

HABITAT USE AND SELECTIVITY BY THE BROWN KIWI (*APTERYX AUSTRALIS MANTELLI*) IN A PATCHY ENVIRONMENT

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ABSTRACT.—The use of different habitats during foraging, roosting, social behavior, and nesting was studied in the North Island Brown Kiwi (*Apteryx australis mantelli*) with the use of radio telemetry. We chose a forest with a patchy distribution of native and introduced habitat types, the Waitangi Forest, to compare habitat availability with habitat use within the ranges of transmitter tagged individuals. During their nocturnal activity phase, Brown Kiwis preferred native forest and seral vegetation over man-made pine forest, marshes, and roads/pasture. During the daytime, kiwis roosted preferentially in marshes and successional vegetation. Social behavior, mostly calling, occurred in the same habitats as did all other nightly activity. Nest sites were preferentially located in or within 25 m of native or seral vegetation. These habitats are selectively used by chicks during foraging in their first weeks after hatching, when chicks are only able to walk short distances. Habitat types seem to be used selectively by kiwis because of their availability of food and shelter sites, regardless of whether they are natural or anthropogenic habitats. Additionally, the needs of young have to be considered when spacing patterns of adults are interpreted. Territories included a certain area of "preferred habitats" irrespective of total territory size. With sufficient access to these patches kiwis are able to survive even in poor habitats like pine forests. Only minor changes in forest management practices (e.g. allowing for wide road margins and preserving remnants of native forest and marshes) would suffice to greatly support the survival and propagation of kiwis. We discuss the importance of the selective use of small habitat patches as a precondition for the ability of kiwis to settle in a wide variety of environments, both natural and modified. Received 13 December 1993, accepted 1 April 1994.

THE BROWN KIWI (*Apteryx australis*) typically is regarded as an inhabitant of the native forests of New Zealand, most of which have been destroyed by human settlement and agricultural exploitation (Robertson 1985). Recent evidence suggests, however, that kiwis are capable of living in a diverse range of habitats. Populations have been observed in exotic pine forests (Colbourne and Kleinpaste 1983, 1984, Taborsky and Taborsky 1991, 1992), regenerating forest, and overgrown pasture (Potter 1989), lowland tussock grassland (pers. obs.) and even in sand-dunes (pers. obs., R. Colbourne pers. comm.). This suggests considerable flexibility in this species with regard to habitat use. Understanding the conditions that enable these birds to settle in such diverse environments would greatly improve our knowledge of their exceptional ecology. Kiwis are ecologically more similar to insectivorous mammals than to other birds. Information about habitat use also could help to find management strategies for this threatened species (Butler and McLennan 1991).

We studied the habitat use of a dense popu-

lation of the North Island Brown Kiwi (*Apteryx australis mantelli*) inhabiting Waitangi Forest on the North Island of New Zealand. Until September of 1987, this population was one of the largest known for this species (900 to 1,000 birds in a forest of 2,900 ha; Colbourne and Kleinpaste 1984, Taborsky 1988, Kayes and Rasch unpubl. report). In the Waitangi Forest, large areas planted with North American pine species are interspersed with patches of native forest, marshes and road margins. Colbourne and Kleinpaste (1983) estimated from capture/recapture data that Brown Kiwi territories were larger in nonnative habitats. In comparison to other habitats, native forest gullies and marsh margins had a greater availability of soil invertebrates, which are the major food of the Brown Kiwi. Hence, it is possible that nonpine habitats have an important influence on the ability of Brown Kiwis to settle in exotic pine forests.

If some habitats are more suitable for Brown Kiwis than others, selective habitat use would be expected. The suitability may depend solely on ecological conditions, such as the abundance

of food and roost sites. Alternatively, it may depend on habitats per se to which the species became adapted over evolutionary time. Such habitats include native vegetation, namely primary forest or marshes. We monitored the spacing of adult kiwis during their nocturnal activity and their diurnal roosting phase with the help of telemetry to be able to distinguish between these alternatives.

The choice of a nest site may depend on characteristics of the site itself, like cover from predation or microclimate. Alternatively, it may depend on ecological advantages in the surrounding area, like the proximity to good feeding grounds for chicks or incubating adults. We evaluated nest-site characteristics of and space use by incubating males and young chicks to test these hypotheses.

With regard to competition for preferred areas, the occurrence of social behavior and territory defense in different habitats were compared. Most of the observed social behaviors were long-distance calls. These serve either as contact or mating calls, or in territorial defense (Taborsky and Taborsky 1992).

If kiwis used habitats selectively and there is competition for the preferred areas, then resource-holding potential (Parker 1974) may be important. This may be expressed in characteristics such as body size, body mass or body condition, and we predict a correlation between such a characteristic and either absolute territory size or the fraction of preferred habitat per territory (e.g. Stimson 1973).

Given that the access to certain habitat types is essential for survival and that these habitat types are scarce, competition for access should exist. In this case, we expect that territories enclose only the amount of preferred habitats necessary for survival, making the territory economically defendable (Davies and Houston 1984). Thus, larger territories should contain relatively less of the preferred habitats than smaller ones. If preferred habitats are not limited or access to them is not important, larger territories should contain proportionally more by chance. Then, we expect a positive correlation between territory size and the absolute amount of preferred habitat.

METHODS

Study site and general methods.—North Island Brown Kiwis were studied in the Waitangi Forest on the

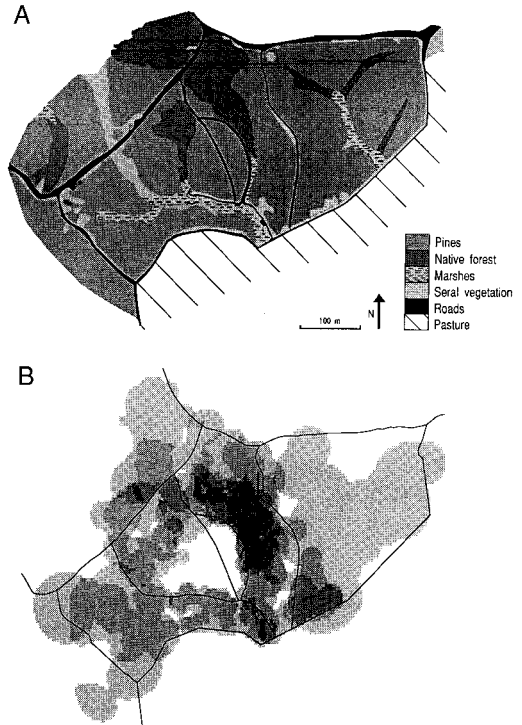


Fig. 1. Distribution of (A) habitat types and (B) territories of paired and unpaired Brown Kiwis in study area in 1987 ($n = 15$; roads serve as reference for comparison of two panels). Shading in lower panel is due to territory overlap (darkest areas indicate highest overlap) and, therefore, represents kiwi densities. Large, nondefended home ranges of floaters omitted from diagram.

North Island of New Zealand ($35^{\circ}15'S$, $174^{\circ}02'E$; size ca. 2,900 ha) between May and November. Most data were collected in a study area of approximately 90 ha from 1985 to 1987. Nearly all of the kiwis that regularly used this main study area were caught and followed using radiotelemetry (for details, see Taborsky and Taborsky 1991, 1992). Additionally, some data on nest-site choice and habitat use by chicks were collected in 1991.

There were no logging activities or any other forestry-management operations within a radius of at least 1 km around the study area during 1985–1987. The study area consisted of a mosaic pattern of distinct vegetation types. We defined five habitat types (pine woods, native forest, marsh, seral vegetation, and roads/pasture) in the study area (Fig. 1A), which were mapped based on fieldwork and aerial photography. Habitats were drawn on a fine-scaled topographic map, which was digitized to calculate the area covered by each habitat. The five habitats are characterized below.

Pines.—*Pinus radiata* and *P. eliottii* were distributed

in large, contiguous areas and covered 72.8% of the study area. The variable undergrowth was dominated by introduced gorse (*Ulex europaeus*) and sometimes included a variety of native shrubs and trees, such as manuka (*Leptospermum scoparium*), hangehange (*Geniostoma ligustrifolia*), mingimingi (*Cyathodes fasciculata*), and various species of *Coprosma*. Also present were tree ferns (*Alsophila tricolor* and *Sphaeropteris medullaris*), some grasses (e.g. *Gahnia*), and thick clusters of bracken (*Pteridium aquilinum*) at places where the canopy was open. Piles of rotting logs left over from thinning were especially important as shelter sites and as food sources (B. Taborsky unpubl. data).

Native forest.—Remnants of the old-growth, primary forest (14.7% of study area) were dominated by kohekohe (*Dysoxylum spectabile*) and tawa (*Beilschmiedia tawa*). Some smaller areas were covered with regenerating native forest dominated by towai (*Weinmannia silvicola*), manuka (*L. scoparium*), and mapou (*Myrsine australis*), or by large black tree ferns (*Sphaeropteris medullaris*). Usually the canopy was very dense with almost no undergrowth, except for a few smaller tree ferns and nikau palms (*Rhopalostylis sapida*), and some supple jack (*Ripogonum scandens*). Additionally, small areas of secondary growth native forest occurred, which were dominated by manuka.

Marsh.—Marsh covered 2.7% of the study area and was characterized by a thick cover of sedge (*Carex sp.*), grasses (*Baumea rubigenosa*, *Typha orientalis*), and ferns (e.g. *Gleichenia dicarpa*). Marsh contained some isolated cabbage trees (*Cordyline australis*) and flax bushes (*Phormium tenax*).

Seral vegetation.—A variety of early successional vegetation stages was found at road margins and in clearings (5.7% of study area). This vegetation was mostly dominated by gorse and/or small manuka trees, and could further contain bracken or other small ferns, herbs, bushes and grasses. Depending on the kind of vegetation and its age, the thickness of undergrowth near the ground varied from sparse to extremely dense, often within only a few meters.

Roads/pasture.—These two habitat types were combined for analyses because of their common feature: lack of ground cover. There was either no vegetation at all, or short grass. Roads and trails made up 3.9% of the study area. Some of the territories overlapped the pasture areas adjoining the forest. The pasture areas were not included in the habitat-type proportions of the "main study area," but they were included for comparisons of habitat availability and use.

Territory mapping.—Territory areas were calculated from telemetry readings of the owner, temporally separated by at least 2 h. At this interval, the locations were found to be independent of each other (Taborsky and Taborsky 1992). The ranges were estimated from the locations recorded in 1987 with the help of an adaptive-kernel method (Worton 1987). This method is "based upon the bivariate probability density function that gives the probability of finding an an-

imal at a particular location on a plane" (Anderson 1982). The range is estimated by the central 90% region, which is obtained from this density function (Taborsky and Taborsky 1992: appendix 1). Territory estimates are presented for 16 adult birds. They are based on 757 locations obtained by cross bearing of radio signals ($\bar{x} = 47.3 \pm \text{SD of } 30.97$ locations per bird).

In our study population, territorial and nonterritorial Brown Kiwis were present. We use the term "territory" for an area defended by a kiwi (for a description of territorial behavior, see Taborsky and Taborsky 1992), whereas "home range" is an area used by a nonterritorial kiwi. "Range" is used as a general term for an area used by a kiwi (including territories and home ranges).

Habitat availability and use.—The use of habitats was compared to their availability on two levels: (1) the proportion of habitat types found in territories compared to their availability in the study area; and (2) how often territory owners were found per habitat type compared to the proportion available in their territories. For the latter comparison, we applied a specific method to measure habitat use (focal-animal search). For this method, we determined randomly a focal animal in each case before any information was obtained on its location. Then the bird was approached. Care was given to reduce the observer effect on its location. The exact location of a focal bird, together with type of habitat, was recorded when the bird was found. Habitat use was calculated as the percentage of total observations for which an individual was found in this habitat. From 10 paired birds (both members of 4 pairs and one member each of 2 pairs), 95 checks were made at night and 99 checks were made during the day. Only once did we fail to determine the exact position of a bird before losing contact. In a few cases, the bird location was on the border between two habitats. These records were split equally between the respective habitats. Only data from 1987 were used in this analysis.

As a measure for selectivity, the difference between habitat use and availability (referred to as "selectivity index" or "selectivity") was calculated. Strauss (1979) developed this linear index, called *L*, in a study of food selection. It has the advantage that availability of a habitat is taken into account, even when it is not or hardly used. Despite its favorable properties of being symmetrical and normally distributed, Lechowicz (1982) stated that Strauss' index cannot potentially attain the full range of values (-1 to 1, or -100% to 100%) and that the index values depend on the relative abundance of other habitats. However, these problems can be overcome by calculating ranks of the selectivity indices for each individual and comparing these between habitats. This was done with Friedman analyses of variance by ranks (Lienert 1986). In our study, we measured habitat use and availability both on an individual basis. Friedman's test proved

to be the best procedure for this design with regard to Type I and Type II errors in a simulation of methods for the analysis of selectivity (Allredge and Ratti 1986). In addition to each Friedman test, the null hypothesis that "the difference between selection and availability for one habitat equals that difference for some other habitat" (Allredge and Ratti 1986) was tested using Fisher's least-significant-difference procedure (Conover 1980). Allredge and Ratti's analysis showed that these multiple comparisons had a lower Type I error when ranks were weighted with the Quade (1979) method instead of using the unweighted ranks generated in the Friedman test. Therefore, the Quade method was chosen for the multiple comparisons with the Fisher's least-significant-difference procedure. Only significant results ($P < 0.05$) are mentioned in the results section.

Nests.—We found one nest for each of eight breeding individuals or pairs, two nests of one pair, and three nests each of three pairs. Thus, the 19 recorded nest sites belonged to 12 males and 11 females. As individuals did not differ in an obvious way with regard to habitat choice for nesting, each nest site was taken as an independent location point. Topographic height and aspect also were measured at nest sites of radio-tagged birds outside of our main study area (i.e. where we had not mapped the habitat). We determined the relative elevation of a nest (i.e. a value between 0 and 1) within the range between the elevation above sea level of the highest and the lowest location at which a particular individual (i.e. the respective nest owner) had been found within its territory.

Habitat use of chicks.—Movements of two chicks were followed by telemetry between day 16/17 and 33 after hatching. A third chick was monitored sporadically between days 14 and 29 after hatching. For the analysis of chick habitat use, bearings had to be separated by at least 2 h, as with the adult data. Due to improved mobility with age, the area available to chicks increased. For the first five weeks after hatching, we calculated the regression of the maximum distance chicks moved from their nests and chick age using data of nine individually known chicks ($r = 0.90$, $P \leq 0.001$, $n = 20$ observations, only the longest distances moved by each chick per five-day interval were used). We assumed that chicks have a circular area available around their nest. With the help of the regression equation, we determined the radius of this area for four age classes (16–20, 21–25, 26–30, and 31–34 days). For each age class we determined the habitat that was available to the two radio-tagged chicks.

Social behavior.—The habitat types at locations where birds were recorded exhibiting social behaviors were compared to the habitat types in those places where recorded birds did not exhibit these behaviors. They also were compared to the available habitat proportions within the respective territories. In order to minimize the effect of sampling error, data of an in-

dividual were only used when five or more records of social behavior existed. Four habitat types were included in this analysis: pine, native forest, marsh, and seral vegetation. The habitat type "roads and pasture" was omitted because the expectations calculated on the basis of habitat area were very low due to the elongated and extremely narrow shape of roads and the rare presence of kiwis in pasture.

Calls made up 86% of all recorded social behaviors (Taborsky and Taborsky 1992). For the analysis, only calls heard within the study area from an estimated distance of up to 200 m (and where the caller was identified) were used. The remaining 14% were direct contacts between two kiwis, which we could only observe by ear. We judged these contacts to be either nonaggressive encounters between pair members, or encounters between neighbors with aggressive or unknown context. The data of all social behaviors were combined for this analysis.

Area of selected habitats.—We calculated the extent (absolute area in hectares, and relative to territory size in percent) of preferred habitats of 16 territories, using data from 1986 and 1987. The classification of preferred habitats was based on the results of habitat-selectivity analyses. We evaluated the extent of preferred habitat within a territory relative to the owner's mass, beak length, ratio of mass to beak length, territory size, and breeding success. The ranks for the latter variable were: unpaired; paired but no clutch; paired, clutch laid, but no young hatched; paired, one chick fledged; and paired, two chicks fledged.

Generally, medians and interquartile ranges are given, and nonparametric statistics were used. When data met the assumptions of a normal distribution, arithmetic means and standard deviations were calculated.

RESULTS

Habitat availability and use.—In Waitangi Forest, Brown Kiwis exhibit territoriality even though there is some range overlap (Taborsky and Taborsky 1992). The extent of overlap was greater for unpaired males than for paired birds. A comparison of Figures 1A and 1B shows that the highest density of territorial kiwis (represented by the number of overlapping territories) occurred: in a large patch of native forest in the center of the study area; in the marsh south of this area; and around small seral vegetation areas (clearings) at the southern forest border to the east of this marsh. This suggests that territories enclose certain habitats to a larger extent than expected based on their availability in the study area. However, this expectation was not supported by the statistical anal-

TABLE 1. Difference between habitat availability and use (daytime and nighttime data combined). Numbers are deviations from 0 (in percent). Positive numbers represent greater and negative numbers represent lesser use of habitats than expected based on availability of respective territories. Observed distribution differs from random distribution (Friedman's rank ANOVA, $P = 0.01$).

Habitat	First quartile	Median	Third quartile
Pines	-21.0	-12.2	3.7
Native	-0.6	0.4	9.0
Swamps	-2.5	3.4	11.4
Seral vegetation	2.0	11.5	16.5
Roads/pasture	-13.5	-3.4	2.0

ysis of habitat distribution in 16 territories (data from 1986 and 1987; habitats included in analysis were pines, native forest, marsh, and seral vegetation; Cochran Q -test, $Q = 3.79$, $df = 3$, $P > 0.1$).

Habitat use of 10 territory owners was compared against the proportions of different habitat types available in their territories. In seven of these territories, four different habitat types were available. The remaining three territories contained all five habitat types. In these 10 territories, a median of 55% of the area was planted in pines (interquartile range 44–73%), 6% in native forest (interquartile range 0–50%), 5% in marsh (interquartile range 2–17%), and 8% in seral vegetation (interquartile range 1–15%); roads and pasture together made up for 5% (interquartile range 3–13%; medians do not sum up to 100% because data are asymmetrically distributed).

Based on daytime and nighttime data combined, marshes and seral vegetation were used preferentially, whereas pines and roads/pasture were used less frequently than expected (Table 1). The use of native forest approximately matched the expectation. A Friedman's rank ANOVA showed that the differences between use and availability (selectivity) were not the same for all habitats ($X^2 = 13.25$, $df = 4$, $P = 0.01$, two-tailed, $n = 10$). Selectivity of native forest, marshes and seral vegetation differed significantly from selectivity of pines and roads/pasture, respectively (multiple comparisons, $P < 0.05$).

The same analyses were done separately for daytime (roosting phase) and nighttime (active phase) data (Fig. 2). Marshes were the preferred habitat for roosting, followed by seral

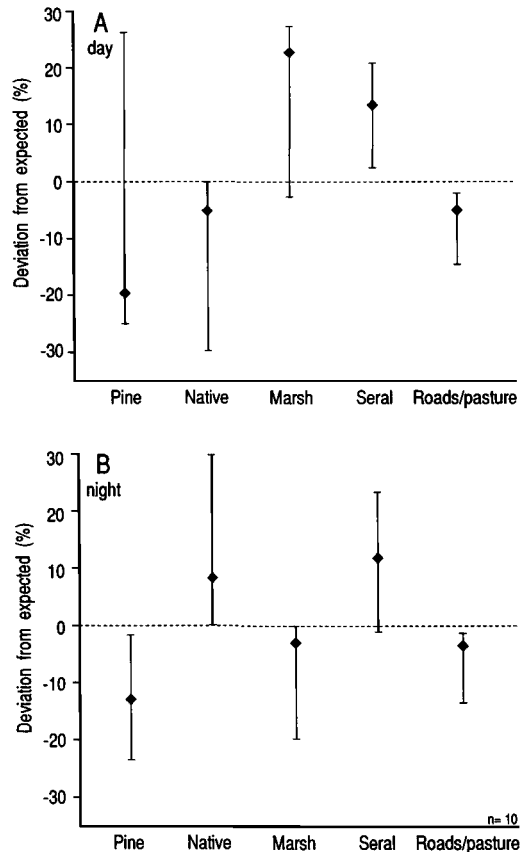


Fig. 2. Use of five available habitat types by 10 kiwis during (A) daytime and (B) nighttime (medians and interquartile ranges). Zero line indicates habitat use as expected from habitat availability within respective territories.

vegetation. The other three habitat types were used less often than expected. Active birds used native forest and seral vegetation more often than expected. Pines clearly were avoided, whereas marshes and roads/pasture were used only slightly less than expected. The selectivity differed significantly among the habitats, both for the daytime and nighttime data (Friedman's rank ANOVA, daytime, $X^2 = 13.51$, $df = 4$, $P < 0.01$, $n = 9$; nighttime, $X^2 = 13.53$, $df = 4$, $P < 0.01$, $n = 10$; all analyses two-tailed). During daytime, the selectivity of marshes and seral vegetation differed significantly from the selectivity of pines and native forest. The selectivity of roads/pasture differed significantly only from the selectivity of seral vegetation (multiple comparisons, $P < 0.05$). During nighttime, the selectivity of native forest and seral

TABLE 2. Numbers of nests found in five habitat types during three breeding seasons compared to expected numbers calculated from availability of habitat types in study area. No significant difference was found between observed and expected (see text).

Habitat	Number of nests	
	Observed	Expected
Pines	14.5*	15.3
Native	5.5*	3.1
Marsh	0	0.6
Seral vegetation	1	1.2
Roads/pasture	0	0.4

* Nests located on border between two habitats were assigned 0.5 to each.

vegetation differed from the selectivity of pine, marshes and roads/pasture, respectively (multiple comparisons, $P < 0.05$).

The patterns of habitat use were compared between daytime and nighttime by calculating the differences between daytime selectivity and nighttime electivity. Overall, the differences approached statistical significance (Friedman's rank ANOVA, $X^2 = 8.77$, $df = 4$, $0.05 < P < 0.1$, $n = 9$). The multiple-comparison tests showed that the use of native forest and marsh vegetation differed significantly between daytime and nighttime ($P < 0.05$).

Nests.—The distribution of 21 nests among habitat types was compared to an expected distribution based on the amount of land in each habitat type in our study area (Table 2). There were no differences between the two distributions. Because of the low expected frequencies in three of the categories, we pooled all nonpine habitats (native forest, marsh, seral vegetation and roads) in one category for a chi-square goodness-of-fit test; the distribution of nest sites in pine areas versus other areas did not differ from expected ($X^2 = 0.12$, $P > 0.1$).

Most nests were situated in the habitat that was most abundant in the owner's territory. Only two exceptions occurred. These involved two of the four pairs with more than one nest. In the first case, one of three nests was on the border between the habitat types with the highest and second-highest availability. In the second, one of three nests was in the habitat with the third-highest availability.

Nests were situated on an average relative elevation of $0.58 \pm SD$ of 0.33 ($n = 21$) of their male owners, and 0.54 ± 0.32 , ($n = 17$) within those of their female owners. Relative altitu-

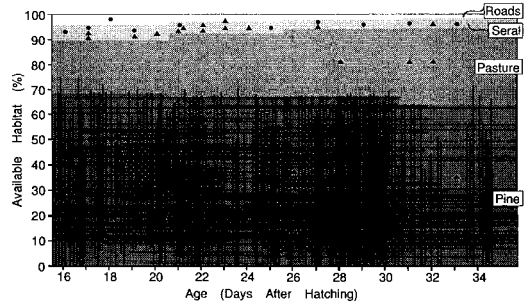


Fig. 3. Use of four habitat types (relative areas represented by different shadings) by two chicks (one indicated by circles and one by triangles) hatched in same nest. Total area available to chicks increased with age and improving mobility.

dinal ranges and aspects of slope for nest sites did not differ significantly from chance expectations (Kolmogorov-Smirnov goodness-of-fit tests, $P > 0.1$).

We tested whether nests were placed more often than expected by chance in or close to habitats preferred during nighttime. In the study area, we found 17 of 20 nests (85%) in or within 25 m of native forest or seral vegetation, which was significantly different from the frequencies expected based on the availability of these areas ($X^2 = 13.64$, $df = 1$, $P < 0.001$, $n = 20$). Furthermore, 16 of 20 nests (80%) were within 25 m of a road or trail, which also differed from expected ($X^2 = 27.65$, $df = 1$, $P < 0.001$, $n = 20$). An arbitrary margin of 25 m was chosen for these analyses as small chicks could already travel across such distances a few days after hatching. This is the age when chicks have resorbed their yolk and start to feed by themselves. Seven days after hatching one chick was found 30 m away from its nest. At day 10, the average distances chicks were found from their nests were already slightly above 25 m.

Habitat use by chicks.—We followed two chicks for almost three weeks using telemetry. They had hatched in the same nest, situated only five meters from an intersection of three trails. The proportion of different habitat types within the areas available to chicks (i.e. habitat availability) did not vary conspicuously among five-day intervals (see Fig. 3). They used seral vegetation nearly exclusively, which was found along the three trails. The number of records for habitat use deviated notably from expected use based on habitat availability (Fig. 3; Kolmogorov-Smirnov tests; chick 1, $D = 0.673$, $P < 0.05$, $n =$

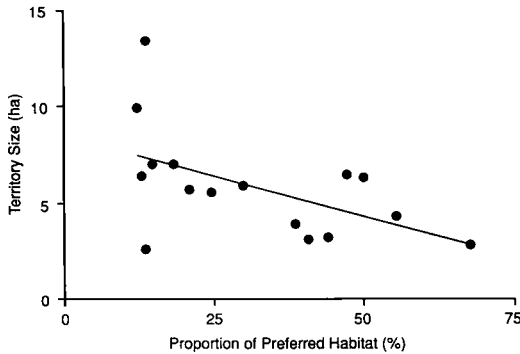


Fig. 4. Relation between percentage of preferred habitat (i.e. native bush, marshes and seral vegetation in each territory) and territory size ($r = -0.54$, $P = 0.03$).

11 locations; chick 2, $D = 0.516$, $P < 0.05$, $n = 19$ locations; use of this test with discontinuous data is conservative [Siegel 1956]).

We observed these chicks several times for 1 to 2 h continuously at close distance using a night-vision scope. During these periods the chicks rarely left the trail margins.

A third chick with a transmitter (chick 3) was located three times in native forest, which compares to an availability of 83% ($n = 1$) and 41% ($n = 2$) of this habitat in the respective five-day intervals. The rest of the area available to this chick was pine forest.

During our study, we recorded 26 night locations of 10 chicks without transmitters. Of these, 65% were in seral vegetation, 31% in pine areas, and 4% in native forest. However, an observational bias—caused by an increased chance of encounters with these birds when they are close to roads or trails—cannot be excluded from these data.

We searched 10 times for chicks 1 and 2 in their daytime shelters, after they stopped returning to the nest. In six of these checks, chicks were found in pines and in four cases they were in seral vegetation, which contrasts with habitat use by these chicks at night. Another chick, which was found on five different days by a dog (trained to find kiwis), roosted in seral vegetation in all cases.

Social behavior.—The distribution of locations where kiwis engaged in social behavior (given as percentages in each of four habitats) differed from habitat availability (Friedman's rank ANOVA, $X^2 = 8.6$, $df = 3$, $P < 0.05$, $n = 9$). The multiple comparisons showed that this was due

to a difference between pine habitat (median = -10.2% , interquartile range -12.1 to -6.8%) and all other habitats (native forest, median = 3.2% , interquartile range 0.05 to 5.9% ; marsh, median = 0% , interquartile range -2.6 to 16.2% ; seral vegetation, median = 0% , interquartile range -4.3 to 3.5% ; $P < 0.05$).

Monopolization of preferred habitats.—Native forest, marsh, and seral vegetation were used more often than expected during daytime, nighttime, or both (Fig. 2, Table 1). Therefore, we assume that the availability of these habitats in a territory contributes to its quality. The three preferred habitat types made up on average about one-fifth of the territories (median = 1.3 ha, interquartile range 1.2 to 1.8 ha; total territory size, median 5.8 ha, interquartile range 3.3 to 6.8 ha; $n = 16$). Neither the absolute areas of these favored habitats nor their proportion in territories of eight paired males and paired females (data from 1986 and 1987) were correlated with the bird's beak length (as a measure of body size), body mass, or the ratio between mass and beak length (as a measure of condition; Pearson's product-moment correlations). Also, there was no correlation between the gradient of breeding success (see Methods) and the absolute or relative amounts of preferred habitats contained in the respective territories (data from three territorial unpaired males were included in this analysis; Spearman rank correlation, $n = 12$, $P > 0.1$). Territory size did not correlate with the absolute amount of preferred habitats in individual territories, whereas it correlated negatively with the proportion of preferred habitat types in territories ($r = -0.54$, $P = 0.03$, $n = 16$; Fig. 4).

DISCUSSION

Our study has shown that Brown Kiwis do not use habitat types in proportion to their availability (see also McLennan et al. 1987, Potter 1989). This finding is similar to that found for other species, including the Ruffed Grouse (*Bonasa umbellus*; Maxson 1978), Dunnock (*Prunella modularis*; Tuomenpuro 1989), and European Blackbird (*Turdus merula*; Landmann 1991). Our study area consisted of a mosaic pattern of clearly separable habitat patches of man-modified and native vegetation. Brown Kiwis used pine areas less often than expected. They preferred some of the nonpine habitats, which occurred only in small patches. These selected

habitats included not only native vegetation (native forest, marsh), but also man-modified habitats (seral vegetation). During nighttime, Brown Kiwis preferred regions of native forest and seral vegetation, which held the highest numbers of potential prey items (unpubl. data, Kleinpaste 1990, Czeika et al. 1994). Daytime roost sites were preferentially chosen in marsh and seral vegetation. These habitat types had thicker undergrowth (unpubl. data, Taborsky 1994) and, therefore, have probably a greater availability of high-quality roost sites.

Despite the selective habitat use within territories, there was no evidence that territories included relatively more of the preferred habitat than available in the study area. This may have been due to the high population density, which caused the use of nearly all area for territories.

The choice of a nest site should play an important role for habitat use during the reproductive period. Our data suggest that habitat type, relative topographic height, and aspect are not important for nest-site selection in the Brown Kiwi. These variables reflect the microclimate of a location. Hence, microclimate may not be important for nest-site selection. It also is unlikely that nest sites were chosen in order to avoid nest predation. The only known native predator of kiwi eggs, the Weka (*Gallirallus australis*; Jolly 1989), does not occur in the Waitangi Forest. In other areas, habitats used by wekas (Robertson and Beauchamp 1985) seem to overlap completely with those used by Brown Kiwi. Therefore, mechanisms to use the habitats selectively by Brown Kiwis probably would not help to avoid nest predation by wekas. Kiore rats (*Rattus exulans*) were introduced by Polynesian settlers about 1,000 years ago. Kiore and even the larger Norwegian rats (*R. norvegicus*) did not harm Little Spotted Kiwi (*Apteryx oweni*) eggs or chicks in the wild and were unable to break kiwi eggs in an experiment (Jolly 1989). All other introduced predators of kiwi chicks and adults have arrived in New Zealand so recently that antipredator adaptations of kiwis seem unlikely.

Incubating males did not feed in close vicinity to their nests (unpubl. data). Our data rather suggest that nest sites are chosen with respect to the needs of newly hatched chicks. When chicks leave their nests for the first feeding trips at an age of about five to six days, they do not move far and return regularly to the nest to be

brooded by their male parent. This situation continues for about one or two weeks. Three radio-tagged chicks used nonpine habitats nearly exclusively, suggesting that these habitats may be relatively more important for chicks than for adults. Indeed, nests were placed preferentially within 25 m of native forest or seral vegetation, indicating that Brown Kiwis select areas where food will be readily accessible to small chicks. This also may explain why the majority of nests were placed close to roads and trails; much of the seral vegetation is found along these structures (i.e. road margins).

Chick survival seems to be the most important bottleneck in the population ecology of the Brown Kiwi, apart from the vulnerability during incubation (Butler and McLennan 1991). Most habitat-selection studies have focussed exclusively on the selectivity of adult animals. Our study has shown, however, that it may be crucial to consider the needs of young when spacing patterns of adults are interpreted.

Calls and other social behaviors occurred very infrequently (Taborsky and Taborsky 1992). The distribution of records of kiwis engaged in these behaviors suggests that they were not restricted to particular habitats.

In the population we studied, larger territories contained a smaller proportion of preferred habitat areas than smaller ones. This suggests that kiwis adjust the size of their territories to include a certain amount of preferred habitat. Davies and Houston (1984) argued that territory owners adjust their territory size depending on either the availability of a resource or the number of intruding competitors.

Our data do not provide any evidence that body size or other morphological characters relate to the defensive abilities of Brown Kiwis. There was a tendency for territories to overlap to a greater extent in regions containing preferred habitat types (Fig. 1). This could suggest a limited ability of Brown Kiwis to defend territories. Furthermore, territories are large in relation to the mobility of their owners, and vision in Brown Kiwis is virtually ineffective. In our study area, birds could hear us (and probably also conspecifics) up to distances of approximately 50 m, whereas the average maximum diameter of territories was around 400 m (Taborsky and Taborsky 1992). Hence, intruding birds would escape detection by a territory owner far away.

According to reports from the nineteenth

century, Brown Kiwis were very abundant before the spread of Europeans in New Zealand (e.g. Buller 1888). Several life-history traits of Brown Kiwis (longevity, low reproductive rate, and production of large precocial young) suggest that they are adapted to stable environments. Nevertheless, our results suggest that they easily are able to adapt to new environments such as exotic pine forests by selectively using small patches of favorable habitat, with the result that Brown Kiwis are distributed over a surprising variety of habitats.

Brown Kiwis are threatened on mainland New Zealand. Conservationists are considering releasing Brown Kiwis in areas which are currently not populated. Our data suggest that only small changes in the forestry management of pine plantations, found all over the country, may suffice to provide suitable habitat for use by the Brown Kiwi. These changes include allowing wide, unmanaged road margins, clearings and forest aisles, as well as preserving remnant native forest and marsh areas.

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