeks. In 1986 and 1987 we succeeded in capturing almost all adult kiwi which used our core study area regularly. Data on space use presented here are from these birds plus an additional pair from the northern edge of the forest (n = 18 birds in 1986, n = 29 birds in 1987). These adults plus three juvenile birds were observed for an average period of 68 days (= $\bar{x}$; SD = 43.5) with the help of telemetry. We took 1846 location records (545 daytime and 1301 nighttime fixes) of these birds with a mean number of 39 records per bird and study season. Radio-tagged kiwi were recaptured in their day time shelters about every 4 weeks so that their transmitters could be checked. Detailed tracking and observation methods are described in TABORSKY & TABORSKY (1992).

In the hilly study area reflections could result in faked signal directions. However, most bearings were taken from tracks along ridge tops, where reflections are fewer. If we encountered great deviations of the first three bearings we took up to three more bearings from different locations.

The kiwi density was 20 birds and 17 birds per 100 ha for 1986 and 1987, respectively, estimated from the range sizes of kiwi using the 90-ha core study area (i.e. 5.4 ha per bird averaged for the years). The respective ratios of males to females were 1.3 : 1 and 1.54 : 1 (average 1.42 : 1) of males to females for the two years. For calculating these figures birds with ranges only partially within the 90 ha were counted proportionally. In 1986 87.6 % (i.e. 77.9 % of all males plus all females) of kiwi were paired, 5.1 % were unpaired territorial males and 7.3 % unpaired floating males. The respective figures for 1987 were 77.0 % (i.e. 42.7 % of all males plus all females), 10.0 % and 12.9 %. This was before the dog predation happened in Aug./Sep. (see TABORSKY 1988).

Processing of Data

All bearings were drawn with date and time onto topographic maps. The sampling error of the triangulation readings (i.e. the deviation of the fix determined by the cross bearings from the real position of the animal as checked independently; "telemetry error") was found to be 18.2 m for 85 % of the data. The remaining 15 % of cases produced "uncertain" fixes with an average telemetry error of 50.3 m, because of interpretation problems of cross bearings (see Appendix 1).

Distances between two locations are underestimated when viewed as straight lines between the map positions because of the geometrical properties of the telemetry error area ("distance estimation error"). This bias is mainly important for small distances. A correction factor was applied to distances when the differences between corrected and unaltered values exceeded 1 %. It was based on the average telemetry error values 18.2 m and 50.3 m for the two types of fixes ("normal" and "uncertain", respectively; see Appendix 1).

Data of all observers were pooled. Telemetry errors of fixes obtained by the two observers which provided the majority of spacing data (i.e. the authors) were tested against each other and did not differ significantly ($p > 0.1$, $n = 18 + 10$, Mann-Whitney U-test).

The locations drawn on a two dimensional map relate to positions of birds living in a three dimensional hilly landscape. This is another error source by which distances are underestimated. Approximately 24 % of the core study area had slopes between 0 and 20 %, 67 % had between 20 and

39 % and 9 % had slopes over 39 %. The resulting weighted average slope of 26.2 % corresponds to an underestimation of distances by 8 % if the beeline between two individuals were rectangular to the contour lines. Assuming the angles of beelines to contour lines were distributed randomly, the mean underestimation of distances would be 4 %. Data were not corrected for this.

Data Analysis

In some analyses, data of the study seasons 1986 and 1987 were combined. This was done by averaging the data of individuals from each year and then calculating the total average for each individual over both years. 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 to decide about the difference from normality. Means ($\bar{x}$) and standard deviations (SD) or medians ($\tilde{x}$) and interquartile ranges (iqr) are given as appropriate. If not otherwise mentioned, two-sided non-parametric tests were used (Siegel 1956).

The inter-individual distances were not normally distributed and the number of simultaneous fixes was small, so a check for underlying frequency distributions did not often appear to be useful. Therefore, we did not apply a parametric test to investigate whether the animals behave independently of each other (H_0) or not (H_1; MacDonald et al. 1980). Instead, we compared the distances between a specific location of kiwi a and a simultaneously-taken record of kiwi b with the median distance between this location of a and all records of b. When applied to all simultaneous records of kiwi a and b significant differences would suggest either attraction or avoidance between the two respective birds. Comparisons were made with Wilcoxon matched-pairs signed-ranks tests, using only data from 1987. In most cases, day and night fixes were treated separately. For 2 of the 10 individuals tested and for all 6 floaters the number of day or night fixes was too small for analysis, so day and night data were combined in these cases.

Only one observer tracked the birds at a time, therefore a truly simultaneous recording of two individuals was impossible. A bias towards smaller distances would result from classifying only those fixes as "simultaneous" which were taken in *quick* succession, because the time spent by moving from one tracking position to the next depends necessarily on the current distance between the respective individuals. To avoid this bias we excluded those data affected by this bias with help of a statistical analysis (App. 2) and we defined *simultaneous* fixes for this special analysis as taken at intervals of 11—60 min for pair members; at tracking intervals of ≥ 10 min the likeliness of two mates being tracked in that interval was independent of the distance between them. By choosing these intervals for comparisons of "simultaneous" positions, there is an inaccuracy introduced by the birds' movements, which could not be avoided. The average distance kiwi travelled between successive fixes taken at intervals of up to 30 min was 44 m (= $\tilde{x}$; iqr = 39—61 m, n = 9 medians of individuals) and of 30—60 min it was 55 m (= $\tilde{x}$; iqr = 41—94 m, n = 7 medians of individuals). The pairwise comparisons between expected and observed inter-individual distances were done for all pairs of mated birds.

However, partners were generally tracked *directly* after each other, in contrast to neighbours (see Taborsky & Taborsky 1992). The spatial distance between mates was hence not causally involved in the decision which individuals were tracked successively. Therefore we analysed also those distances of pair members which resulted from observations taken at less than 15-min intervals. We compared the frequency distribution of intra-pair distances of these fixes taken in quick succession with those taken at greater than 2-h intervals (i.e. the respective *subsequent* fix of the partner). For this analysis the data were divided into two classes: distances within and above 50 m. 50 m is probably close to the maximum distance at which two kiwi may hear (i.e. sense) each other, when not calling. Additionally, "direct contacts" (i.e. night distances ≤ 5 m and joint roosting at daytime) were quantified.

An adaptive kernel method (Worton 1989) for deriving home range estimates from telemetry fixes was used which is described in Taborsky & Taborsky (1992). Two successive locations of an individual were autocorrelated when taken within 2 h, but not beyond this interval (Taborsky & Taborsky 1992). Therefore, only fixes taken at intervals exceeding 2 h were used in statistical analyses demanding independence of sample points.

For a comparison of territoriality between different classes of males we calculated the "relative calling rates", which are the percentages of fixes *with* calls from total night fixes. The absolute calling rates were approximately 0.85 and 0.35 calls/h for males and females, respectively (Taborsky & Taborsky 1992). However, they could not be determined for the single individual.

Results

Paired Males and Females

a) Size. Females were nearly 20 % heavier than males (p < 0.001, n = 14 + 12, Students t-test) and had 28 % longer beaks (p < 0.001, n = 21 + 16) in our population (Fig. 1). The weight averages were calculated only from non-reproductive birds measured at the same season, as seasonal weight change has been demonstrated (Colbourne & Kleinpaste 1983) and the weights of breeding males and egg-producing females fluctuate considerably during the reproductive season (M. Taborsky unpubl. data).

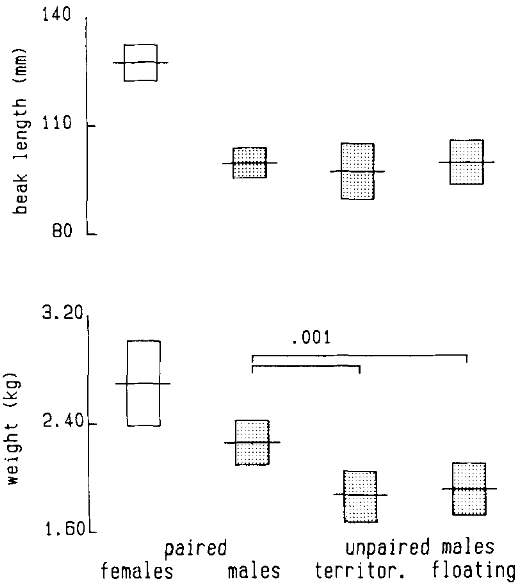

Fig. 1: Beak lengths and weights of kiwi females and different types of males (x̄ and SD). Apart from the significant differences marked in the graph female values are higher than those of all male types (p < 0.001)

b) Spacing. The territories of pair members overlapped extensively, those of neighbours only slightly (Table 1). The territories of females (x̄ = 6.7 ha) were on average 22 % larger than those of males (x̄ = 5.5 ha; Fig. 2), but this difference

Table 1: The use of paired males' and females' territories by 5 classes of kiwi, expressed as average proportions (x̄ + iqr) of overlap

		Partner	Neighbours of		Unpaired ter. males	Floaters
			same sex	other sex		
Males	%	79.2	0.5	5.3	29.9	61.8
	iqr	22.8	4.9	15.4	31.3	51.2
	n	6	9	9	4	7
Females	%	63.6	8.3	2.2	37.1	45.1
	iqr	35.9	13.3	3.1	29.5	56.2
	n	6	8	8	4	6

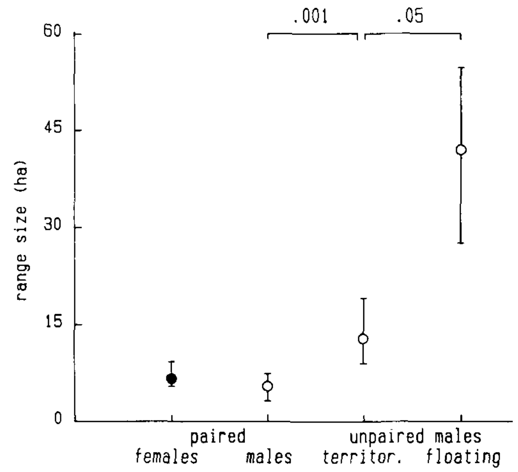

Fig. 2: Range sizes of kiwi females and different types of males (x̃ and iqr)

was not statistically significant (p > 0.1, n = 8 + 9, U-test). The comparison of *simultaneously*-recorded inter-individual distances with overall median distances (see Methods) showed that members of two of five pairs were found significantly closer to each other than expected when inactive during daytime, and one pair was closer to each other than expected at night (p < 0.05, respectively, Wilcoxon tests; in one of the daytime cases the male's relation to the female only was significant, p for the female was 0.059).

Direct contacts (i.e. individuals were within 5 m of each other when tracked *within 15 min*) of pair members occurred at 32 % (= x̃, iqr = 0—12.5 %, n = 5 pairs) of night fixes and they roosted together in the *same* daytime shelter at 15.8 % (= x̃, iqr = 0—34.5 %, n = 5 pairs) of all occasions at which they were tracked at the same day. The respective figures for ≤ 50 m distances were 45.2 % (= x̃, iqr = 34.7—64.2 %, n = 5 pairs) for night and 50.0 % (= x̃, iqr = 16.6—60.7 %, n = 5 pairs) for daytime checks. In three pairs out of five these close (≤ 50 m) distances (night data only) occurred more often than expected by chance (Fisher exact probability tests).

c) Calling pattern. Partners may call immediately after or even partly overlapping each other. We define all calls separated by up to 1 min as "response calls" or, when performed by pair members, as "pair calls". Both males and females reacted to approximately half of their mate's calls (x̃ = 45.2 % reactions by males, iqr = 15.0—60.0 %, x̃ = 46.2 % reaction by females, iqr = 25.8—63.8 %). The average distance between birds giving a pair call was for all six pairs tested below the average distance of non-calling simultaneously tracked mates (p = 0.05, Wilcoxon test). In 11 cases the position of a pair member could be determined shortly (i.e. ≤ 15 min) before *and* after a call by a series of fixes. The "listening" partner approached the location where the call had been produced on three occasions, on four it moved away and on four occasions the distance did not change. Males and females did not differ significantly in these reactions (p = 0.08, n = 11, two times three contingency table exact test after Freeman and Halton; Lienert 1986).

d) Social interactions. We never found more than two birds together. We could not visually observe interactions, but recognized if social contacts happened by the noises produced at these occasions. Most direct contacts (33 out of 36) were judged to be non-aggressive and between pair members. The three non-pair contacts were either aggressive (1 case) or of unknown context. In 39 % of the 33 within-pair contacts, the birds were roosting together in the same daytime shelter, in 39 % mates were located close to each other at night while continuously making grunting and wheezing sounds. The contexts were unknown in the other 22 % of direct meetings.

The grunting and wheezing sounds were described by REID & ROWE (1978) as a "purring noise" and by COLBOURNE & KLEINPASTE (1984) as "mewing and purring". These noises are uttered rhythmically, with a frequency of 1—2 sounds/s, and alternate with arhythmical phases. In the rhythmical parts the noise swells at times. These noisy interactions lasted from a few min to up to 2 h 17 min. For these time spans the birds stayed at the same site or eventually moved away together for a few m. No feeding sounds (see COLBOURNE & KLEINPASTE 1984) could be heard during these times. During the longer sequences, short silent breaks of up to 10 min occurred intermittently.

e) Long-term territories and pair bonds. 8 of 10 adult birds banded in 1981 and 1982 by COLBOURNE & KLEINPASTE and recovered by us between 1985 and 1987 used exactly the same areas in these two periods. A 9th bird was found dead within the area where it was caught in 1982. Of the remaining bird we do not know the 1982 capture site. 18 birds were captured in two study seasons and two in all three seasons from 1985 to 1987. 19 of these 20 birds were territorial and used the same ranges in these different years. The set of 18 birds captured in two years contains 5 pairs which were paired in both seasons in which they were studied. One pair had already been captured in 1981 and was thus paired for at least six years. "Divorce" never occurred in the animals investigated.

Possibilities for cuckoldry could result from short-term excursions and long-term "journeys" (see TABORSKY & TABORSKY 1992) into neighbouring ranges. We observed such trips in two reproductive males and three females (n = 1 trip each), and in five non-reproductive males (n = 1 or 2 trips each) and two females (n = 4 and 6 trips). These were 20 % and 37.5 % of the reproductive birds and 39 % and 41.5 % of the non-reproductive birds, males and females. Another potential source for partner infidelity is the use of large parts of pair territories by unpaired territorial and floating males (see below). Once a probably paired female (mate unbanded) answered a call of an unpaired male while close to him (within at least 50 m). However, we never observed social interactions other than calling between individuals of opposite sexes which were not paired with each other, while this was relatively often detected in pair members.

Unpaired Birds

The sex ratio in the study population was male biased, with 1.4 males to 1 female (see Methods). Only in 1987 we found two unpaired females, and they had been widowed shortly before. The partner of one of them was killed by a dog on

8th Sep. 1987 (TABORSKY 1988). The other female had been paired with a male which was caught in 1985 and 1986 but not found in 1987, although the area was repeatedly and thoroughly searched. It is likely that he was killed by the same marauding dog. *All* other unpaired adults (n = 12) were males. Their beak lengths did not differ from those of paired territorial males, but they were lighter (Fig. 1).

1) Unpaired Territorial Males

a) Spacing pattern. The five males of this category had ranges which were twice the size of those of paired males (Fig. 2, size difference: $p = 0.001$, U-test; core areas $\tilde{x} = 3.3$ ha, iqr = 1.2—5.0 ha, size not significantly different from paired males: $0.05 < p < 0.1$). They used neighbouring territories more extensively than did paired males (Table 1; $p < 0.005$, $n = 5 + 9$, U-test). Sufficient data for a comparison of *simultaneously*-recorded inter-individual distances with overall median distances were only available for one male of this category. The observed distances of this male from its five neighbours did not differ from the expectation. On 3 of 7 occasions of neighbours being within 50 m when tracked within 15 min, unpaired territorial males were together with a paired bird.

b) Territorial behaviour. The relative calling rates of unpaired territorial males did not significantly differ from those of paired males ($p > 0.1$, $n = 10 + 5$, U-test), although the median was somewhat lower (Fig. 3). There was no difference between the calling frequencies within and outside of regions overlapping with other territories. In 7 cases the percentage of calls was larger than the percentage of area overlap, and in 3 cases it was smaller. Altogether, 21.8 % of the calls of unpaired territorial males were uttered in regions of overlap with pair males. Calling was also stimulated in *un*paired territorial males by human intrusion.

c) Contacts with females. We never observed a direct contact between an unpaired territorial male and a female, nor did we find such a male breeding. One response call by an unpaired territorial male to a female call was recorded, and four times an unpaired male's call elicited the response of a female. In all these cases with one exception the *same* male was involved.

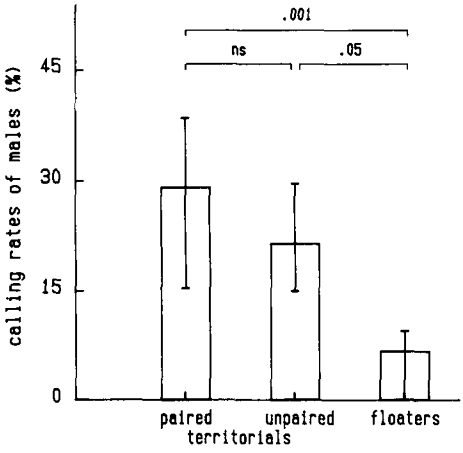

Fig. 3: Relative calling rates (i.e. % of locations with calling records from the total sum of night locations) of three male types ($\tilde{x}$ and iqr)

This male differed from all other birds of this category in his spacing pattern and the frequency of closeness to conspecifics: His territory overlapped 60 % of the territory of one of the widowed females (= 26 % of his range), which is an exceptionally high degree of overlap between neighbours. Two of the response calls mentioned above were between these two birds. Three of 7 recorded distances $\leq$ 50 m between night locations of neighbours were between these two individuals. However, other facts suggest that these kiwi were not (yet?) paired: Firstly, two other calls of this male were answered by a different, unbanded female. Secondly, his ratio of close distances to distances > 50 m from that female and the rate of response calls were far below all values of pair members.

2) Unpaired Floating Males

a) Spacing pattern. These males used wide home ranges an average of six times the size of paired males' territories (Fig. 2, range size and core areas of floaters larger than paired male's territories, $p < 0.001$, $n = 7 + 9$, and from unpaired male's territories, $p < 0.05$, $n = 7 + 5$, U-tests; core areas $\tilde{x} = 10.0$ ha, iqr = 3.8—11.9 ha). The 90 % areas of 2 of the 7 floaters were not contiguous, but were divided into three to four larger areas. Each floater used several territories of other males on average to an extent of about 50 % (Table 1), but *up* to 100 %. Floaters returned more or less regularly to the same areas, i.e. they had definite home ranges. The only male of this type caught in two years was still floating around in the same area in the second year.

b) Territorial behaviour. Relative calling rates of floaters were lower than those of both territorial male types (Fig. 3; $p < 0.01$, $n = 7 + 10$, and $p < 0.05$, $n = 7 + 5$, U-tests). We never observed response calls or territorial reactions of floaters to playbacks or to human disturbance.

c) Relation between floaters and territory owners. We found no trend for either attraction to or avoidance of territory owners by floaters. The distances between "simultaneous" fixes were 12 times closer and 10 times greater than average distances between these floater locations and all other fixes of the respective territory owners (night and day data pooled; n = 6 floater individuals + 8 territory owners). We found no evidence for contacts between floaters and females.

Out of a total of 8 recorded floater calls, five were uttered within a territory of a pair or unpaired male, two were in an area which was apparently not occupied by a territorial bird, and in one case the territorial system at the calling location was not precisely known. Once a floater called within 20 m of an unpaired territorial male.

3) Juveniles

The range sizes of three juveniles were 17.2 ha (= $\tilde{x}$; range: 17.1—33.4 ha; core areas $\tilde{x} = 2.7$ ha, range: 1.9—4.3 ha, n = 3). Each juvenile used the territories of four pairs, on average to 53.6 % per pair member (range: 26.7—62.6 %). One adult male had been banded as juvenile in 1981 at a location 2.1 km away from its 1985 capture site. Another male, which was unpaired, held a territory in 1987 exactly within the same area where it was banded as a juvenile in 1981.

Health and Condition of Kiwi

Most birds appeared to be in good condition (immaculate plumage, few or no parasites). Moult occurred in all categories and at all phases of the breeding cycle, to strongly varying degrees. 7 birds were judged to be lean and/or showed signs of poor health like a worn-out plumage or parasites. One of these was a paired territorial male before breeding, one was an unpaired territorial male, and one was a floater. The other 4 birds were males after incubation.

Discussion

In Waitangi Forest, North Island brown kiwi females are about 20 % heavier than males, their beaks are 28 % longer, and males do all the broodcare. Sole paternal broodcare is quite common in bird species in which males are smaller than females (e.g. *Jacana spinosa*, JENNI & COLLIER 1972; *Eudromias morinellus*, NETHERSOLE-THOMPSON 1973). However, the female kiwi investment in offspring is also very high: The egg is one of the largest among birds and it contains the most energy relative to female body weight. Although smaller, males are the more territorial sex (TABORSKY & TABORSKY 1992). Here we discuss how spacing and social systems reflect the peculiar features of kiwi reproduction.

In our male biased study population all females were paired monogamously. We found three different types of space use by males, which can be partly explained by their pairing status.

a) Monogamously Paired Males

The majority of kiwi males in the study area lived in monogamous pairs (78 % in 1986, 63 % in 1987). Territories of pair members matched widely, whereas there was little overlap with neighbouring pairs. Non-random attractions between mates could be detected within some pairs by comparing simultaneous and average inter-individual distances and the frequencies of distances below and above 50 m. Similar analyses could not reveal an influence of spacing between neighbouring territorial kiwi (TABORSKY & TABORSKY 1992). Non-aggressive social contacts occurred nearly exclusively between partners. The latter stayed frequently within 50 m of each other, which is in contrast to only 7 such cases found in neighbours.

When partners meet they may utter grunting and wheezing sounds, which may take more than 2 h. Kiwi making these sounds have been watched copulating (COLBOURNE & KLEINPASTE 1984). On two occasions we heard birds making the noises even though there was no second bird in close vicinity. From this and the length of those vocalizations we conclude that they are not tied to the process of copulating, but birds may copulate during these periods.

The wide-ranging kiwi calls which are given at rates of less than one call per h play an important role for territory maintenance (TABORSKY & TABORSKY 1992). However, nearly 50 % of calls are responded to by calls of the respective partners within a min. These "pair calls" may serve to give information about the partners locations and/or may function to strengthen the pair bond. We could not observe immediate effects of calls on the spacing behaviour of potential receivers.

All banded birds repeatedly caught with intervals of one to 6 years used the same ranges at these different occasions and were mated with the same partners. Six additional birds recaptured by KAYES & RASCH (1985) were all in the same area where the birds had been banded in 1981/82. These data suggest that the territories are very stable and the pair bond lasts for many years. This agrees with the results of a two year study on brown kiwi by MCLENNAN (1988) on a population of three pairs and two unpaired females. All pairs stayed together throughout the study period within the same territories.

In another population in Paerata the pair bond was relatively unstable (POTTER 1989). According to POTTER's classification, 50 % out of 12 pairs did not remain together from one to the next breeding season. This high divorce rate could not be attributed to differential breeding success, and the acquisition of a new partner was accompanied only by minor changes in home range use. However, the Paerata population was twice as dense as that in Waitangi and had a female biased instead of male biased sex ratio; and the spacing behaviour of members of both sexes was very different. The birds used widely overlapping home ranges instead of defending territories. POTTER suggests that the intensive competition between females for mates, together with the opportunities for mate change given by the high density and by non-territoriality might be responsible for the high rate of divorces.

In North Island brown kiwi only the males incubate and they are limited to two egg clutches, which is the average clutch size a female produces. Hence, paternal care is not shareable between females. This is one prerequisite for the evolution of monogamy (WITTENBERGER & TILSON 1980), as is the defendability of one mate or its range (EMLEN & ORING 1977). Therefore, monogamy may be regarded as being the logical consequence for kiwi males. This is not the case in females. They are free from parental duties after egg laying. Therefore, kiwi females have a high potential for polyandry (EMLEN & ORING 1977). Females should be capable of laying replacement clutches if (a) there is a high probability of egg loss, and (b) there are no strong environmental limitations causing a short reproductive season. Both conditions hold in the Waitangi kiwi, and two females indeed produced replacement clutches (unpubl. data). This capability of females to lay replacement clutches again favours polyandry (JENNI 1974). However, there is no evidence for polyandry to occur in kiwi from our behavioural data.

b) Unpaired Territorial Males

Unpaired males maintaining territories defended areas of twice the size of pair male territories, and overlapped the latter's extensively. The territorial behaviour of paired and unpaired males did not differ with regard to calling rates and reactions to human intrusion. There was no strong evidence for reproductive activities of unpaired territorial males. However, one of them called in a territory of a receptive female when she was carrying a progressed egg, and in a territory of a breeding male. One unpaired territorial male which differed from others in his spacing pattern and behaviour was apparently just about to pair up with a widowed female.

c) Unpaired Floating Males

About 42 % of the unpaired males did not defend a territory. These males roamed about in wide ranges overlapping several territories of other males to a large extent. However, they still used well defined areas and did not disperse indefinitely. These floaters called very rarely (Fig. 3), but we do not know the function of these calls. They might serve for mate attraction, but we have no evidence that floaters attempt to mate. When calling in an area overlapping with a pair male's territory, floaters take the risk of being pursued and attacked by the heavier, and probably stronger paired territory owners. It may hence be expected that these intruders call only when the paired male is likely to be at some distance from them. However, we observed one floater calling within 20 m of a territorial male, and our spacing data suggest that floaters do not avoid male territory owners markedly; they appear to be largely ignored by them.

Three juveniles of unknown sex had smaller ranges than floaters, but used areas occupied by several territories. Their spacing system hence resembled that of floaters.

BROWN (1969) introduced the term "floater" and suggested that their occurrence is bound to population density levels at which "all habitats where breeding could possibly occur are occupied by territorial individuals". Then "a *surplus* of potential breeders exists as non-breeding *floaters*". In kiwi, floating males could be mature but still young birds which are unable to gain a territory. The crucial experiment to clarify the breeding potential of kiwi floaters by removing breeding males cannot be done because of the protected status of kiwi. However, in Sep. 1987 several territorial males as well as complete pairs were killed by a marauding dog (TABORSKY 1988). This allows to check whether BROWN's habitat saturation hypothesis applies to kiwi, which is studied at present.

BIRKHEAD & CLARKSON (1985) suggested that surplus individuals have four possibilities of where to stay: 1) living in a flock separated from the breeding population in marginal habitats, 2) living solitarily and inconspicously on territories of other conspecifics, 3) using a home range (alone or as a flock) which overlaps with territories of the breeding birds, 4) staying at the territory of the parents often as helpers at the nest. Kiwi floaters match the third of these suggested options.

Surplus individuals floating among a territorial population are known from several other species (e.g. *Zonotrichia capensis*, SMITH 1978, juvenile *Sitta europaea*, MATTHYSEN 1989). A system phenomenologically similar to that of kiwi is found in yearling male song sparrows, *Melospiza melodia*. These are monogamous and have the same three categories of males as kiwi do (territorial mated and unmated, floating unmated). Also, there are no differences in size, plumage and morphology between males of these different classes. SMITH & ARCESE (1989) investigated the life-time reproductive success of the male types: Territorial yearling males obtaining mates reproduced more than twice as well as floaters, whereas those not obtaining a mate reproduced about as well as the floaters over their lifespan. But floating males were more likely to die after their first year compared to both types of territorials, hence suggesting that they were making the best of a bad job. Non-resident individuals may be stressed to a higher degree than territorial males. This was suggested by their higher cortisol concentrations and shorter periods of resting in cheetahs (*Acinonyx jubatus*, CARO et al. 1989).

d) Male types in Comparison

Beak lengths as a measure of size did not differ between the three male types, therefore we assume that they were all adult and mature birds. We have no evidence that health is related to the pairing or territorial status of male kiwi. However, the lower weights of the unpaired males of both categories indicate that these males were probably not as strong or as fit as paired territory owners. We cannot tell at this stage whether weight is cause and/or effect of territorial and pairing status.

The two types of unpaired males have not been described in kiwi before. COLBOURNE & KLEINPASTE (1983) only recorded three straying *females* which did not seem to hold a territory and two of which were thought to be unpaired. As they did not use telemetry this suggestion remained unconfirmed. The populations of MCLENNAN et al. (1987) and POTTER (1989) contained more females than males, and the spacing system of their unpaired birds did not differ basically from that of pair members.

Why do Most Kiwi Defend a Territory?

There are several arguments for kiwi territories having a reproductive function. Distribution and availability of food and roost sites do not appear to be responsible for the occurrence of territory defence (TABORSKY & TABORSKY 1992). A reproductive function is suggested by the spatial organization of males and females. Ranges of pair partners match to a large extent. The spacing pattern of territorial males differs between mated and unmated kiwi with regard to territory sizes and overlap regions. On the other hand, the nutritional state of *unpaired* males (as measured in weight) does not differ between those defending territories and those floating about in huge home ranges. A reproductive rather than a nutritional function of kiwi territories is further supported by the differences between the degrees of male and female territoriality, which run counter to the direction of size dimorphism. Finding and keeping a mate may be the most important functional variable for spacing and territorial behaviour of kiwi.

Defence of a territory for the purpose of maintaining a partner should be especially important for males: They invest more time and energy in offspring than females do (M. TABORSKY, unpubl. data). They should assure that they really father the eggs they are incubating. One way to obtain this security would be mate guarding, another to defend a pair territory against potential competitors. Combined with a shortage of females in the population to pair up with, this may explain the stronger territoriality of males as compared to females (TABORSKY & TABORSKY 1992). Keeping a long-term territory and partnership is advantageous if both partners incur high reproductive costs. It assures the availability of suitable space and a proved partner ready to breed when conditions are favourable.

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Appendix 1

From 85 % of cross bearings a location could be derived unequivocally. The remaining 15 % of fixes were judged to be uncertain. Either the triangles constructed from these cross bearings were very large or the cross bearings gave equivocal results.

Estimation of the "telemetry error": We analysed 28 cases of day-time fixes in which three or more cross bearings of a bird were taken before it was subsequently approached until found roosting in its shelter. Within this set of data, the errors of the "uncertain" fixes did not show significantly higher deviations than the normal fixes ($p > 0.1$, $n = 9 + 19$, U-tests). Therefore, normal and uncertain fixes were treated equally in the analyses unless otherwise mentioned.

As expected, the telemetry error (*not* the error angle of the single bearing, see SPRINGER 1979) was positively correlated with the distance between observer and transmitter (distances from the different positions of the observer were averaged; $r_s = 0.56$, $p < 0.01$, $n = 28$, one tailed, Spearman rank correlation coefficient). In a sample drawn from the fixes of 1987 we found that the "uncertain" locations were tracked from larger distances on average than the normal locations ($\tilde{x} = 170$ m, iqr = 93.7—240 m and $\tilde{x} = 50$ m, iqr = 25—100 m, respectively; $p < 0.001$, $n = 63 + 21$, U-test). The regression function of observer distances from transmitters and the telemetry errors depict that the average distance of 50 m for normal fixes relates to an error of ±18.2 m and the average distance of 170 m for "uncertain" fixes to an error of ±50.3 m.

We calculated a correction factor to overcome the "distance estimation error" with the help of the following geometric logic: The true location of a transmitter may be assumed to lie within a concentric area a around fix p_1, with the radius of the average telemetry error r_e (Fig. 4). A second fix, p_2, is the centre of a circle with the radius r_{dist}, which is the distance between p_1 and p_2. The area a is hence separated into two parts, a_1 and a_2. As $a_2 > a_1$, p_1 is more likely to lie in a_2, i.e. there is a higher probability that the true distance between the two fixes is larger than r_{dist}. The correction factor was calculated as follows:

$cor = (1 — a_1/\pi r_e^2)\ 2r_e — r_e$ with

$a_1 = r_{dist}^2/2\ (4x_1 — \sin[4x_1]) + r_e^2/2\ (2x_2 — \sin[2x_2])$ with

$x_1 = \arcsin(r_e/2\ r_{dist})$ and

$x_2 = \arcsin(r_{dist}(\sin[2x_1])/r_e)$.

The respective value was added to the distances measured by telemetry. The correction factor was only applied if no additional information about the true locations by acoustic tracing was available.

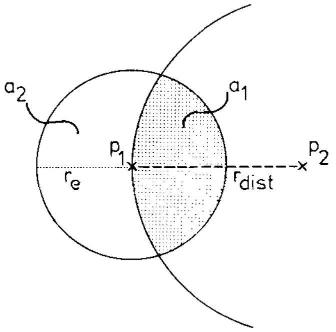

Fig. 4: Graphical expression of the "distance estimation error" (for symbols see text)

Appendix 2

Spatial information of two individuals should be recorded *simultaneously* when interested in the distance between two birds at a given time. But in our study two kiwi were more likely to be tracked simultaneously when they were close to each other because then the short distance would be quickly covered between successive bearing points. Therefore, our data set would be biased towards short distances. To overcome this problem we chose a rather narrow range of time intervals between subsequent recordings and defined them as "simultaneous" (21—60 min for neighbouring individuals [TABORSKY & TABORSKY 1992] and 11—60 min for pair members). To find the limit of these ranges, we determined the lowest time interval at which the inter-individual distances were no longer biased by walking time. When all distances between every two kiwi were plotted (separately for neighbours and pair members) against the time interval in min between the recordings (medians of 5 min-classes, up to intervals of 120 min), we found an asymptotic relationship. We determined the first median, which was not significantly lower than the asymptotic plateau ($p > 0.1$, U-tests); this was the class 21—25 min for neighbouring kiwi and 11-15 min for pair members. The upper limit of 60 min was chosen because the movement data of individuals were still highly autocorrelated up to record intervals of 60 min, hence most individuals would on average have moved only little on that time scale.

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