

Home range size and carrying capacity of the South Island takahe (*Porphyrio hochstetteri*) on Tiritiri Matangi Island

M.J. BABER

School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand
Present address: Department of Natural Resources, University of New Hampshire, 226 James Hall,
Durham, NH 03824, U.S.A.
matthew.baber@unh.edu

J.L. CRAIG

School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

Abstract The South Island takahe (*Porphyrio hochstetteri*), an endangered flightless rail, has been released on 4 predator-free islands to reduce the risk of its extinction. To determine the ability of these islands to support takahe populations, we studied takahe home range size and carrying capacity on one of the islands. We plotted the location of 4 takahe family groups (13 individuals) from Nov 1994 to Oct 1995 on Tiritiri Matangi Island. Mean home range size (95% Minimum Convex Polygon) was 20.7 ha, and tended to be smaller when the proportion of suitable habitat within each home range was higher. We estimate that Tiritiri Matangi can support up to 8 breeding pairs, based on the availability of suitable habitat and estimated individual habitat requirements. However, this number is likely to change in the future depending on the influence of population density increases and successional habitat changes on takahe spatial requirements.

Baber, M.J.; Craig, J.L. 2003. Home range size and carrying capacity of the South Island takahe (*Porphyrio hochstetteri*) at Tiritiri Matangi Island. *Notornis* 50(2): 67-74.

Keywords carrying capacity; home range; New Zealand offshore islands; *Porphyrio hochstetteri*; South Island takahe

INTRODUCTION

The South Is takahe (*Porphyrio hochstetteri*), has declined as a result of anthropogenic changes such as habitat destruction and modification, hunting, and the introduction of mammalian predators and competitors (Beauchamp & Worthy 1988; Holdaway 1989, 1999; Clout & Craig 1995). The wild population of South Island takahe is confined to an alpine region in the Murchison Mountains, Fiordland. However, since 1984, takahe management has included the use of 4 islands (Kapiti, Tiritiri Matangi, Maud, Mana). Fossil evidence indicates that South Is takahe inhabited lowland regions (Beauchamp & Worthy 1988; Atkinson & Millener 1991; Bunin & Jamieson 1995; Clout & Craig 1995). Nevertheless, translocations have placed these birds outside their historic range, and the lowland habitat on the selected islands differs markedly from the alpine-tussock habitat of the source population on the mainland.

Compared to the mainland population, South Is takahe on islands have a lower chance of extinction given the relatively mild climate, abundant food

supply, and freedom from introduced predators and competitors (Bunin *et al.* 1997). However, unlike the mainland population, the area limitations on islands result in low carrying capacities (the maximum potential population size that can be supported) for takahe. Moreover, impending successional habitat changes on several islands may decrease the potential size of takahe populations even further (Baber & Craig 2003). Specifically, South Is takahe on Tiritiri Matangi Island frequently use revegetated grassland habitats that are expected to revert to forest as part of the restoration process and generally avoided forest (Baber & Craig 2003). Temporal changes in habitat availability as a result of vegetation succession may affect maximum population size as productive habitats become more limited (Pulliam *et al.* 1992). There is some evidence that birds respond to successional changes in habitat quality. For example, at least 9 species of bird that mostly use early successional habitats are declining in parts of the species range as a result of regional reforestation in the northeastern United States (Litvaitis 1993; Hunt 1998).

The intended role of the island populations as stated by the Takahe Recovery Plan is to insure

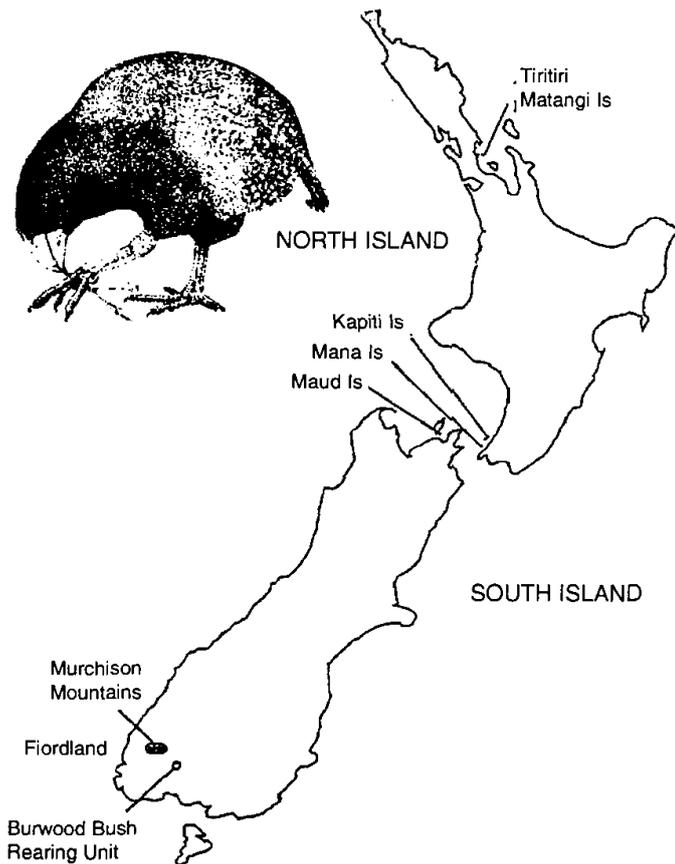


Fig. 1 Present distribution of South Is takahe (*Porphyrio hochstetteri*) in New Zealand. The wild population is now restricted to an alpine area of c. 650 km² in the Murchison Mountains, Fiordland. Translocated populations exist on 4 offshore islands. Eggs from the Fiordland population are artificially incubated and reared to 1 year of age at the Department of Conservation Burwood Breeding Unit, then released back into the wild.

against extinction of the mainland population (Crouchley 1994). To achieve this, the 4 island populations of South Is takahe must constitute a viable metapopulation able to persist indefinitely. This outcome depends on the carrying capacity of the islands, which, in turn, reflects the spatial requirements of takahe coupled with the amount of suitable habitat. If carrying capacities are low, then either additional islands or more intensive management of the current suite of islands may be necessary. Conversely, if the carrying capacities are high, management resources should remain concentrated on islands supporting takahe populations and current management intensity should continue. It is therefore essential for future management planning for takahe on islands to estimate spatial requirements and carrying capacities of the island refuges, to ensure survival of the species (Ryan & Jamieson 1998).

Studies of takahe populations have been limited so far by either small population sizes of non-free-ranging birds (Dawson 1994) or

observations over a short period (Ryan & Jamieson 1998). Our study is the 1st to investigate the factors influencing spatial requirements of takahe populations on an offshore island throughout a year and at different stages of chick rearing (hatchlings to subadults). Furthermore, the impending reforestation of some islands has largely been overlooked in the context of takahe management. Thus, the consequences of these changes on takahe spatial requirements and the ability of islands to support takahe are largely unknown. Moreover, supplementary feeding of birds was terminated 5 months into this study, allowing us to examine the influence of food manipulations on takahe home range size. Our objectives were: 1, to quantify the sizes of takahe home ranges on 1 of the 4 islands on which they have been established; 2, to examine the effects on takahe home range size of breeding condition, seasonal variation, the presence or absence of supplementary feeding, overall population density, and habitat quality; 3, to determine if the variability in home range size among family groups was related to spatial patterns in habitat availability; 4, to estimate the carrying capacity of South Is takahe on Tiritiri Matangi Is; and 5, to use these data as a basis for discussion on the value of islands for takahe conservation.

METHODS AND MATERIALS

Study area

The study was conducted on Tiritiri Matangi Island (Fig. 1), an open wildlife sanctuary in the inner Hauraki Gulf, 3.5 km east of Whangaparaoa Peninsula and 28 km north of Auckland City, New Zealand (36°30'S, 174°55'E). Tiritiri Matangi (220 ha) has a maximum elevation of 91 m asl, a relatively low rainfall (1026 mm yr⁻¹), and an average temperature of 10–20°C. Droughts are uncommon because the rainfall is evenly distributed throughout the year and the humidity is generally high. The island was farmed until 1971 when it was retired for conservation. Following over 100 years of farming, 94% of the island's forest had been removed. However, between 1984 and 1994, volunteers planted 250,000–300,000 trees in an attempt to restore the native forest. In addition, the Polynesian rat (*Rattus exulans*), the island's only introduced mammalian predator, was eradicated in 1995. Subsequently, several threatened and endangered birds have been introduced, and have established self-sustaining populations. Excluding rocky coastline and beach areas, the vegetation cover of Tiritiri Matangi consists of mature forest (18.9%), open areas of native grasses (32.8%), managed grass tracks (3.2%), a mosaic of native grassland and shrubs (42.6%), and a small (2.5%) area of farmland.

Takahe on Tiritiri Matangi

Takahe were introduced to Tiritiri Matangi in 1991. At the beginning of the study (Nov 1994) the population was 10, and by the end of the study (Oct 1995) the population had increased to 16. Resident birds were translocated from other islands, hand-reared at the National Wildlife Centre at Mt Bruce (southern North Is), or were born on Tiritiri Matangi. We studied 3 free-ranging family groups and a group that had established their home range around the lighthouse and housing area on the island (total of 13 individuals). The lighthouse group was not considered to be free-ranging because the birds sought human contact, and were given supplementary food all year. Each of the 4 family groups studied consisted of an adult male and female and their offspring. Offspring of the lighthouse group and 2 free-ranging family groups consisted of 1 chick, while 1 free-ranging takahe group consisted of 1 chick and 1 subadult. Management of island birds includes supplementary feeding, egg monitoring and manipulation. Supplementary feeding began on all islands for the 1994/1995 breeding season to facilitate breeding and enhance chick growth, and to allow for easier observation and capture if necessary. Family groups were fed organic turkey breeder pellets (c. 100 g bird⁻¹ day⁻¹) from Nov 1994 to Mar 1995. In addition, chicks were fed a 60/40 vegetable/grain and mealworm mix for the 1st 4-6 weeks. Family groups were given the supplementary feed near their nesting sites.

Data collection

We fixed the location of 4 takahe family groups 517 times on Tiritiri Matangi from Nov 1994 to Oct 1995. Each family group was located 7-12 times month⁻¹ with at least 24 h between consecutive location fixes on the same family group, to ensure that data were independent among sampling periods. We determined the location of each takahe family group using the distance and direction of the birds from several predetermined reference points on the island. Searches for family groups were evenly spread over the entire day within 3 predetermined periods, dawn-midmorning, midmorning-midafternoon, and midafternoon-dusk. A plot of home range size on the number of location observations reached an asymptote after 42-97 fixes. Hence, the number of independent location observations for each group (105-156) was sufficient for accurate estimates of home range size over the course of the study. The non-free-ranging group was given supplementary feed over the course of the study, and hence served as a control to measure the effects of supplementary feeding on home range size.

Data analyses

We calculated home range sizes of the 4 takahe family groups over the course of the study using the 95% minimum convex polygon method (MCP, Mohr 1947) and 95% Harmonic Mean (HM) method (Dixon & Chapman 1980). The MCP method was used because of its objectivity and comparability among studies, but because MCP is influenced significantly by outlier fixes (White & Garrott 1990; Harris *et al.* 1990), HM was chosen as an alternative descriptor of home range size. The HM method places less emphasis on the boundaries and allows for the accurate representation of the areas of the home range with the greatest intensity (core areas) (Kaufmann 1962; Jaremovic & Croft 1987; Harris *et al.* 1990). Differences between home range estimators were analyzed using a non-parametric Mann-Whitney *U* test. We defined the 75% HM home range for each group as the core area because at that point, the home range size generally reached an asymptote (Harris *et al.* 1990). Home ranges were estimated using the software package RANGES IV (Kenward 1990). Differences in the absolute amount of each major habitat type (managed grassland tracks, grass/shrub mosaic, native grassland) in each home range were determined using non-parametric Kruskal Wallis analyses.

Home range sizes (95% MCP) were also calculated for each season, by breeding stage (age of chick), and for periods with and without supplementary feeding. However, location fix asymptotes were not reached when home ranges were divided into season, breeding condition or the presence or absence of supplementary feeding, so differences in size of home range among these parameters were not analyzed statistically. Furthermore, seasonal categories and breeding condition were strongly correlated, making it impossible to determine the relative importance of each factor on home range size. Most notably, summer home range was likely to be influenced by the presence of young chicks.

Potential takahe population size (carrying capacity) on Tiritiri Matangi

To estimate the potential maximum size of the takahe population on Tiritiri Matangi, the total area of suitable takahe habitat (grass/shrub mosaic and managed grass tracks; Baber & Craig 2003) was delineated and measured. These habitats were used for foraging on grasses and invertebrates, offered adequate protection from Australasian harriers (*Circus approximans*), and the grass/shrub habitat provided many nesting and roosting sites (Baber & Craig 2003). Artificial ponds are also important for takahe. Broad

habitat components were mapped using aerial photograph interpretation, aided by ground checks. The availability of each habitat type on Tiritiri Matangi was then calculated from the sum of proportions of habitat types in 25 m × 25 m (625 m²) grid squares. Habitat availability within home ranges was then calculated from 95% HM home ranges to estimate the average amount of grass/shrub and managed grass track habitat required individual⁻¹. Carrying capacity was then determined by dividing the total available area of suitable habitat into the average amount of suitable habitat required by each individual.

RESULTS

Home range size

Mean annual home range of free-ranging takahe groups calculated using 95% MCP (20.7 ± 6.9 ha) did not differ significantly ($U = 0.48$, $P > 0.05$) from mean home range calculated using 95% HM (22.15 ± 6.4 ha). The core area over the course of the study (designated as 75% HM) averaged 7.3 ± 2.2 ha. There were large differences in the habitat composition of home ranges among takahe family groups (Fig. 2). However, there was no significant difference in the amount of grass/shrub habitat ($H_2 = 0.55$, $P > 0.05$, Fig. 2) or managed grass tracks ($H_2 = 1.2$, $P > 0.05$, Fig. 2) among takahe groups. Furthermore, the smaller the home range of any takahe family, the greater the proportion of suitable habitat (grass/shrub mosaic and managed grass tracks) within the home range (Fig. 3).

Effects of seasonal, breeding condition, and supplementary feeding on home range size

The mean size of takahe home ranges (95% MCP) for free-ranging families differed significantly ($U = 19.8$, $P < 0.01$, Table 1) between periods of supplementary and non-supplementary feeding. Mean home range sizes averaged 4.1 ± 0.87 ha during the supplementary feeding period (Nov 1994 to Mar 1995) and increased 6-fold to 25.0 ± 7.4 ha during the non-supplementary feeding period (Mar 1995 to Oct 1995) (Table 1). There was also a 2-fold increase in home range size (2.24 – 4.37 ha) during the same period in the lighthouse group that was fed throughout the course of the study. The mean size of home range of family groups increased steadily from 1.7 to 17.2 ha (Table 1), as chicks aged from 0-2 months (newborn) to 6-10 months (close to adult size) (Table 1). The mean sizes of takahe home ranges (MCP 95%) were similar, although summer home ranges were generally smaller.

Home range overlap and aggressive encounters

The only overlap among study birds was in the outer periphery of home ranges between Groups 2 and 3. Based on infrequent observations of

Table 1 Factors influencing home range sizes (ha) of South Island takahe (*Porphyrio hochstetteri*) on Tiritiri Matangi Island, Nov 1994 – Oct 1995. Values are means of Minimum Convex Polygons ± SE. () = no. of fixes; *, difference significant at $P < 0.05$.

Category (no. of fixes)	Home range (ha)
Supplementary feeding*	
Supplementary feeding (155)	4.10 ± 0.9
Supplementary feeding (270)	25.0 ± 7.4
Age of chick*	
0-2 months (119)	1.7 ± 0.7
3-5 months (139)	9.4 ± 5.4
6-10 months (172)	17.2 ± 7.5
Season	
Summer (176) (Dec-Feb)	4.4 ± 1.7
Autumn (127) (Mar-May)	10.7 ± 2.8
Winter (106) (June-Aug)	13.3 ± 3.2
Spring (71) (Sep-Nov)	10.1 ± 3.3

non-study birds, no other home range boundaries overlapped to any extent, although all home ranges were bordered by the home range of at least 1 other individual or family group. Aggressive behaviour was observed whenever individuals from different family groups met. Such circumstances were rare, but were more common during the breeding season. In the nonbreeding season (Jan-Aug) there were 0.06 encounters pair⁻¹ month⁻¹, however this increased 10-fold to 0.6 aggressive encounters pair⁻¹ month⁻¹ during the breeding season (Sep-Dec).

Habitat quality and the potential takahe population size on Tiritiri Matangi

The vegetation of Tiritiri Matangi included 79 ha of grass/shrub mosaic and 7 ha of managed grass tracks, making 86 ha of habitat considered suitable for takahe. Measurements of the composition of home range habitat indicated that each takahe family group required an average of 11.7 ha of native grass/shrub mosaic and 1.3 ha of managed grass tracks with at least 1 permanent water supply. Together, the 3 free-ranging family groups (10 birds) occupied a total of 35 ha of grass/shrub habitat and 4 ha of grass tracks. The average individual therefore used *c.* 3.5 ha of grass/shrub habitat and 0.4 ha of grass tracks. The entire free-ranging takahe population of 14 birds at the end of this study used an estimated 54.6 ha, which left 31.4 ha of suitable habitat, sufficient to support 7 additional individuals (under the current regime of supplemental feeding). The carrying capacity of Tiritiri Matangi therefore may have been 25 individuals, or *c.* 7 breeding pairs (including chicks) under the environmental conditions at the time of study.

DISCUSSION

Home range size

The takahe home ranges on Tiritiri Matangi were

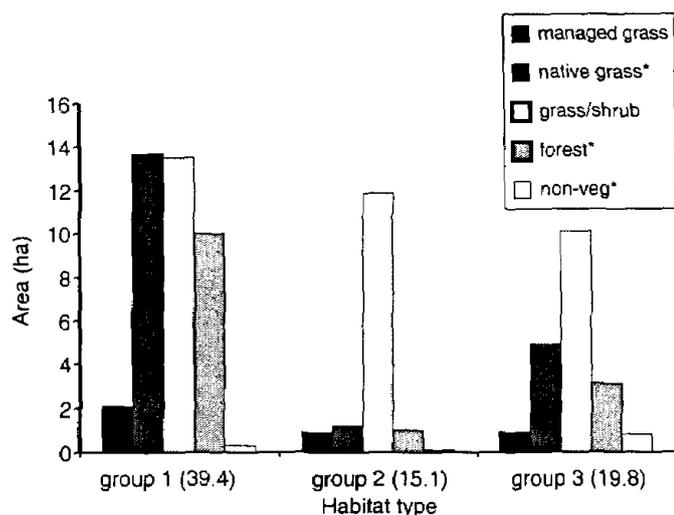


Fig. 2 Area (ha) of each habitat available within home ranges of 3 free-ranging South Is takahe (*Porphyrio hochstetteri*) groups on Tiritiri Matangi, Nov 1994 - Oct 1995. *, significant differences in area among group home ranges; solid, managed grass; open, native grassland; coarse horizontal hatch, grass/shrub; diagonal hatch, forest; fine horizontal hatch, non-vegetated.

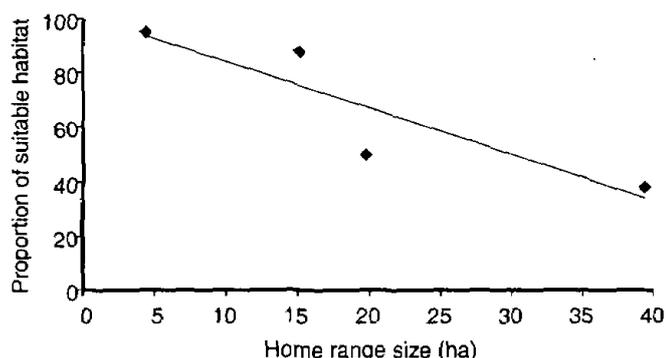


Fig. 3 Home range size (ha) and the proportion of suitable habitat (grass/shrub mosaic + managed grass tracks) of South Is takahe (*Porphyrio hochstetteri*) within home ranges of all groups ($n = 4$) on Tiritiri Matangi Is, Nov 1994 - Oct 1995.

larger than estimated home ranges on other offshore islands, and on Tiritiri Matangi in the past. Dawson (1994) estimated average home range sizes on Tiritiri Matangi and Maud Is at 5.5 ha. Likewise, Ryan & Jamieson (1998) estimated home ranges of c. 2.8 ha on Mana Is, and 8.0 ha on Kapiti Is. Differences among studies probably resulted from a combination of factors, including the use of human-conditioned birds, and differences in study duration, methodology, and habitat quality. Dawson (1994) and Ryan & Jamieson (1998) included "human influenced" takahe family groups, which tended to have much smaller home ranges than the more free-ranging groups. Furthermore, Ryan & Jamieson's (1998) study on Mana Is was conducted during the breeding season only (Sep- Feb), which

corresponded to the period in which home ranges were smallest on Tiritiri Matangi during this study. The duration of sampling may have important effects on estimates of home range size because home range coverage and boundaries change over time (Buskirk & McDonald 1989). Variation in estimates of home range size between sites has also been attributed to calculation methods. Furthermore, Ryan & Jamieson (1998) used a modified minimum area method, which is likely to give smaller estimates relative to other methods (Harvey & Barbour 1965), such as those used in this study. Differences in home range sizes among offshore islands may also result from differences in habitat quality among islands. The drier conditions on Tiritiri Matangi may result in reduced habitat quality (Ryan & Jamieson 1998), and explain the larger home range sizes compared to Mana Island. The home ranges of South Is takahe on Tiritiri Matangi and other islands are smaller than those in Fiordland, which average 30-35 ha (Reid & Stack 1974), and range between 2.5 and 80 ha (Mills 1973).

Home range size versus habitat quality

Home ranges of the 3 free-ranging family groups varied widely (10.1-33.8 ha) but contained similar amounts of preferred habitat (10.1-13.5 ha of grass/shrub mosaic, 0.8-2.1 ha of managed grass tracks) despite large differences in overall size. The negative correlation between home range size and habitat quality suggested that home range size of family groups was dependent on the spatial distribution of grass/shrub mosaics and grass tracks. Where there were suitable habitats in sufficient quantity over a small area, the group home ranges were small. Conversely, where these habitats were widely distributed and patchy, home ranges were large. Habitat quality may be reflected in home range size, which is often assumed to reflect underlying resource levels (Storch 1995), a perception supported by the smaller home range sizes on Mana, where suitable habitat may be less patchy (C. Ryan pers. comm.). The response is likely to ensure that sufficient resources necessary for survival are included within the home range. Specifically, birds in habitats with more concentrated or higher quality food resources may not need as much space to meet their resource needs (Hunt 1996). For example, the size of home ranges of capercaillie (*Tetrao urogallus*) in the Bavarian Alps, Germany, were inversely related to the proportion of suitable habitat (late successional forest) within the home range (Storch 1995).

Forest and open areas of native grassland were generally avoided by South Is takahe. It is particularly noteworthy that high proportions of forest appear to correlate with large home ranges of takahe family groups because much of Tiritiri

Matangi Is (60%) is expected to revert to mature forest. The remaining 40% will remain as open areas of grassland to support associated wildlife, including the red-crowned parakeet (*Cyanoramphus novaeseelandiae*), and for aesthetic reasons such as views of the surrounding Hauraki Gulf. Despite an abundance of food resources, open areas of native grassland were avoided by takahe, which may be associated with a high risk of predation in open habitats (Baber & Craig 2003).

Seasonal and breeding condition effects on home range size

Over the course of the study, home range size was likely to be influenced by season, the birds' breeding condition, and the presence or absence of supplementary feeding. We were not able to interpret the relative importance of each of these factors statistically, but trends were apparent. Home ranges during summer were <50% of those in autumn, spring, or winter. The reduction in home range size during summer may correspond partially to a greater availability of food resources (availability of grass seedheads, Baber & Craig 2003) and the use of supplementary feed. Small summer ranges may have also resulted from the presence of small chicks in all family groups during most of this period (see below).

The effect of supplementary feeding suggests that the use of space was largely influenced by resource availability, because a decrease in resource availability (termination of supplementary feeding) corresponded to a significant increase in home range size: the average home range size (95% MCP) increased 6-fold after supplemental feeding was stopped, whereas supplementary feeding was continued in the "control" group and there was only a 2-fold increase in home range size of this group. From a review of food supplementation experiments on terrestrial vertebrates, Boutin (1990) concluded that supplementary feeding led to a decrease in home range in 19 of 23 instances. Supplementary feeding obviously allows nutritional and energetic requirements to be met in a small area (Arcese & Smith 1988), and the increase in the home range of the "control" group over the same period suggests that other factors, such as season and breeding condition, that differed during and after supplementary feeding may also account for the changes.

Home range increased in size as the chicks grew. A young chick may limit mobility of the family group. Alternatively, the resource requirements of the chick may be available in a much smaller area given its size and the dominance of invertebrates in the chick diet (Baber & Craig 2003). Adult takahe may be able to obtain their total energy requirements from a smaller area by increasing foraging efficiency

(energy gained unit⁻¹ feeding time) or by feeding on suboptimal food resources (Krebs & Davies 1993). Seasonal effects (takahe chicks reached maturity in the late autumn and winter months when food resources were likely to be less abundant) and the presence or absence of supplementary food? (family groups were fed only when chicks were young) may have influenced home ranges simultaneously with the age of the chick.

Population density

Under higher population densities, as in Fiordland, "takahe occupy territories which they defend aggressively against other takahe" (Crouchley 1994). Takahe also occupied territories on Tiritiri Matangi Island, as indicated by aggressive encounters (Baber & Craig 2003) and mutually exclusive home ranges. Aggressive encounters were most frequent during the mating season when single adults moved about the island in search of mates. Ryan & Jamieson (1998) considered that the South Is takahe on Mana Island occupy home ranges rather than territories, but this is likely to result from differences in interpretation rather than differences in spatial behaviour between islands. Based on the presence of unoccupied but suitable habitat (grass/shrubs; grass tracks), we believe that maximum supportable population density had not yet been reached on Tiritiri Matangi during this study. Home ranges are not, therefore, likely to have been compressed or constrained by the presence of neighbouring birds (Hunt 1996). Moreover, aggressive encounters between conspecifics were low, except during the mating season when single adults in search of mates frequently entered the home ranges of family groups. Alternatively, the contrast in levels of aggressive encounters between the Fiordland and Tiritiri Matangi populations might be related to the predictability of resources in time and space, which would influence the energetic defensibility of a resource (Krebs & Davies 1993).

Potential takahe population size (carrying capacity) on Tiritiri Matangi

Conservation planning for takahe in the future may depend largely on the number of takahe that can be supported on islands (Ryan & Jamieson 1998). In the absence of detailed autecological information, Crouchley (1994) estimated that the carrying capacity of Tiritiri Matangi to be 7-10 breeding pairs, or 20-30 birds. In contrast, Dawson (1994) suggested that Tiritiri Matangi Island may be able to support up to 100 takahe, though a conservative figure of 50 was considered more realistic (Clout & Craig 1995). However, Dawson's study was restricted to a single group of supplementary-fed human-influenced birds with an artificially small

home range. From our study, we propose a maximum carrying capacity of 25 birds (~7 breeding pairs) which is similar to Crouchley's (1994) estimate. Our estimation is based on home range size and the amount of suitable habitat available on Tiritiri Matangi Is and assumes that home ranges will not compress as population density increases. The estimated carrying capacity of all 4 islands range from 25-35 pairs (Crouchley 1994) to a maximum of nearly 100 pairs (Ryan & Jamieson 1998).

Levels of inbreeding higher than those assumed acceptable in population modeling (*e.g.*, Vucetich & Waite 1999) are common in New Zealand birds where population sizes are small (Craig 1991; Clout & Craig 1995). Populations as low as 7-10 pairs may have at least medium-term viability (Craig 1991). In addition, because birds are also moved among islands, island populations of South Is takahe represents a managed metapopulation (Levins 1970; Hanski & Gilpin 1991), which reduces the risk of extinction from genetic, demographic, or environmental factors (Hanski & Gilpin 1991). A total carrying capacity of 25-35 pairs on all islands combined, as estimated by Crouchley (1994), may therefore be viable. Ryan & Jamieson (1998) estimated that Mana Island alone was capable of supporting up to 53 pairs (assuming habitat restoration), and may therefore sustain a viable population on its own.

Carrying capacity is notoriously difficult to predict and depends largely on population densities and habitat and resource availabilities at the time of study (Hobbs & Hanley 1990). Seasonal effects and breeding condition may also be important, but not measured if a study does not continue for at least 1 year, or preferably for several years. The effect of future increases in population density on home range sizes is also difficult to determine because increased densities may be accommodated by reduced home range size, increased overlap or home ranges, or use of presently unoccupied habitat (Donnelly 1989; Broughton & Dickman 1991). Furthermore, the behavioural flexibility of takahe (Dawson 1994; Baber & Craig 2003) suggests that they may use vegetation types avoided at the time of study, such as native grassland, beaches, and forest, if competition for resources increases. These factors suggest that carrying capacity could be higher than 25 individuals on Tiritiri Matangi, but any increase in carrying capacity is likely to be offset by a gradual decrease in the proportion of the grass/shrub mosaic through time as they mature into forest (Baber & Craig 2003). A visit to the island in Mar 2002, revealed that several core grass/shrubland areas used frequently by takahe in 1994/1995 now have a leaf litter layer,

suggesting that they may now be suboptimal foraging habitat for takahe. The carrying capacity of the other islands with large areas of re-vegetated habitat — Mana and Maud — may also be affected in future. Thus, habitats will to be managed to maximize the number of takahe that these islands can support (Baber & Craig 2003).

Implications for conservation

The carrying capacity of Tiritiri Matangi for South Is takahe based on home range size, habitat requirements, and suitable habitat availability, was estimated to be 25 individuals. Based on the estimated carrying capacities for all islands and the ability of many New Zealand birds to survive high levels of inbreeding, populations of takahe on offshore islands are expected to be viable under current environmental conditions (Craig 1991). Therefore, at the time of this study, these islands fulfilled their role as an insurance against extinction on the mainland. Nevertheless, given the impending habitat changes on Mana, Tiritiri Matangi, and Maud islands, it is unclear whether South Is takahe populations on management islands will continue to be viable in the future without an active management plan. The need for a larger island to insure against extinction on the mainland is therefore not clear, but is recommended if feasible. Further research on the responses of South Is takahe to changes in habitat and associated population densities will be necessary to ensure better management of this critically endangered species.

ACKNOWLEDGEMENTS

Special thanks go to Ray and Barbara Walter whose warmth and hospitality help make Tiritiri-Matangi Island what it is today. Research on Tiritiri Matangi was supported by the University of Auckland, and Supporters of Tiritiri Matangi Island. Earlier drafts from this manuscript benefited greatly from comments by Dan Childers, Maureen Donnelly, Ian Jamieson, Graham Ussher, Jeremy Wilson, the South Florida Ecosystems Lab at Florida International University, and 2 anonymous reviewers. Finally, I thank Sara Tompkins for editorial assistance.

LITERATURE CITED

- Aitkinson, I.A.E.; Millener, P.R. 1991. An ornithological glimpse into New Zealand's pre-human past. *Acta XX Congressus Internationalis Ornithologici* 1: 129-192.
- Arcese, P.; Smith, J.N.M. 1988. Effects of population density and supplemental food on reproduction in song sparrow. *Journal of animal ecology* 57: 119-36.
- Baber, M.J. 1996. Offshore islands and management of the Takahe: can islands support a viable population? Unpubl. MPhil thesis. University of Auckland, Auckland, New Zealand.

- Baber, M.J.; Craig, J.L. 2003. The relationship between resource availability, foraging behaviour and habitat use by the South Island takahe (*Porphyrio hochstetteri*). *Notornis* 50: 59-67.
- Beauchamp, A.J.; Worthy, T.H. 1988. Decline in the distribution of the takahe *Porphyrio mantelli*: a re-examination. *Journal of the Royal Society of New Zealand* 18: 103-112.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian journal of zoology* 68: 203-220.
- Broughton, S.K.; Dickman, C.R. 1991. The effect of supplementary food on home range of the southern brown bandicoot, *Isodon obesulus* (Marsupialia: Peramelidae). *Australian journal of ecology* 16: 71-79.
- Bunin, J.S.; Jamieson, I.G. 1995. New approaches towards a better understanding of the decline of the takahe (*Porphyrio mantelli*). *Conservation biology* 9: 100-106.
- Bunin, J.S.; Jamieson, I.G.; Eason, D. 1997. Reproductive success of the endangered takahe (*Notornis mantelli*). *Ibis* 139: 144-151.
- Buskirk, S.W.; McDonald, L.L. 1989. Analysis of variability in home range size of the American martin. *Journal of wildlife management* 53: 997-1004.
- Clout, M.N.; Craig, J.L. 1995. The conservation of critically endangered flightless birds in New Zealand. *Ibis* 137 (Supplement): S181-S190.
- Craig, J.L. 1991. Are small populations viable? *Acta XX Congressus Internationalis Ornithologici* 4: 2546-2551.
- Crouchley, D. 1994. Takahe Recovery Plan. *Threatened species recovery plan series no. 12*. Wellington, Department of Conservation.
- Dawson, N. 1994. The behavioural ecology and management of the takahe. Unpubl. MPhil thesis. University of Auckland, Auckland, New Zealand.
- Dixon, K.R.; Chapman, J.A. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61: 1040-1044.
- Donnelly, M.A. 1989. Effects of reproductive resource supplementation on space use patterns in *Dendrobates pumilio*. *Oecologia* 81: 212-218.
- Hanski, I.; Gilpin, M.E. 1991. *Metapopulation dynamics*. London. Academic Press.
- Harris, S.; Cresswell, W.J.; Forde, G.P.; Trehwella, W.J.; Woollard, T.; Wray, S. 1990. Home range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal review* 20: 97-123.
- Harvey, M.J.; Barbour, R.W. 1965. Home range of *Microtus ochrogaster* as determined by a modified minimum area method. *Journal of mammalogy* 46: 398-402.
- Hobbs, N.T.; Hanley, T.A. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? *Journal of wildlife management* 54: 515-522.
- Holdaway, R.N. 1989. New Zealand's pre-human avifauna and its vulnerability. *New Zealand journal of ecology* 12 (Supplement): 11-25.
- Holdaway, R.N. 1999. Introduced predators and avifaunal extinction in New Zealand. pp. 189-238 In: MacPhee, R.D.E. (ed.) *Extinctions in near time: causes, contexts, and consequences*. New York, Kluwer Academic/Plenum Press.
- Hunt, P.D. 1998. Evidence from a landscape population model of the importance of early successional habitats to the American redstart. *Conservation biology* 12: 1377-1389
- Hunt, P.D. 1996. Habitat selection by American redstarts along a successional gradient in northern hardwood forests; evaluation of habitat quality. *Auk* 113: 875-888.
- Jaremovic, R.V.; Croft, D.B. 1987. Comparison of techniques to determine eastern grey kangaroo home range. *Journal of wildlife management* 51: 921-30.
- Kaufmann, J.H. 1962. Ecology and social behaviour of the *Coati nasua nitrica* on Barro Colorado Island Panama. *University of California publications in zoology* 60: 95-222.
- Kenward, R.E. 1990. RANGES IV. Software for analyzing animal location data. Cambridge, Institute of Terrestrial Ecology, Natural Environmental Research Council.
- Krebs, J.R.; Davies, N.B. 1993. *Behavioural ecology – an evolutionary approach*. 3rd ed. Cambridge, Blackwell Scientific Publications.
- Levins, R. 1970. Extinction. pp. 175-186 In: Gasterhaber, M. (ed.). *Some mathematical problems in biology*. Providence, R.I., American Mathematical Society.
- Litvaitis, J.A. 1993. Response of early successional vertebrates to historical changes in land use. *Conservation biology* 7: 866-873.
- Mills, J.A. 1973. Takahe research. *Wildlife: a review* 4: 24-27.
- Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. *American midland naturalist* 37: 223-249.
- Pulliam, H.R.; Dunning, J.B.Jr.; Liu, J. 1992. Population dynamics in complex landscapes a case study. *Ecological applications* 2: 165-177.
- Reid, B.; Stack, D.J. 1974. An assessment of the number of takahe in the "special area" of the Murchison Mountains during the years 1963-1967. *Notornis* 21: 296-305.
- Ryan, C.J.; Jamieson, I.G. 1998. Estimating the home range and carrying capacity for takahe (*Porphyrio mantelli*) on predator-free offshore islands: implications for future management. *New Zealand journal of ecology* 22: 17-24.
- Storch, I. 1995. Annual home ranges and spacing patterns of capercaillie in Central Europe. *Journal of wildlife management* 59: 392-400.
- Vucetich, J.A.; Waite, T.A. 1999. Erosion of heterozygosity in fluctuating populations. *Conservation biology* 13: 860-868.
- White, G.C.; Garrot, R.A. 1990. Analysis of wildlife radio-tracking data. New York, Academic Press.