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New Approaches Toward a Better Understanding of the Decline of Takahe (Porphyrio mantelli) in New Zealand

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Abstract: Island populations of endemic birds are known to be particularly susceptible to extinction. This paper focuses on factors behind past and present declines of the highly endangered Takahe (Porphyrio mantelli), a flightless rail endemic to New Zealand. Subfossil evidence indicates that Takahe were once found throughout this island nation, being most abundant along forest margins and streams in lowland regions. Their numbers have declined dramatically since human colonization about 800–1000 years ago, probably due to a combination of habitat destruction and hunting by early Polynesian settlers. Today, the wild Takahe population consists of about 100 adult birds in an isolated alpine habitat and approximately 30 individuals recently released on several small offshore islands. Despite protection and intensive management, including removal of an introduced competitor (red deer, Cervus elaphus), the alpine population has continued to decline. In contrast, the Takahe’s nearest relative, the Pukeko (Porphyrio porphyrio), has expanded its range across New Zealand despite heavy hunting pressure since its colonization from Australia less than 1000 years ago. We suggest that, unlike Pukeko, Takahe lack appropriate behavioral responses to cope with mammalian predators such as stoats (Mustela erminea), which have been introduced relatively recently by European colonists. A study comparing predator defense behavior between these two closely related species is currently underway.

Nuevas propuestas para una mejor comprensión de la declinación del Takahe (Porphyrio mantelli) en Nueva Zelandia

Resumen: Es sabido que las poblaciones endémicas de aves insulares son particularmente susceptibles a la extinción. Este trabajo se centra en los factores de declinación pasados y presentes del Takahe (Porphyrio mantelli), un ave zancuda no voladora endémica a Nueva Zelandia, que se encuentra en peligro de extinción extrema. Evidencias de subfósiles Takahe se le encontraba alguna de toda esta nación insular, siendo más abundante a lo largo de los bosques y en arroyos en regiones de tierras bajas. Sus números disminuyeron dramaticamente desde la colonización humana, hace unos 800 o 1000 años, probablemente debido a una combinación de la destrucción del hábitat y la cacería por parte de los primeros colonos Polinesios. En la actualidad, la población silvestre del Takahe consiste en alrededor de 100 aves adultas en un hábitat alpino aislado y unos 30 individuos que fueron dejados en libertad recientemente en varias islas pequeñas a escasa distancia de la costa. A pesar de la protección y del manejo intensivo, que incluye la remoción de un competidor introducido (el ciervo rojo, Cervus elaphus), la población alpina ha continuado su declinación. En forma opuesta, el pariente más cercano del Takahe, el Pukeko (Porphyrio porphyrio), ha expandido su área de distribución a través de Nueva Zelandia, a pesar de las presiones de la caza desde su colonización desde Australia, menos de 1000 años atrás. Sugerimos que, a diferencia del Pukeko, el Takahe carece de respuestas de comportamiento apropiadas para enfrentar predadores mamíferos, tales como el armiño (Mustela erminea), que ha sido introducido en tiempos relativamente recientes por colonos Europeos. Actualmente se está llevando a cabo un estudio, que compara el comportamiento defensivo contra predadores de estas dos especies estrechamente relacionadas.

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Introduction

At least one-third of all bird species on the planet remain endemic to islands, despite the observation that the diversity of bird species on practically all oceanic islands has been reduced by 30–50% since human colonization (Olson 1989). In fact, over 90% of land and freshwater bird extinctions that have occurred since 1600 have been of island forms (King 1985; Atkinson 1989). Within New Zealand alone, 36 native bird species have disappeared since human arrival only 800–1000 years ago (Gill & Martinson 1991), and this island nation has one of the largest proportions of endangered bird species of any country in the world (Halliday 1978). Investigation into the demise of these extinct and endangered species is complicated by the fact that declines have usually occurred in prehistoric times or were poorly documented by the earliest island settlers. As a result, the causes of decline are often poorly understood. This, in turn, can lead to misdirected and largely ineffective conservation efforts. Such may be the case with one of New Zealand's endemic rails, the Takehake (Porphyrio mantelli), whose decline has been the subject of heated debate within New Zealand for much of the past decade.

Formerly in their own genus, Notornis, Takehake are now recognized as very close relatives of Pukeko (Porphyrio porphyrio), elsewhere known as Purple Swampheens. The two species share many morphological and behavioral characteristics, although Pukeko are smaller, have longer legs, neck, and wings, and are able to fly. Since their invasion of New Zealand within the past 1000 years, Pukeko have flourished in lowland swamps, moist pastures, and croplands (Millener 1981). They have become one of this country's most successful native birds. Despite many similarities to Pukeko, Takehake have been declining steadily at least since the arrival of humans (Beauchamp & Worthy 1988). Takehake were actually considered extinct for the first half of this century until an expedition in 1948 discovered a remnant population in the Murchison Mountains, Fiordland—a rugged, mountainous region in the southwestern corner of the South Island. Although their progress has been closely monitored, with much time and resources being allocated to Takehake conservation, the population has continued to decline, from early estimates of 500 birds throughout Fiordland (Reid & Stack 1974) to the approximately 100 adults presently in the wild (D. Eason, personal communication).

One reason for the apparent ineffectiveness of efforts to halt Takehake decline may be a lack of understanding of the factors affecting the Takehake population. Again, this is characteristic of the majority of rare island endemics that have been reduced to remnant populations before detailed biological studies could be carried out. The aims of this paper are, therefore, to critically review theories on past and present Takehake decline and to discuss implications of this review for future research. We suggest that the possible inability of Takehake to recognize and respond to introduced mammalian predators has been largely overlooked in earlier explanations of their decline, as has the potential of behavioral manipulation as a management technique (see also Maloney 1991; McLean & Rhodes 1991). Many of the arguments presented in this paper are highly relevant to other endangered species, particularly the wide variety of threatened endemic bird species on islands.

Evolution of Takehake in New Zealand

Why are large, flightless rails found on a variety of isolated islands around the world? The most widely accepted explanation involves volant ancestral dispersal, followed by rapid evolution in an environment free from terrestrial predators, and the need to migrate (Olson 1973, 1992).

This theory likely explains the presence of the flightless Takehake in New Zealand as well. It has been suggested that a small population of Pukeko-like invaders became established here several million years ago (Millener 1981). In the absence of terrestrial predators and in the presence of some very effective avian predators (Holdaway 1989), they evolved into their large, flightless form (Takehake are approximately three times heavier than Pukeko). While volant dispersal has been challenged on panbiogeographic grounds (Beauchamp & Worthy 1988; Beauchamp 1989), it does seem to be the most likely explanation in this case because Takehake and Pukeko lines apparently diverged about two million years ago (Sibley & Ahlquist 1990). This is much too recent for a panbiogeographical argument because New Zealand separated from Gondwanaland approximately 80–85 million years ago (Gill & Martinson 1991).

Morphological changes in Takehake evolution have been accompanied by certain behavioral and life-history changes. The modal clutch size of the Takehake is smaller (two eggs) than that of most other gallinules, and they are not restricted to wetlands. Subfossil evidence indicates that their range expanded to include a variety of habitats as they attained a widespread distribution across New Zealand (see Reid 1974; Mills et al. 1984). By the time of European colonization (beginning in 1769), however, Takehake had already become quite rare (Halliday 1978).

Pre-European Decline of Takehake

The first widely accepted explanation of the pre-European decline of Takehake in New Zealand was proposed by Williams (1962) and was later supported in a detailed report by Mills et al. (1984). They believed that climatic changes were primarily responsible for the de-
cline in Takahe range and numbers before European settlement.

Mills et al. (1984) use knowledge of current Takahe ecology in an attempt to explain past distribution and palaeoecology. They suggest that Takahe are specialized tussock-feeders, behaviorally and morphologically adapted to live in alpine grasslands. They claim that climate change since the post-glacial Holocene resulted in increased forest coverage and, therefore, reduced Takahe range. They support this claim by citing an apparent lack of Takahe bones in swamps formed 5000–6500 years ago, which indicates that Takahe had declined prior to this time. With Takahe reduced to islands of grassland in a sea of forest, they became easy prey for early Polynesian settlers (the Maori), who dealt them a further blow. Mills et al. (1984) recommended, therefore, that future Takahe management be aimed at preserving Takahe in their natural alpine environment to which they are so well adapted.

Beauchamp and Worthy (1988) proposed an alternative theory of the prehistoric decline of Takahe. They based their argument on a detailed examination of the geographical distribution of subfossil remains. They point out that the majority of Takahe remains have been found in lowland areas, many of which had been covered by forests at the time of deposition (see also Millener & Templar 1981; Caughey 1989). They also note that Takahe bones have been found in swamps and are not rare relative to those of similar-sized birds. The presence of Takahe bones in middens indicates that Takahe were hunted and eaten regularly by the Maori, who used dogs (Kuri, Canis familiaris) to assist in capturing their prey. In addition, Beauchamp and Worthy (1988) suggest there is no evidence of a decline in Takahe numbers relative to other ground-dwelling birds prior to the arrival of Polynesians nor that Takahe were previously restricted to or even found in the alpine tussock zone.

They also note that Takahe recently translocated to offshore island reserves show a high level of adaptability to their new food resources and habitats, indicating that Takahe morphology may be well-suited to feeding on a variety of monocot species other than tussock (see also Gray & Craig 1991). This is supported by the fact that numerous gallinules that resemble Takahe in morphology thrive on monocots growing in and around swamps. Beauchamp and Worthy (1988) believe, therefore, that the Polynesian invasion of New Zealand was primarily responsible for Takahe decline, and that Takahe should be experimentally released into new habitats while the traditional population is maintained.

The debate outlined above highlights the difficulties associated with drawing conclusions about the past decline of a currently endangered species. Today it is generally accepted that, prior to their decline, Takahe lived primarily along lowland forest margins and stream banks, where plants with basal meristems are plentiful (see, for example, Atkinson & Millener 1991). In these habitats they were probably capable of feeding on both forest and grassland plants as they still do in the Murchison Mountains (see Mills 1975; Mills et al. 1991).

If Takahe were primarily lowlands birds prior to human invasion, then how can we explain their presence in the Murchison Mountains today? We believe that this area of Fiordland has served as a final refuge for these birds, not because it is optimal habitat or preferred in any way (see Gray & Craig 1991), but simply because of its isolation. This reflects the trend, described by Olson (1989), whereby most island species persisting in wet montane forests do so because these tend to be the last habitats modified by humans.

The most widely accepted hypotheses relating to the decline or extinction of a variety of birds across Pacific islands involve either (1) human impact (including hunting, habitat destruction, and the introduction of novel predators) or (2) climate change leading to habitat alteration (Anderson 1984; Cassels 1984; Diamond 1984; Mills et al. 1984, 1988; Gill & Martinson 1991). Subfossil evidence indicates that the decline of Takahe was relatively recent—much closer to 1000 than the 10,000 years ago required for the climate change hypothesis of Mills et al. (1984, 1988). In the most detailed published report involving Takahe subfossil deposits, Horn (1983) describes the results of excavations at Hawkes Bay, North Island, where avian remains were collected from a 3500-m² area over nine years. According to these data, the minimum number of Takahe, the total number of Takahe bones, and the proportion of Takahe to all other bird species actually increased from Layer 3 (deposited 4000–7000 years ago) to Layer 2 (deposited 1000–4000 years ago). This implies that Takahe actually became more abundant over this time, before declining substantially in Layer 1 (deposited within the past 1000 years). Beauchamp & Worthy (1988) also found that most (18 out of 21) of the Takahe bones that were dated at the time their paper was prepared were less than 5000 years old.

These findings suggest that humans were directly or indirectly responsible for the pre-European decline of Takahe, because it seems clear that Takahe were common well after the last major climate and habitat changes in the late Pleistocene—approximately 14000 years before present, according to Mills et al. (1984). This agrees with the conclusions of Beauchamp and Worthy (1988), as well as those of a variety of other authors who have argued that humans are behind the decline of numerous bird species on a variety of Pacific islands (Anderson 1984; Cassels 1984; Diamond 1984; Trotter & McCulloch 1984; Olson & James 1984; Olson 1989). Some authors focus on habitat destruction by humans (Millener 1981; Cassels 1984), while others emphasize the effects of hunting and predator introduction (Diamond & Veitch 1981; Beauchamp & Worthy...
1988; Holdaway 1989). It is extremely difficult to distinguish between the effects of these various aspects of human colonization, however, because the negative effects of human hunting, deforestation, and introduction of mammalian predators were concurrent and mutually reinforcing.

Post-European Decline of Takahe

While the direct effects of humans on Takahe have been greatly reduced over the past century (soon after "rediscovery" in 1948, a 500-km² special area within Fiordland National Park was set aside for their protection), Takahe numbers have continued to fall. Their range in Fiordland has diminished from a maximum of 16,000 km² late last century to the present 500 km² of the Murchison Mountains and adjacent Doon River Catchment (Crouchley 1994).

Competition with introduced deer (Cervus elaphus) for a limited food resource, namely snow tussock (Chionochloa pallens), has been cited as the primary cause of Takahe decline since their rediscovery (Lee et al. 1988; Mills et al. 1989). Competition has been inferred from dietary overlaps between these species and from the fact that Takahe numbers were declining as Red Deer abundance in Fiordland increased (Mills et al. 1989; Crouchley 1994). In light of this hypothesis, New Zealand's Department of Conservation initiated a program of intensive deer control in 1962 that involved hunting on the ground and from helicopters. Deer numbers have since decreased considerably in Fiordland, with an apparent subsequent increase in vegetative growth (see Mills et al. 1989). Takahe numbers, however, have fallen to their lowest level since population estimates were first recorded (D. Eason, personal communication). Alternate theories must now be investigated. It is possible, for example, that the extreme and often harsh climate of Fiordland will simply preclude a recovery of the Takahe population, assuming that this area is a final refuge rather than historically preferred habitat. With respect to Takahe, Reid (1978) has stated, "The environment of Fiordland is too harsh to allow enduring stability—let alone permit a recovery in numbers."

Another explanation often proposed for the demise of endemic New Zealand bird species (and other island endemics renowned for their "tameness") involves susceptibility to introduced predators (Halliday 1978; Diamond & Veitch 1981; Holdaway 1989; Gill & Martinson 1991; Lovegrove 1992). Having evolved in isolation from terrestrial mammalian predators native New Zealand species felt no selection pressure to evolve or maintain defense mechanisms against these animals. When humans arrived with a variety of mammalian species, New Zealand's avifauna was easy prey for the introduced predators. The first terrestrial predators to arrive were the dog and the Polynesian rat, or kiore (Rattus exulans), which were introduced by the Polynesian settlers. Early European colonists brought two more species of rats (the Norway rat, *R. norvegicus* and the ship rat, *R. rattus*), the cat (*Felis catus*), and three mustelid species (stoats, *Mustela erminea*, weasels, *M. nivalis*, and ferrets, *M. furo*) (King 1990).

While stoats were introduced too recently to be held responsible for the pre-European decline of most of New Zealand's threatened birds, they have undoubtedly increased the predation pressure on several already rare species such as the Takahe, the Kakapo (*Strigops habroptilus*), and the Little Spotted Kiwi (*Apteryx owenii*) (King 1990). Stoats are known to prey upon Takahe eggs, chicks, and even adults (Reid 1967; Crouchley 1994), although it has also been reported in at least one instance that an adult Takahe has successfully fended off and actually killed a stoat (Lavers & Mills 1978). But the degree to which Takahe are able to defend themselves and their offspring against stoats remains largely unknown. Given the low fecundity of the Takahe, even marginal levels of stoat predation could be responsible for the low level of recruitment of young Takahe into the adult population.

One line of action recently employed by New Zealand's Department of Conservation has been the transfer of small groups of Takahe onto selected offshore islands free of mammalian predators. Island populations are intended to act as a safety net should some unforeseen catastrophe strike the larger mainland population (Crouchley 1994). Although transferred Takahe have survived on these islands and achieved limited breeding success, suitable islands are small and few in number. The long-term goals outlined in the recently released Takahe Recovery Plan involve the establishment and conservation of at least two large populations on the mainland (approximately 500 birds each) in addition to four much smaller island populations. The estimated carrying capacities of these islands range from 7 to 10 pairs (Crouchley 1994). Because mainland Takahe will still be faced with the threat of predation from introduced predators, it would be highly advantageous to learn as much as possible about the predator recognition and defense capabilities of Takahe before the population dwindles any further. It is here that comparative studies with the Takahe's closest relative, the Pukeko, become relevant.

History of Pukeko in New Zealand

The story of the Pukeko is quite different from that of the Takahe. It is generally agreed that Pukeko have re-
cently invaded New Zealand from Australia. The relative rarity of subfossils indicates that they probably arrived and established viable populations within the past 1000 years (Millener 1981; Mills et al. 1984; R. Holdaway, personal communication). This is also supported by the finding of only four Pukeko bones in Layer 2 (formed 1–4 thousand years ago) and 410 Pukeko bones in Layer 1 (formed within the past 1000 years) at the excavation site in Hawkes Bay, North Island (Horn 1983).

Since their relatively recent invasion, however, Pukeko have become common in wet grasslands across New Zealand. They have actually expanded their range with the development of agriculture and the resulting increase in open, grassy habitat. Pukeko are now among the most common and widespread of New Zealand’s native bird species, despite heavy hunting pressure (Robertson 1985).

**Potential Behavioral Studies of Takaha and Pukeko**

The close correlation between the establishment and spread of Pukeko across New Zealand and the decline of the Takaha is remarkable. This leads to a variety of interesting questions and hypothetical scenarios: for example, is there a common factor behind these two opposite trends, or is there actually a causal relationship between the Pukeko’s arrival and increase and the Takaha decline? Furthermore, if Porphyrio stock invaded successfully on two occasions, is it probable that they reached New Zealand many times but were unable to establish stable populations? If this is the case, what prevented them from doing so in the past?

While these questions are interesting from a theoretical perspective, it is usually difficult to draw firm conclusions in a historical context. However, these same trends of Pukeko success and Takaha decline persist to this day. Takaha remain highly endangered despite the best efforts of conservationists, and Pukeko, while sharing many characteristics with Takaha, thrive in the face of heavy hunting pressure. It is safe to assume, therefore, that these species differ in some significant way(s). Perhaps most obvious is the fact that Pukeko can fly, although they often seem reluctant to do so, usually choosing to run and hide from apparent danger. As Weka (Gallirallus australis) have demonstrated, flight is certainly not a prerequisite for success in New Zealand, and the flightless rail Gallinula mortierii flourishes in nearby Tasmania despite the presence of terrestrial marsupial predators (Bull & Whittaker 1975).

Rather than flight per se, the act of fleeing may be an important factor in the differing success between species. That is, perhaps terrestrial predator recognition and defense behaviors are more highly developed in Pukeko than Takaha, and this behavioral distinction is the primary cause of the difference in population trends. This is believed to be the case with New Zealand’s endemic Black Stilt (Himantopus novaeseelandiae), which is highly endangered, and the Pied Stilt (H. himantopus leucocephalus), an Australian race of Black-winged Stilt that thrives in New Zealand (Pierce 1986).

Evolution in Australia, like the Pied Stilt, Pukeko have developed the ability to distinguish between aerial and terrestrial predators and give specific alarm calls in each case (J. Jamieson, personal observation). Their response to predators is quick and vigorous. According to Oliver (1955), “Harriers are dealt with by the Pukekos gathering together and driving them away . . . . the Pukeko hunts and kills stoats.” Pukeko are also very wary of humans, hiding or taking flight at the first sign of approach. Undoubtedly, these characteristics have contributed to the Pukeko’s success within New Zealand.

To compare the predator defense behaviors of Takaha and Pukeko, it would obviously be best to study these two species in a similar habitat. The ranges of Takaha and Pukeko may once have overlapped, because bones of both species have been found in the first two layers at Hawkes Bay (Horn 1983), and Takaha subfossils have been found in areas where Pukeko currently thrive (for locations of Takaha subfossil finds, see Reid 1974; Mills et al. 1984). This is no longer the case over their “natural” ranges today. With the recent transfer of a number of Takaha to offshore islands, however, Takaha and Pukeko currently coexist on Mana, Tiritiri Matangi, and Kapiti Islands. This provides an ideal opportunity to study the behavior of these species in greater detail in an attempt to understand their current population trends.

We are now undertaking studies of behavioral differences between Takaha and Pukeko on Mana Island, focusing on species-specific differences in defense behavior. To investigate differences in their behavior, we have designed an experiment in which Takaha eggs will be cross-fostered to Pukeko. Takaha will renest if their first clutch is removed, so this procedure should effectively double their reproductive output, assuming Pukeko foster parents can successfully raise Takaha chicks. Measures such as temporarily enclosing cross-fostered juveniles in a pen with conspecifics or transferring birds to islands lacking Pukeko are being considered to reduce or reverse potential undesirable effects of imprinting. Cross-fostering will provide an opportunity for detailed analyses of the development of predator recognition and defense behavior between Takaha and Pukeko, using model stoats to elicit appropriate responses. In light of conclusions drawn from the cross-fostering experiment, recommendations will be made for future Takaha management and conservation. These may include, for example, using wild Pukeko to “teach” naive Takaha.
foster chicks to recognize and defend against introduced predators.

Conclusion

Species conservation is difficult under the best of circumstances. The task becomes much harder when the biological factors responsible for a species' decline are poorly understood. We have reviewed what is known about the historical and continued decline of Takahe in New Zealand. We conclude that Takahe were most abundant in lowland forest margins and along stream banks prior to the arrival of humans in New Zealand. The Maori have had a strong impact on the Takahe population in the past, through a combination of hunting pressure and habitat destruction. Although direct threats from hunting and habitat loss have been eliminated within the protected Fiordland population since it was discovered in 1948, Takahe numbers have continued to decline. Two largely overlooked factors that have probably contributed to this post-European decline include the harsh and often unpredictable climatic conditions affecting Fiordland and the introduction of mammalian predators, such as stoats, by European colonists.

Most studies investigating the decline of endemic avifauna emphasize aspects of ecology and breeding biology. As Maloney (1991) points out, interpretations of decline are therefore biased towards morphological, reproductive, and habitat-related explanations. He goes on to note that “it may be that behavioral inadequacies in recognition and response towards mammalian predators played a far greater role in the decline of native birds than is indicated by the current evidence.” We have tried partially to redress this bias, which is also evident in explanations of Takahe decline, by emphasizing the need for further research into the predator defense capabilities of Takahe. Our study, which is investigating the possibility that Pukeko foster parents may be able to enhance the predator defense capabilities in their cross-fostered Takahe chicks, may have important implications for the Takahe recovery program here in New Zealand as well as similar conservation programs involving endangered endemic bird species on islands around the world.

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