Responses to a Model Predator of New Zealand's Endangered Takahe and Its Closest Relative, the Pukeko

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Introduction

New Zealand’s avifauna, characterized by several species of endemic flightless birds, has evolved in isolation from terrestrial mammalian predators. Consequently, there has been no selection pressure to develop defense mechanisms against terrestrial predators. When Polynesians (AD 1000-1200) and Europeans (AD 1850) arrived, much of New Zealand’s naïve avifauna became easy prey to predators introduced by these settlers (Diamond & Veitch 1981; Holdaway 1989). Vulnerability may have been exhibited by unusual tameness (lack of defensive behavior) or by nesting, roosting, and perching in areas exposed to introduced predators (Bell 1991).

The Takahe (Porphyrio mantelli) is a large, flightless gallinule endemic to New Zealand. It was thought extinct until its rediscovery in Fiordland in 1948 and is still among the most highly endangered bird species in the world. The Takahe population consists of approximately 120 adult birds in Fiordland’s isolated alpine habitat and 30 others that have been established on four, small, predator-free islands (Crouchley 1994). Subfossil evidence indicates that Takahe were once found throughout New Zealand, apparently most abundant along forest margins and streams in lowland regions (Beauchamp & Worthy 1988). Bunin and Jamieson (1995) review the reasons behind the Takahe’s decline, which began with the arrival of humans 800-1000 years ago.

The main predatory threat to Takahe in their current environment is the stoat (Mustela erminea), first introduced with early European settlers toward the end of the nineteenth century (King 1990). There is a correlation between years of high stoat numbers in Fiordland and dramatic declines in Takahe numbers (Lavers & Mills 1978; Eason & Rasch 1993), and there is evidence of stoat predation on Takahe eggs, chicks, and adults (Reid 1967; Lavers & Mills 1978; Maxwell, in press). Given the current status of Takahe and their low fecundity, even marginal levels of stoat predation could have serious implications for the survival of the species in the wild (Crouchley 1994).

In contrast, the Pukeko or Purple Swamphen (Porphyrio porphyrio), the Takahe’s closest extant relative, invaded from Australia within the past 1000 years (Millener 1981) and has expanded its distribution and numbers since European colonization to become one of New Zealand’s most successful avian species. Pukeko evolved in the presence of a variety of terrestrial marsupial predators in Australia, and in New Zealand will attack stoats near their nests (Oliver 1955; I. Jamieson, pers. obs.) and generally thrive in habitat where introduced predators are present (Bunin & Jamieson 1995).

We suggest that terrestrial predator recognition and defense behaviors may be more highly developed in Pukeko than Takahe, and this distinction may be partly responsible for the difference in population trends of these congeneric species. However, the effects of mammalian predators and their management implications for Takahe have been largely overlooked in the past (Bunin & Jamieson 1995).

Although their natural ranges do not overlap today, following recent transfers of adult Takahe to these predator-free refuges Takahe and Pukeko coexist on Mana, Tiritiri Matangi, and Kapiti Islands off the coast of the North Island. Our research, conducted primarily on Mana Island, compares the behavioral responses of breeding Takahe and Pukeko to the presence of model stoats on their territories. We attempt to show quantitatively that the response of Pukeko to model predators is more intense than that of Takahe. We briefly compare behavioral responses of a cross-fostered Takahe chick that was successfully raised by Pukeko foster parents to
a parent-reared Takahe chick that was raised on Mana Island the same year. If cross-fostered Takahe can learn adaptive behaviors from their Pukeko foster parents, including a heightened response to model predators, it may increase survivorship of Takahe released on mainland New Zealand.

**Study Area and Methods**

Mana Island is 217 ha in area and lies approximately 21 km north of Wellington and 4 km off the North Island's western coast. Three pairs of Takahe were transferred to Mana Island in 1987. There were four pairs breeding by the time our study began in 1993. Although Pukeko were rarely seen a decade ago (P. Todd, personal communication), the self-introduced population has grown to approximately 300 birds. Pukeko breed in family groups ranging in size from 2 to 12 birds, often including several non-breeding helpers (Craig & Jamieson 1990). Data were collected on Mana Island from September 1993 to February 1994 and from September 1994 to January 1995. We also conducted tests with four pairs of Takahe on Tiritiri Matangi Island, northeast of the city of Auckland, and two pairs at the Takahe captive rearing station in Burwood Bush, Southland, at the end of the 1994–1995 breeding season. Tiritiri Matangi Island is also free of introduced mammalian predators, and the Takahe at Burwood Bush are held in large predator-proof enclosures.

To determine whether Takahe and Pukeko differ quantitatively in the intensity of their response to terrestrial predators, adults of both species were exposed to a model predator and their reactions were recorded and compared. All tests were conducted while adults were still caring for their semi-precocial chicks. Both the model predator (a taxidermic mount of a stoat) and the control (a cardboard box similar in size and color to the model stoat, after Maloney & McLean 1995) were attached to radio-controlled vehicles. For each test we placed the model inside a large rectangular wooden box that was attached to a runway situated on the birds’ territory (Fig. 1). Food (pellets of maize) was placed 7 m in front of this runway. When the birds came to feed, the model was driven through a swinging door at the end of the runway. Every 20 seconds the model was driven approximately 30 cm backward and then forward again to the end of the runway. After 2 minutes, the model was reversed into the box.

The behavior of the bird nearest to the model at the beginning of the test was observed and recorded from a nearby blind. Distance from the model (mean and nearest approach), time present (amount of time bird remained in view; i.e., not hiding from model), vigilance (amount of time in alert posture: motionless, with neck outstretched and head held high), number of tail-flicks (upward movement of tail feathers which exposes the bird’s strongly contrasting white rump patch), number of wing-flaps (an alarm response), and number of alarm calls were noted. Behavioral data were collected from 10 pairs of Takahe and 9 groups of Pukeko, although 1 group of Pukeko was only exposed to the control.

Mean responses were compared using two-way nested analyses of variance (ANOVA), with individual pairs or groups nested within species, and with treatment (i.e., stoat or control) as the factors and the behavioral responses listed above as the dependent variables. Discrete data (i.e., number of calls, number of tail-flicks, and number of wing-flaps) were square-root transformed, and continuous data (i.e., time and distance) were log-transformed.

One member of three pairs of Takahe we tested had been raised by hand. Post hoc tests indicated that hand-raised birds did not respond significantly differently from other birds to the models and, thus, were included in the main analyses.

One parent-reared and one cross-fostered Takahe chick were exposed to the models (with their Takahe parents and Pukeko foster parents, respectively) five times in the 1993–1994 season. At the beginning of the following breeding season, we compared the responses to the models (in the manner described above) of each of these two yearling Takahe tested by themselves. The details of the actual cross-fostering procedure are reported in Bunin & Jamieson (in press).

**Results**

Pukeko responded significantly more strongly than Takahe in number of alarm calls (ANOVA, $F_{1,17} = 7.7, p = 0.01$), number of tail-flicks ($F_{1,17} = 42.2, p < 0.0001$), and vigilance ($F_{1,17} = 16.0, p < 0.001$). There was no difference in distance from the models, time present, or
number of wing flaps (Table 1). The only response that differed significantly between the two models was vigilance, which was higher for the stoat than the control when both species were taken together ($F_{1,16} = 7.7, p < 0.01$); although the interaction between model and species was not significant ($F_{1,16} = 7.7, p > 0.05$). Nevertheless, when each species’ responses to both models were compared separately in paired t tests, Pukeko were significantly more vigilant when the stoat was present versus the control ($n = 8, p < 0.05$).

The main differences between the behavioral responses of the cross-fostered and parent-reared yearling Takahe were the amount of tail flicking and vigilance (Table 2). In both cases the cross-fostered juvenile clearly exhibited an elevated response (similar to that of adult Pukeko; Table 1) relative to the parent-reared Takahe. In addition, the cross-fostered Takahe was more likely to leave the testing area than the parent-reared bird, which remained for the full 2 minutes for all tests.

### Discussion

Behavioral responses of both Takahe and Pukeko to the presence of models on their territories included tail-flicking, bouts of vigilance, and alarm calling. However, in each of these behavioral categories, Pukeko exhibited a higher level of response than Takahe. Although responses to the stoat and control were generally quite similar for both species, Pukeko exhibited an increased level of vigilance in the presence of the stoat relative to the control. These findings support our hypothesis that Pukeko exhibit more highly adaptive behavioral responses than Takahe in the presence of a perceived mammalian threat.

Given the degree of individual variation in the behavioral responses of the birds we tested, it is not surprising that no differences were found between Takahe and Pukeko responses that involved distance from the model or time present because neither response can be directly related to level of alertness. Moving away from a predator or remaining still and alert, for example, may both be adaptive, but this variation in adaptive responses confounds interpretation of the data (McLean et al. 1996). This can be contrasted with tail-flicking, vigilance, alarm calling, and wing-flapping. An increase in any of these behaviors implies an increase in alertness.

Results of predator defense tests on the two yearlings reared on Mana Island in the 1993-1994 breeding season were promising. As predicted the cross-fostered yearling displayed an elevated response to the models relative to the parent-reared yearling. No evidence of mal-imprinting was apparent as the cross-fostered juvenile quickly established a pair bond with a conspecific after being penned together, and they remained together after their release. Although it is too early to draw any firm conclusions, these preliminary findings indicate that cross-fostering to Pukeko could play an important role in the future management of Takahe in New Zealand, particularly if they are to be released on mainland sites where terrestrial mammalian predators are present. Our results should encourage further research into the behavioral effects of cross-fostering on Takahe in particular and on endangered birds in general.

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