

## The relationship between foraging behaviour and habitat use by South Island takahe (*Porphyrio hochstetteri*) on Tiritiri Matangi Island

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**Abstract** We investigated the habitat use and foraging behaviour of 3 South Island takahe (*Porphyrio hochstetteri*) family groups on Tiritiri Matangi Island, from Nov 1994 to Oct 1995. Takahe used habitats that offered abundant grasses, specifically grass/shrub mosaic and managed grass tracks, but open grassland was avoided. The preference was attributed to the higher risk of predation by Australasian harriers (*Circus approximans*) in this habitat as a result of a lack of sheltering trees or shrubs. Temporal patterns in habitat use reflected seasonal changes in food availability and breeding condition (age of chick). Most importantly, takahe family groups used the seasonally available grass seedheads in the grassland/shrub mosaic and the invertebrates in forest when chicks were young. The ability of Tiritiri Matangi to support takahe is likely to decrease as the suitable grass/shrub mosaic reverts to forest under the revegetation programme.

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**Keywords** foraging behaviour; habitat use; *Porphyrio hochstetteri*; South Island takahe; Tiritiri Matangi Island

### INTRODUCTION

The South Is takahe (*Porphyrio hochstetteri*) is currently restricted to an area of alpine-tussock grassland in the Murchison Mountains of Fiordland, South Island. As with many endangered species in New Zealand, takahe have declined as a result of anthropogenic changes including habitat destruction and modification, hunting, and the introduction of mammalian predators and competitors (Beauchamp & Worthy 1988; Bunin & Jamieson 1995). Since 1984, takahe management has involved the use of 4 predator-free islands to ensure against extinction in the wild. The island birds are managed as a single population and now comprise over 25% of the total takahe population. The translocations are particularly unusual given that the lowland habitat on selected islands differs markedly from the alpine-tussock habitat of the source population on the mainland. As such, the success of these efforts relies heavily on the behavioural flexibility of takahe. For example, takahe populations in

Fiordland eat mostly snow tussocks (*Chionochloa pallens*, *Chionochloa flavescens*, and *Chionochloa crassiuscula*) and the fern *Hypolepis millefolium* (Mills *et al.* 1984; Crouchley 1994). In contrast, offshore island populations forage primarily on various native and introduced pasture grasses (Crouchley 1994; Dawson 1994; Treweek 1996) and are known to eat live prey opportunistically, including earthworms, cicadas, small lizards, and possibly brown teal (*Anas aucklandica*) chicks (Dawson 1994; Baber 1996).

The takahe may be the most widely researched bird species in New Zealand (Lee 2000), but there are few studies of its behavioural ecology on offshore islands. This study therefore examined habitat use and foraging behaviour of takahe on Tiritiri Matangi Island, one of the 4 offshore islands currently supporting takahe populations. The translocation of South Island takahe to Tiritiri Matangi Island, off the east coast of the North Island, has extended the species known historical range (Fig. 1), and hence exposed this species to a novel environment. However, as a result of restoration efforts, much of the island is undergoing ecological succession and eventually

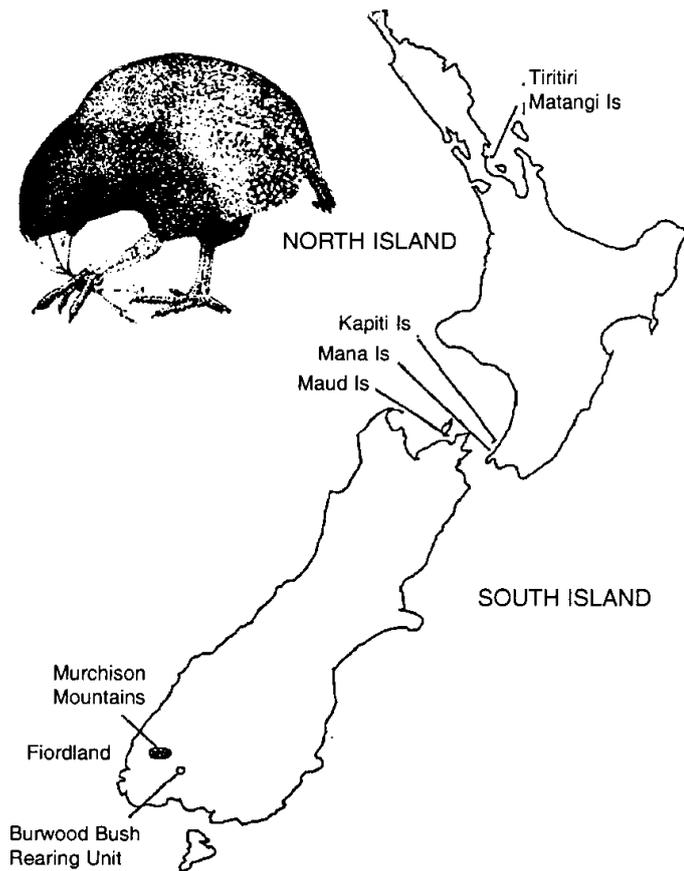


Fig. 1 Present distribution of South Is takahe (*Porphyrio hochstetteri*) in New Zealand. The wild takahe population is now restricted to an alpine area of c. 650 km<sup>2</sup> in the Murchison Mountains, Fiordland, but populations have been established on 4 offshore Islands.

will revert to forest (Baber 1996). The impact of this successional change on the takahe population is unclear. In addition, Australasian harriers (*Circus approximans*), a potential predator of takahe (Bunin & Jamieson 1995), are reported to be seasonally abundant (Moller & Craig 1988).

Our objectives were to quantify habitat use and foraging behaviour of takahe family groups on Tiritiri Matangi Island, to determine how seasonal changes in food availability or breeding condition (e.g., the age of the chick being reared in each family group) influenced habitat use and foraging behaviour by family groups, and to develop recommendations for the management of takahe populations on islands, with specific reference to the impending successional habitat changes in re-vegetated habitats.

## METHODS

### Study area

This study was conducted on Tiritiri Matangi Is (36°30'S, 174°55'E), 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 (Fig. 1). Tiritiri Matangi (220 ha) is 2.7 km long, has an average width of 0.7 km, and has gentle slopes rising to

only 91 m a.s.l. Mean annual rainfall is 1026 mm and temperatures are mild (monthly mean 10-20°C); droughts are uncommon because of year-round rainfall and high humidity.

The vegetation of Tiritiri Matangi consists of mature bush, open areas of native and introduced grasses, mown grass tracks, a small area of farmland, a mosaic of native grassland and shrubs, and non-vegetated areas (artificial ponds, gravel road) and coastline. The island was farmed until 1970, and was classified as a conservation island by the Department of Conservation in 1987. During 120 years of farming the island lost 94% of its native forest (Dawson 1994). However, between 1984 and 1994 volunteers planted 250,000-300,000 trees and eradicated the Pacific rat (*Rattus exulans*), the island's only introduced mammalian predator. Several threatened and endangered birds have been introduced and have established self-sustaining populations.

### Data collection

#### Study population

We studied 10 free-ranging, colour-banded individuals in 3 separate family groups. Two of the 3 family groups consisted of an adult female, adult male, and 1 chick, and 1 family group consisted of an adult female, adult male, sub-adult offspring, and 1 chick. The 3 groups comprised the entire population of free-ranging takahe family groups on Tiritiri Matangi during the study period from Nov 1994 to Oct 1995.

#### Collection methods and time frame

Data on takahe habitat use and foraging behaviour on the island were collected over 405 h. We sampled each family group 7-12 times month<sup>-1</sup>, and each sampling period lasted from 30 to 120 min. Consecutive samples on the same takahe group were conducted at least 1 day apart to ensure that data were independent among sampling periods. Observations were spread evenly over the day and pooled into the time periods dawn-mid-morning, mid-morning-mid afternoon, and mid-afternoon-dusk. Birds rapidly habituated to the observer and data could be collected within the 1st month, except that 1 pair appeared stressed in that 1st month of observation, during which the adults were incubating and hatching a chick. We began to collect data for this group when the chick was 2 weeks old.

Within each sampling period we recorded habitat use and foraging behaviour using 1 min instantaneous focal sampling (Altmann 1974). Habitat categories included managed (mowed) grass tracks, open areas of native grassland, forested habitat (predominant leaf litter base), native grass/shrub mosaic (re-vegetated areas), and non-vegetated areas (artificial ponds, beaches, a gravel road). Foraging activities included foraging for and consuming vegetation, foraging for and consuming invertebrates, and non-foraging activities such as standing still, allopreening, and preening. We also divided vegetation consumption

into 3 categories: tillering (consuming the basal meristems of grass); consuming grass blades or clover leaves; and stripping grass seedheads.

Time budgets for all individuals in a group could be recorded simultaneously (for up to 4 individuals). In many situations where an individual or individuals were momentarily separated or obscured from view, observations were recorded for the visible bird(s). Birds were observed from at least 15 m from the nearest bird to minimise behavioural changes associated with disturbance or stress.

### Data analyses

We examined habitat selection for each family group at 2 levels. Level I habitat selection concerned the selection of a home range from the available habitat on Tiritiri Matangi Island, and Level II habitat selection concerned the use of habitats within a home range (Johnson 1980). The relative proportion of each habitat type (habitat availability) on Tiritiri Matangi and the relative proportion of each habitat type within each of the 3 95% Harmonic Mean (HM) home ranges (RANGES IV, Kenward 1990) (Baber & Craig 2003) were calculated based on analysis of aerial photographs and field examination. We subdivided a aerial photograph taken in 1993 into 25 m × 25 m (625 m<sup>2</sup>) grids and estimated the proportion of each habitat type to the nearest 10%. This allowed us to determine the estimated availability of habitat on the island as a whole, and within each family group's home range. We did not include beaches, unavailable habitat types (small area of farmland), or habitats that constituted <2% of the total habitat (open areas of managed grassland; lighthouse area,) in our measurements.

We used  $\chi^2$  homogeneity analyses to determine if takahe groups used habitat non-randomly. Only the 1st recorded habitat observation during each sampling period was used in the analyses to ensure that data were statistically independent. Bonferroni 95% simultaneous confidence intervals were constructed to compare observed proportions (habitat use) with expected proportions (habitat availability) (Neu *et al.* 1974). Habitats were considered "selected" by takahe if the expected value was above the confidence interval, "avoided" if the expected value was below the confidence interval, and neither selected or avoided if the expected  $\chi^2$  value was within the confidence interval.

Habitat use and foraging behaviour budgets were calculated for each individual by dividing the observations recorded in each habitat and for each foraging behaviour by the total number of observations in a predetermined time period (*i.e.* over the entire study period, for each season, and within each chick-rearing stage). Habitat and foraging budgets of individuals within a group were then averaged to obtain a family group mean for the entire study period, each season, and within each chick-rearing stage. The small sample sizes undermined the validity of using statistical

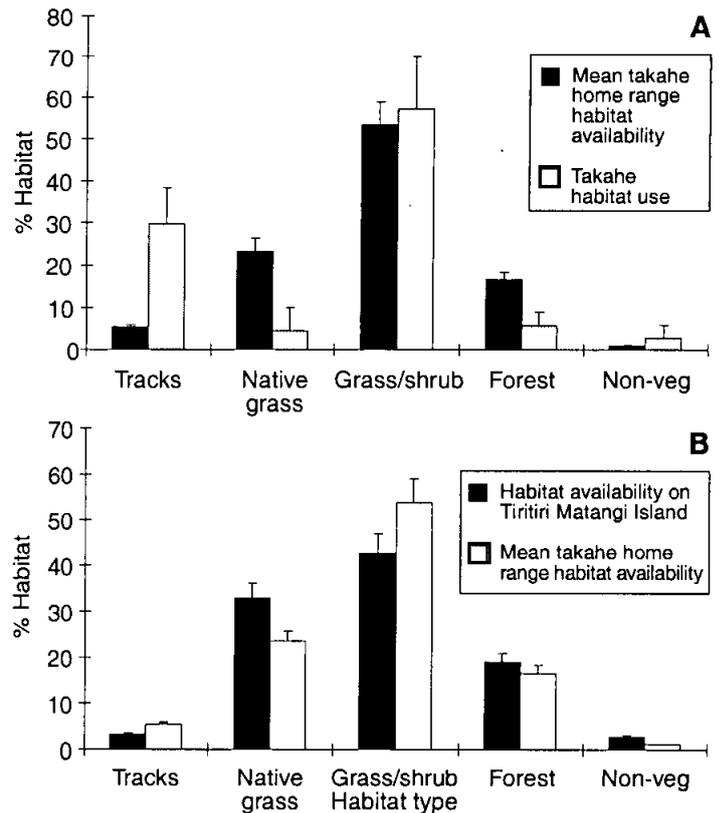


Fig. 2 A, Relationship between habitat availability and home range habitat availability within home ranges (Level I) for South Is takahe (*Porphyrio hochstetteri*) on Tiritiri Matangi Island, Nov 1994-Oct 1995. B, Relationship between habitat availability within South Is takahe home ranges and habitat use (Level 2).

analyses to determine differences in habitat use and foraging behaviour with respect to season, and breeding condition, or differences in foraging behaviour among habitats. We did not investigate sexes or age classes (adult/chick) separately because we were concerned with the behavioural ecology of the takahe family unit as a whole.

## RESULTS

### Habitat use

The habitat composition within takahe home ranges differed significantly from the relative availability on Tiritiri Matangi (Level I:  $\chi^2_4 = 32.7$ ,  $P < 0.001$ , Table 1, Fig. 2A). The grass/shrub mosaic was included within home ranges significantly more than expected based on availability on Tiritiri Matangi. The availability of managed grass tracks and forest within the home range were not significantly different from availability on the island. Native grassland and non-vegetated areas in home ranges were significantly less represented than expected.

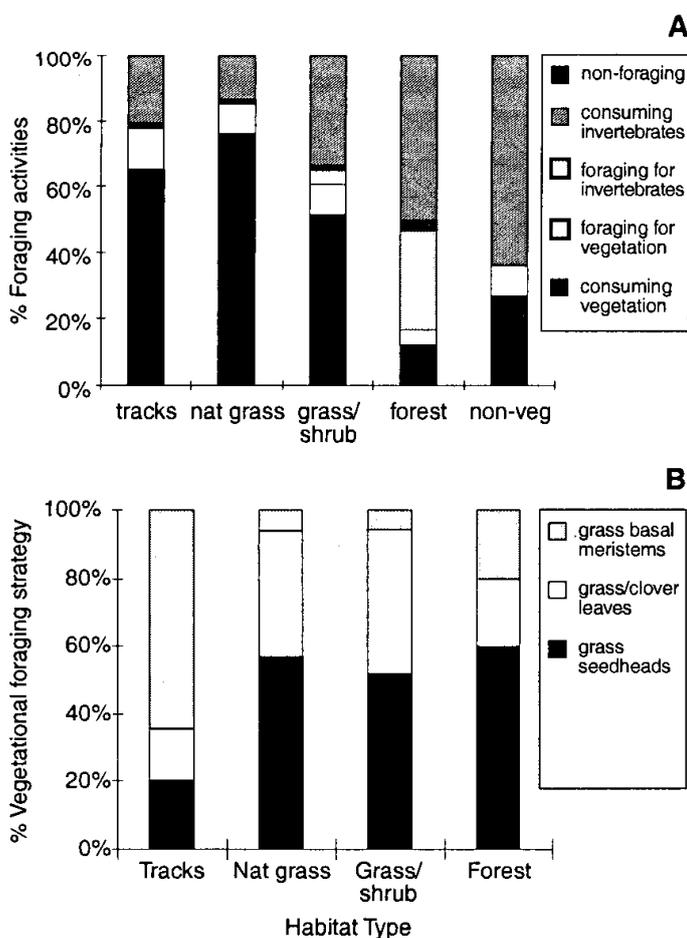
Habitat use differed significantly from habitat availability within home ranges (Level II:  $\chi^2_4 = 529.7$ ,  $P < 0.001$ , Table 1, Fig. 2B). Based on availability within home ranges, managed grass tracks were used more than expected, grass/shrub and non-vegetative habitats were used as expected, and native grassland and forest were used less

**Table 1** Bonferroni Confidence Interval tests for significant differences in the proportion of habitat type available within the study area versus the proportion of habitat type available within the home range of South Is takahe (*Porphyrio hochstetteri*) on Tiritiri Matangi Is (Level I). Level of significance, 0.01; ns, neutral selection; \*, habitat avoided; \*\*, habitat selected.

Vegetation type	Study area availability	Home range habitat availability (observed)	Bonferroni Intervals
Grass tracks	0.032	0.054	0.024 < P < 0.084**
Grassland	0.328	0.234	0.178 < P < 0.290*
Grassland /shrub	0.426	0.536	0.470 < P < 0.602**
Forest	0.189	0.166	0.117 < P < 0.215 NS
Non-vegetative	0.027	0.01	0 < P < 0.023*

**Table 2** Bonferroni Confidence Interval tests for significant differences in the proportion of habitat type available within the home range versus the proportion of habitat type use within the home range of South Is takahe (*Porphyrio hochstetteri*) (Level II). Level of significance, 0.01; ns, neutral selection; \*, habitat avoided; \*\*, habitat selected.

Vegetation type	Study area availability	Home range habitat availability (observed)	Bonferroni Intervals
Grass tracks	0.054	0.297	0.237 < P < 0.357**
Grassland	0.234	0.045	0.018 < P < 0.072*
Grassland /shrub	0.536	0.563	0.470 < P < 0.602 NS
Forest	0.166	0.058	0.027 < P < 0.089*
Non-vegetative	0.01	0.027	0 < P < 0.057 NS



than expected. Furthermore, takahe family groups averaged 52% of their time in grass/shrub mosaic, 36% in managed grass tracks, 7% in forest, 3% in native grassland, and 2% in non-vegetated habitat.

**Foraging behaviour**

South Is takahe family groups spent an average of 70% of their total time foraging, and 30% of their time engaged in non-foraging activities. Of the time spent foraging by each family group, 79% was spent consuming vegetation (grasses and clover), 13.8% searching for vegetation, 3.8% searching for invertebrates, 2.4% consuming invertebrates, and 1% consuming other (supplementary feed, dead twigs, and small stones). Of the foraging time allocated to the consumption of vegetation, 34.4% was spent consuming grass blades and clover leaves, 36.5% consuming seedheads, and 29.2% consuming grass basal meristems. The proportion of total time spent consuming vegetation was highest in native grassland at 74.1%, followed by 62.7% in managed grass tracks, 50.2% in native grass/shrub mosaic, 26.3% in non-vegetated and 12.1% in forest (Fig. 3A).

Invertebrates were consumed most frequently in forest (10%) and grass/shrub mosaic (8%), and much less frequently in non-vegetated (3%), native grassland (1%), and managed grass tracks (0.5%) (Fig. 3A). Invertebrates were consumed opportunistically in all habitats. Takahe searched actively for invertebrates only in the forest and grass/shrub mosaic, accounting for 30% and 2.4% (respectively) of the total time spent in these habitats (Fig. 3A). Consuming seedheads was the predominant method of feeding in forest (59.3%), native grassland (58.4%), and native grass/shrub mosaic

**Fig. 3** A, South Is takahe (*Porphyrio hochstetteri*) foraging activities versus habitat type on Tiritiri Matangi Island, Nov 1994-Oct 1995. B, Vegetation consumption strategies of takahe versus habitat on Tiritiri Matangi Is (n = 3).

(53.0%), whereas consuming grass blades and clover leaves was the predominant feeding activity in managed grass tracks (66.3%) (Fig. 3B); grass seedheads were uncommon on mowed grass tracks.

### Season

#### Habitat use among seasons

Habitat use differed between seasons (Fig. 4A). In summer, most time was spent in grass/shrub mosaic (78%) and only 11% of time was spent in grass tracks. Conversely, in winter only 43% of time was spent in grass/shrub mosaic and 46% of time was spent in grass tracks. Furthermore, time spent in forest peaked in summer and steadily decreased to 0.1% in spring.

#### Foraging behaviour versus season

Foraging activities were generally lower in summer compared to other seasons (Fig. 4B). Foraging for invertebrates was highest in summer and accounted for 12% of the total time spent foraging, followed by spring (5%), autumn (3%) and winter (0.5%) (Fig. 4B). Vegetation consumption strategies differed markedly among seasons (Fig. 4C). The predominant foraging strategy in summer (77.4%) and autumn (72.2%) was consuming seedheads. In winter the predominant foraging strategy was consuming grass basal meristems (48.9%), while in spring consuming grass blades and clover was the predominant foraging strategy (72%).

### Breeding condition (age of chick)

#### Habitat use versus age of chick

The proportion of time spent in each habitat differed among chick-rearing stages (age of chick) (Fig. 5A). The amount of time spent in grass/shrub mosaic decreased from 80.1% to 41.6% as chicks aged from 0-2 months to 6-10 months. Conversely, there was a gradual increase in the time takahe groups spent in managed grass-track habitats from 9.2% to 52.3% from the ages of 0-2 to 6-10 months. The proportion of time takahe groups spent foraging in forest was 10.1% when the chicks were aged 0-2 months, and 15% when chicks were aged 2-5 months. This decreased markedly to 0.9% when chicks were aged 6-10 months.

#### Foraging behaviour versus age of chick

Foraging behaviour differed among chick rearing stages (Fig. 5B). The time that family groups spent foraging steadily increased from 61.3% when the chicks were aged 0-2 months to 79.4% when the chick was 6-10 months. When chicks were young (0-2 months), parents spent much of their time foraging for invertebrates, which were immediately given to the chicks. At c. 2-3 months, the parents also began feeding the chick vegetation (e.g., grass blades and tillers). After 3 months chicks began foraging for themselves, consuming both vegetation and invertebrates. After c. 6 months, chick diets consisted almost exclusively of vegetation. Correspondingly, the time that family groups spent foraging for vegetation increased steadily from 41.1% when chicks were aged 0-2 months to 78.2%

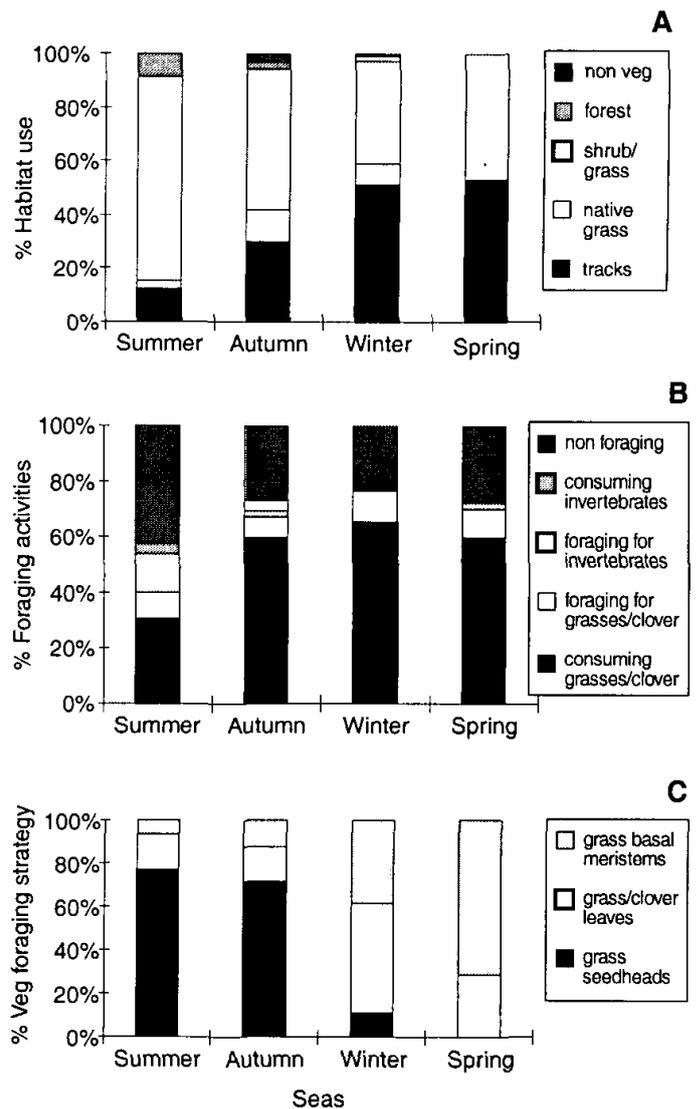


Fig. 4 A, Proportion of time South Is takahe (*Porphyrio hochstetteri*) spent in different habitats on Tiritiri Matangi Island for each season ( $n = 3$ ). B, Relative foraging behaviour of takahe by season. C, Relative vegetation consumption strategies of takahe for each season on Tiritiri Matangi Is, Nov 1994 - Oct 1995.

when chicks were 6-10 months. Over the same period, the proportion of time family groups spent foraging for invertebrates decreased from 19.2% to 0.2%. The relative proportion of time takahe family groups spent foraging differed among chick-rearing stages (Fig. 5B).

### DISCUSSION

Takahe appear to use habitats primarily in response to food resource abundance, food requirements, and the degree of protection from a potential predator (the Australasian harrier) on Tiritiri Matangi. Managed grass tracks and grass/shrub habitats were selected by takahe; these habitats contained abundant food resources, as indicated by the proportion of foraging time (93%) spent searching for or consuming various species of grasses and clover. In addition, these habitats provided protection from harriers, in the

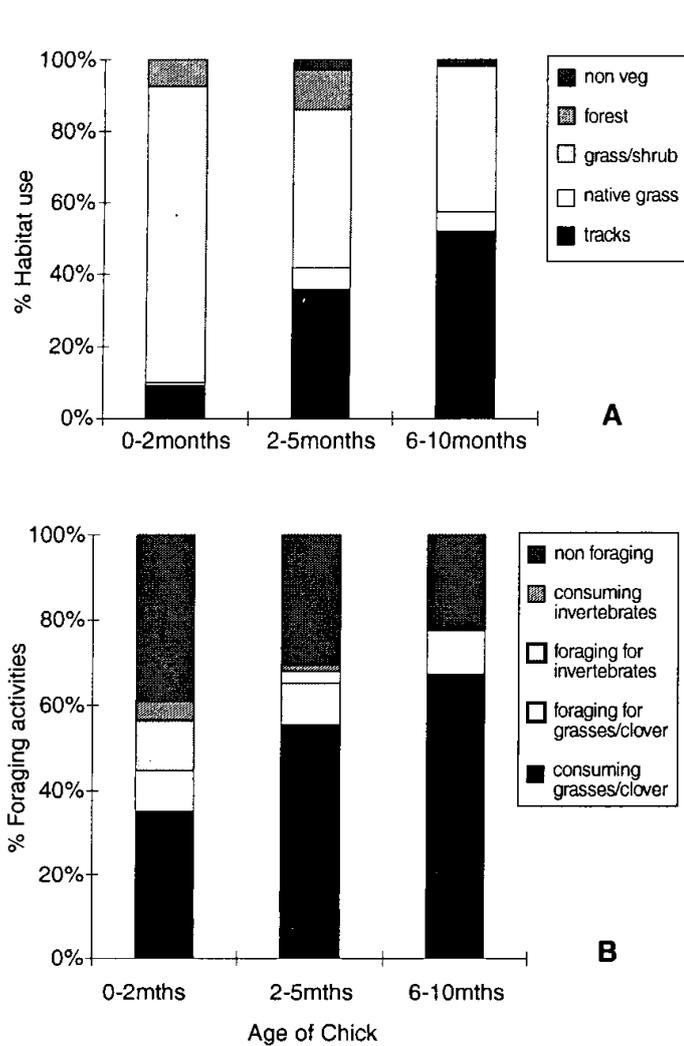


Fig. 5 A, Habitat use versus age of chick by family groups by South Is takahe (*Porphyrio hochstetteri*) on Tiritiri Matangi Island, Nov 1994-Oct 1995 ( $n = 3$ ). B, Takahe foraging activities in relation to age of chick.

form of shrubs and trees (within grassland and bordering grass tracks). Forests on Tiritiri Matangi were also generally avoided because of a relative lack of food resources (but see below). Non-vegetated areas also lacked food, but these areas included small ponds, which were used for bathing and drinking. Open areas of native grassland also contained abundant food, but this habitat was avoided by takahe, possibly because of the lack of protection (trees and shrubs) from harriers.

It is likely that harriers are a potential threat to South Is takahe, and that the risk of predation influences habitat selection. Over the course of the study, we witnessed 3 unsuccessful predatory strikes by harriers. There is circumstantial evidence that an adult takahe was killed by a harrier in 1992 (Crouchley 1994), and an adult was attacked but not injured on Tiritiri Matangi (G. Ussher pers. comm.). Takahe alarm response varied according to perceived danger, which may include the distance from harrier to takahe and the level of protection offered by the surrounding vegetation.

Alarm response varied from darting to cover and hiding (e.g., beneath a shrub), to watching the harrier until it was out of sight. Many studies (e.g., Ludwig & Rowe 1990; Houston *et al.* 1993) have reported a tradeoff in habitat use between resource abundance and the threat of predation.

Changes in foraging behaviour and habitat use partially reflected seasonal changes in the distribution, availability and abundance of food resources. The grass/shrub mosaic was the predominant habitat used during summer when grass seedheads were present. However, as seedheads became less available there was a gradual switch in habitat use to grass tracks and a corresponding switch in foraging methods to consumption of grass and clover leaves, and grass basal meristems. Similarly, takahe in Fiordland consumed the seeds of tussocks and grasses when available from Jan to Mar (Mills *et al.* 1984, 1988) and moved into forested valleys in winter, where their major food source was the rhizome of a fern *H. millefolium* (Mills *et al.* 1984; Crouchley 1994).

Differences in habitat use and foraging behaviour among stages in the breeding cycle (chick age categories) suggested that birds were responding to variations in food resource requirements and changing food availability and distribution, or both. Most importantly, the observed changes in habitat use correlated with the reduced dietary importance of invertebrates as chicks aged. When chicks were <6 months old, family groups spent a relatively large portion of their time in forest foraging for invertebrates. Typically, family groups would forage in leaf litter or rotten logs for earthworms and other invertebrates, most of which were fed to the chick. Most birds, even if strictly herbivorous as adults, consume a high protein animal diet when young to maximise growth rates (Begon *et al.* 1990). It was likely that the sharp decrease in use of forest as the chicks reached 5-6 months corresponded with a reduction in invertebrate foraging as chicks switched to a predominantly herbivorous diet.

Alternatively, reduction in the availability of invertebrates in the winter months may have also accounted for differences in habitat use and foraging behaviour among breeding stages. Studies of seasonality of terrestrial invertebrates in New Zealand forests and alpine habitats indicate that peak abundances occur in spring and autumn, with the lowest abundance in winter months (Moeed & Meads 1985, 1987). The perceived decrease in vulnerability to harrier predation as the chicks grew may also have contributed to the higher proportion of time spent in habitats that offered better protection when chicks were young — forest and grass/shrub mosaic. This is also suggested by the observation that takahe chicks often remained under cover waiting for food while adults foraged. In contrast to our study, Dawson (1994) found invertebrates to be of little significance, accounting for only 1% of their diet; her results probably reflected the absence of chicks.

### Impending successional habitat changes

All 4 islands currently holding takahe populations contain grassland habitats, although the relative proportions differ among islands. Kapiti Island (2023 ha) is largely forested, Mana (217 ha) includes the largest proportion of grassland habitats, and Maud Island (309 ha), like Tiritiri Matangi, has a mixed forest/grassland vegetation. Currently, Tiritiri Matangi Island contains a large proportion of suitable habitat. However, habitat quality is expected to change over time as the grass/shrub association is replaced by forest; with a consequent reduction in the availability and abundance of food (particularly native grasses). This is expected to reduce the carrying capacity of the island for takahe significantly, given that 42.6% of the island currently consists of native grass/shrub habitat (Baber & Craig 2003). Based on a visit to the island in Mar 2002, several core grass/shrub areas used frequently by takahe in 1994/1995 now have a ground cover consisting mostly of leaf litter base, suggesting that these and other areas frequently used by takahe in 1994/1995 may now be poor foraging habitat.

### Population density

Takahe habitat use and foraging behaviour on Tiritiri Matangi are also likely to be influenced by population density. Individuals under nutritional stress at high population densities may trade increased predation risk for access to higher quality diets in open areas, such as native grassland (Brown 1988). Use of native grassland might, therefore, be expected to increase, assuming that the takahe population on Tiritiri Matangi continues to grow. This may, to some extent, offset the reduction in quality of the area of grassland/shrub through time. Based on the presence of unoccupied but suitable habitat (grass/shrub and grass track habitats) in 1994/1995, we believe that maximum population density had not yet been reached. As of Mar 2002, there were 20 South Is takahe on Tiritiri Matangi. The spatial and foraging changes associated with this increased population density are unclear because of an absence of research. However, the 2000/2001 breeding season was largely unsuccessful, attributed primarily to the increase in territorial disputes among proximal family groups (Dunning, pers. comm.).

### Conclusion and recommendations for management

Suitable habitat for takahe on Tiritiri Matangi includes managed grass tracks and the grass/shrub mosaic. However, an expected successional change from grass/shrub habitats to forest is likely to reduce the availability of this habitat, and consequently, may reduce the takahe carrying capacity on Tiritiri Matangi Island (Baber & Craig 2003). About 40% of the island is to remain as native grassland to provide views of the surrounding Hauraki Gulf for visitors, and to provide suitable habitat for other species, such as the red-crowned parakeet (*Cyanoramphus*

*novaezelandiae*). However, open native grasslands are not used by takahe. To improve the island's capacity to support takahe, while minimising negative effects on other grassland species and scenery, we recommend planting shrubs in the grassland. Planting small clusters of shrubs such as *Coprosma* spp. throughout the native grassland areas may encourage takahe to use them, by providing cover from harriers. We recommend clusters spaced 20-30 m apart, in areas that do not detract from the view of the surrounding Hauraki Gulf.

Successional changes on Tiritiri Matangi (and possibly on Maud and Mana Is) may make it necessary to move takahe to islands that can support larger takahe populations (Baber & Craig 2003). Selected islands may require appropriate cover to escape harrier predation: shrubs may need to be planted in pasture or native grassland. Takahe spatial dynamics should be monitored again on Tiritiri Matangi, to understand the effects both of successional changes, and the projected increase in population density on the behavioural ecology of the population. Such monitoring may provide information on which to base decisions on whether additional or larger islands might be necessary to ensure the long-term persistence of this critically endangered species.

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