Survival and Recruitment of Captive-Reared and Wild-Reared Takahe in Fiordland, New Zealand

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Abstract: *Captive rearing for release back into the wild is considered a useful management tool for endangered species because it can potentially increase the rate of recruitment by bypassing the early, high-risk stages in an individual's life history. In evaluating the benefits of captive rearing to conservation, it is important to monitor the survival rate of animals after release, to be sure that they have the skills necessary for survival in the wild. Using radio telemetry, we compared the movement and survival of captive-reared Takahe (*Porphyrio mantelli*), a large flightless rail endemic to New Zealand, to wild-reared Takahe in the rugged mountains of Fiordland over a 5-year period. The results indicated that captive-reared birds survived at least as well as wild-reared birds. Survival of wild-reared Takahe up to 1 year of age, which is prior to the release of captive-reared birds, was poor over two winters marked by particularly cold temperatures, which made the benefits of captive rearing more pronounced. Differences in post-release movements and habitat selection of the two groups did not have a detrimental effect on survival rate of captive-reared birds. Although there was no difference in the survival rate of captive-reared females versus males, eight out of nine (89%) surviving females have formed pairs since their release compared with only two of eight (25%) males. This unexpected result suggests there may be a shortage of females in the wild population. We conclude that captive rearing for release back into the wild increases the adult Takahe population in Fiordland.*

Sobrevivencia y Reclutamineto del Takahe Obtenido en Cautiverio y en Condiciones Silvestres en Fiordland, Nueva Zelanda

Resumen: *La reproducción en cautiverio para posterior liberación en áreas silvestres es considerada una herramienta de manejo muy valiosa para especies en peligro de extinción, puesto que potencialmente incrementa la tasa de reclutamiento al sobrepasar los estados de desarrollo temprano de la historia de vida de un organismo con altos riegos. Durante la evaluación de los beneficios de la reproducción en cautiverio, es importante monitorear la tasa de sobrevivencia de los animales después de ser liberados, para estar seguros de que han adquirido las habilidades necesarias para sobrevivir en condiciones silvestres. Usando radiotelemetría, comparamos el movimiento y sobrevivencia de organismos obtenidos en cautiverio del Takahe (*Porphyrio mantelli*), un ave no voladora endémica de Nueva Zelanda, con organismos silvestres de las montañas de Fiordland, por un periodo de cinco años. Los resultados indican que los organismos obtenidos en cautiverio sobrevivieron al menos tan bien como los silvestres. Sobrevivencia de organismos silvestres por mas de un año de edad, el cual es previo a la liberación de aves cautivas, fue pobre durante dos inviernos marcados por temperaturas particularmente bajas. Este evento ocasionó que los beneficios de producción en cautiverio fueran mas pronunciados. Las diferencias en movimientos post-liberación y selección de hábitat de los dos grupos no tuvieron un efecto negativo en la tasa de sobrevivencia de organismos de cautiverio. A pesar de que no existió diferencia en la tasa de sobrevivencia entre hembras y machos de organismos de cautiverio, ocho de nueve (89%) de las hembras sobrevivientes formaron parejas desde su liberación, comparados con dos de ocho machos (25%). Estos inesperados resultados sugieren que podría haber una escasés de hembras en la población silvestre. Concluímos que la producción de organismos en cautiverio para liberación en condiciones silvestres incrementa la población adulta de Takahe en Fiordland.*

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Introduction

For the recovery of endangered species, conservation management attempts to increase the size of populations and restore them to a self-sustaining level in the wild. Restoring species to former ranges requires that the areas from which they earlier disappeared are currently suitable habitat and no longer display those qualities that led to the decline of the species (Ounsted 1991; Stanley–Price 1991). Given suitable habitat, some populations could be left to increase at their own rate and eventually reach the carrying capacity of the environment. Captive rearing for release, however, can increase the rate of population growth and range extension, thus aiding the population to reach a larger size more quickly (Page et al. 1989; Powell & Cuthbert 1993). Captive rearing has the advantage of bypassing high-risk stages of an individual's life history in the wild and in birds can increase the overall productivity of wild parents because removal of eggs or young may induce repeated breeding attempts (Derrickson & Snyder 1992).

However, potential problems of captive rearing for release may also arise. Some captive-reared animals may be behaviorally unable to cope with the wild environment (Hutchins et al. 1995; Snyder et al. 1996). An individual's behavior is likely to be shaped not only by genetic factors but also by experience. Development of species-typical behavior may require an individual's exposure to an environment normal for its species (Johnston 1984), which a captive situation may be unable to provide (Hutchins et al. 1995). Therefore, although captive rearing for release may increase the survival rate during early stages of an endangered species' life history, recruitment rate of captive-reared animals into the breeding population may be low. If the aim of management is an increased breeding population, then captive breeding or rearing, which is usually very labor-intensive and expensive, may not be the most cost-effective means of restoring an endangered population (Snyder et al. 1996).

Overall, captive-rearing and release programs for birds have met with varying degrees of success (Fyfe 1978; Scott & Carpenter 1987; Beck et al. 1994). The underlying message from all of these attempts is that individuals need to be monitored after their release back into the wild, with their ability to survive and breed being the ultimate measure of a reintroduction's success.

The Takahe, a large flightless rail endemic to New Zealand, is highly endangered with less than 120 individuals remaining in the alpine grassland and forest of the mountainous Fiordland National Park. Since 1984, 15–20 eggs have been collected from nests each year and artificially incubated and chicks reared to 1 year of age before being released back into their wild habitat. Hatching and rearing rates in captivity have been very high relative to birds in the wild (Eason 1992), but there has been no assessment of how well the birds do once they are released. Thus the important questions for Takahe management in Fiordland that we hope to address in this study are: (1) Do captive-reared birds survive in the wild as well as their wild-reared counterparts? (2) Are there differences in behavior (i.e. movement, habitat selection, and foraging) between captive-reared and wild birds that might affect their survival? and (3) Are captive-reared birds being recruited into the breeding population?

The Takahe Recovery Program

The Takahe population was once spread throughout New Zealand as shown by the subfossil record (Beauchamp & Worthy 1988; Atkinson & Millener 1991). Reasons for its decline have been debated, but habitat destruction and hunting by early Polynesian settlers have been implicated for the period before European colonization of New Zealand (ca. 1800 A.D.), and introduced predators and competitors have negatively affected the population since European settlement (Clout & Craig 1995; Bunin & Jamieson 1995). The Fiordland population currently exists in a very small part of its former range (i.e., primarily in the Murchison Mountains). This population has also been used as a source of stock for four predator-free offshore islands onto which small groups of Takahe have been released (Crouchley 1994; Clout & Craig 1995; Bunin et al. 1996).

The New Zealand Department of Conservation is in the midst of an intensive management program intended to increase the size and range of the Murchison Mountains Takahe population. Some habitat restoration is being achieved by the on-going culling of red deer (*Cervus elaphus*), an introduced competitor of food (Mills et al. 1989). Captive rearing and release was initiated in an attempt to improve the survival rate of juvenile Takahe between egg stage and 1 year of age. In an unmanaged population only 30–40% of chicks survive to 1 year of age (Mills 1978), which contrasts with an approximate 85% annual adult survival (Reid 1967). Two main causes of juvenile mortality have been proposed: the cold, wet mountain climate and predation on eggs and chicks by introduced stoats (*Mustela erminea*) (Crouchley 1994).

Takahe normally breed in pairs and both parents care for eggs and chicks. Clutches normally consist of two eggs but parents rarely raise two chicks (Mills 1978). The Takahe management program involves the fostering of single eggs to pairs that laid non-viable eggs (to ensure each pair has at least one viable egg to raise), as well as the removal of eggs for artificial incubation and rearing at Burwood Bush Rearing Unit (Crouchley 1994). At the rearing unit the rate of survival to 1 year of age has been 90% (Eason 1992), an improvement of 50–60% on that of the wild population. Captive-reared birds are released into the wild at approximately 1 year of age. From 1987 until 1991, 90% (n = 58) were released into the Stuart Mountains, an area adjacent to the Murchison Mountains, in an attempt to repopulate a part of the species' former range. However, during an extensive survey of the area in 1995–1996 only eight birds (14%) were resighted and the Stuart Mountain releases have been deemed unsuccessful, possibly due to poor habitat quality (J. Maxwell, unpublished data). Since 1992, the focus of the Takahe recovery program has changed with 82% (n = 35) of captive-reared birds being released in the Murchison Mountains to augment the natural remnant population.

Takahe chicks in the wild remain with their parents at least until the following spring, and some remain until their second winter. Wild Takahe are known to move between topographical and vegetational types to take advantage of different food plants at the most nutritious stage of their annual cycle (Mills et al. 1980, 1991). Foraging behavior may be passed on to each individual by its parents through observational learning during the young bird's first 1 to 2 years. The ability of a bird to select good feeding areas and suitable foods is likely to have an effect on its survival. Our study attempts to determine whether habitat selection and use differs between wild and captive-reared birds and whether there is a difference in their rate of survival and recruitment into the breeding population. In this respect the captive-rearing and release program could be seen as an experiment in the effect of experience on behavioral development, done in an ecologically relevant setting.

Methods

Captive-Rearing

Specific methods for collection of eggs, artificial incubation, and rearing procedures for chicks are detailed in Eason (1992). In brief, eggs are taken from the Murchison Mountains in November of each year, usually a single egg from two-egg clutches, and transported by helicopter to Burwood Bush Takahe Rearing Unit for artificial incubation. When the chicks hatch, they are placed under a suspended model of an adult Takahe, with a heated pad and hygienic cloth nest material, to simulate brooding by a parent. A small speaker concealed in the nest material plays quiet calls recorded from brooding parents on natural nests. Up to five chicks may share a model parent and nest inside a small, indoor "brooder" enclosure that is lined with freshly cut, short turf and tall tussock grasses and has a small, shallow pond. Chicks are unable to see their human keepers except during weekly weighing sessions, but they may be observed through one-way glass.

Chicks are fed from a dish of food by a glove puppet simulating a head and neck of an adult Takahe, which is manipulated by the keeper through a hatch in the wall of the enclosure. After about six weeks chicks learn to feed themselves from the dishes and puppet feeding is reduced. For their first month they are fed a soft, wet mash and are then slowly introduced to pellets. They also learn to feed amongst themselves on grass from the turfs, and to break off short pieces from longer leaves held by the glove puppet. At three months of age chicks are moved to 30 × 60 m predator-proof pens and are held in groups of approximately 10 birds. There they feed on sedges, tussock, and pasture grasses and are given supplementary pellet food daily. At 6 months of age they are shifted to larger enclosures containing tussock grassland and small patches of beech forest, where they overwinter. There they are supplied with only small amounts of supplementary food. They are also encouraged to forage in the forest for a winter food that is important to birds in Fiordland, the rhizomes of the fern *Hypolepis millefolium*, by being penned temporarily in a small area containing little other food. Birds learn the skill of digging for rhizomes more quickly if they are penned with an older bird that is experienced at feeding on rhizomes (R. van Mierlo pers. comm.).

Field Methods

Wild birds are caught by hand at approximately 6 months of age in May–June while still with their parents, banded with individual color combinations, and fitted with radio-transmitters with batteries that last for 3 years. Captive-reared birds are released at approximately 1 year of age in November–December, all fitted with transmitters and color bands. They are released in various parts of the Murchison Mountains, in groups of two to four.

The radio transmitters weigh 55 g, less than 3% of the bird's body weight. They are not attached to any bird under 1.7 kg, to allow for further growth. The transmitter is held on the bird's back using a nylon cord harness, with one loop on either side of the transmitter passing under each wing. A weaker, degradable length of finer thread is sewn in, joining two halves of the harness cord. This enables the bird to eventually drop its transmitter should it fail before it can be recovered near the end of expected battery life. It also allows a bird to escape the harness should it become entangled in scrub.

Locations of each radio-tagged study bird were confirmed by close approach using a hand-held radio receiver and a "Yagi" aerial. If the ground search was unsuccessful, aerial searches by helicopter were made, and once located, it was often possible to sight the bird from the air depending on the vegetation. Study birds were checked once every 2 months.

Each time a bird was located, a record was made of its status (dead or alive, with other birds, evidence of nesting), its location, vegetation type, and plants eaten: fresh feeding sign at each site was recorded from examination of droppings, cut plant pieces, and actual observations of feeding birds. Vegetation was recorded by noting dominant species present and categorizing the type of community (i.e. forest, forest clearing, subalpine scrub, or alpine tussock grassland).

Analysis

Survivorship and recruitment data were collected until February 1995 and analyzed by cohort from 1990 through to 1993. Survivorship of captive-reared and released (from here on CR) and wild-reared (WR) birds was compared at two stages: (1) pre-release, from 6 months to 1 year when CR birds are in the large enclosures at the rearing unit and WR birds are still with their parents and (2) post-release, from 1 year to 2 years after the release of CR birds. Movement and habitat selection data were collected and analyzed from cohorts 1990 through to 1992. Habitat data were arcsin transformed for an analysis of variance using a general linear model (some habitat categories were combined because of small sample sizes). Similarly, movement data were log transformed for statistical analyses using *t*-tests.

To compare movement distances between CR and WR birds, location data were analyzed by two methods: (1) mean areas used over a 1 year time period were compared using minimum convex polygon method of home range analysis and (2) mean distances moved over 2 month periods were compared within seasons.

The minimum convex polygon method followed that of Stickle (1954) for delineating a home range estimate. The CR birds were followed for 1 year from their release date at about 1 year of age. The WR birds were also followed for 1 year but from 6 months of age when they were first radio tagged to 18 months (Fig. 1). Birds' locations were recorded as grid references (NZMS topographical map) with an accuracy of ± 46 m horizontally. The number of locations for each study bird varied considerably; some had extra locations provided by Department of Conservation field staff whereas others lost their transmitters part way through the study. To make home range figures for the two groups as comparable as possible, the sample was extracted in the following way: only birds with at least 7 locations were used to estimate area. For those with more than 10 locations, we used the 10 locations most evenly spread in time. Each individual had at least one observation in each of the 4-month periods (Jan.–Apr., Mar.–Aug., Sep.–Dec.). This treatment is based on that recommended by Harris et al. (1990) for home ranges that do not reach an asymptote with continued sampling.

The distance between observations method followed Koeppl et al. (1977) for obtaining an estimate for the average home range index of a population. The advantage of this method is that even individuals with as few as two locations can be used in calculating this weighted index because it is based on the assumption that the reliability of each individual's contribution varies directly in relation to its sample size. The index was calculated by

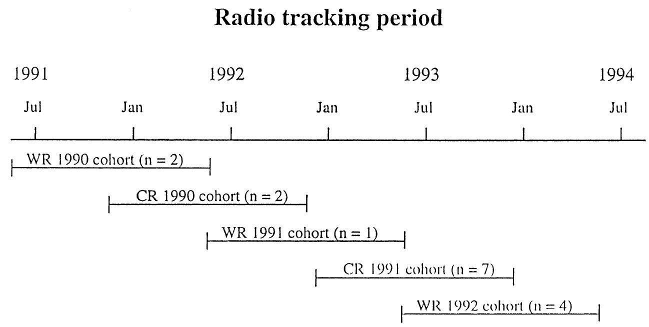

Figure 1. Period during which captive-reared (CR) and wild-reared (WR) birds were radio tracked for movement analysis. Although birds within both groups were of similar ages, WR birds were approximately 6 months younger than CR birds when radio tagged. The small number of WR birds followed in the first two cohorts was due to their poor survival rate over the first two winters of the study.

measuring the distance between a pair of locations observed a standard time interval apart (i.e., the minimum distance an individual actually travels in a given time). Sequential distances were then summed for all individuals of the group and divided by the total number of distances that had been summed (i.e., the mean over all individuals). To compare mean distances moved by CR and WR Takahe, pairs of locations observed 2 months apart (± 2 weeks) were used. Separate indices (means) were calculated for summer (Dec.–Feb.), autumn (Mar.–May), winter (Jun.–Aug.), and spring (Sept.–Nov.) to check for seasonal effects. Each distance measurement was considered to belong to that season into which the first observation of any pair fell.

Results

Survivorship

The survivorship of CR birds varied from year to year but overall was as good if not better than that of WR birds (Fig. 2). In three of the four cohorts, survivorship for the pre-release stage (6 months to 1 year of age) was significantly greater for CR birds than their WR counterparts. In the 1990 cohort 20 of 20 (100%) CR birds versus 3 of 6 (50%) WR birds survived (Fisher's exact test, $p < 0.01$); in the 1991 cohort 17 of 17 (100%) versus 1 of 4 (25%) survived ($p < 0.01$); and in the 1993 cohort 11 of 11 (100%) versus 4 of 8 (50%) survived ($p < 0.01$). However, in the 1992 cohort, all six WR birds alive at 6 months of age survived to 1 year of age, as did the 14 CR birds. The winter was comparatively milder in this year but the higher proportion of WR birds surviving to 1 year

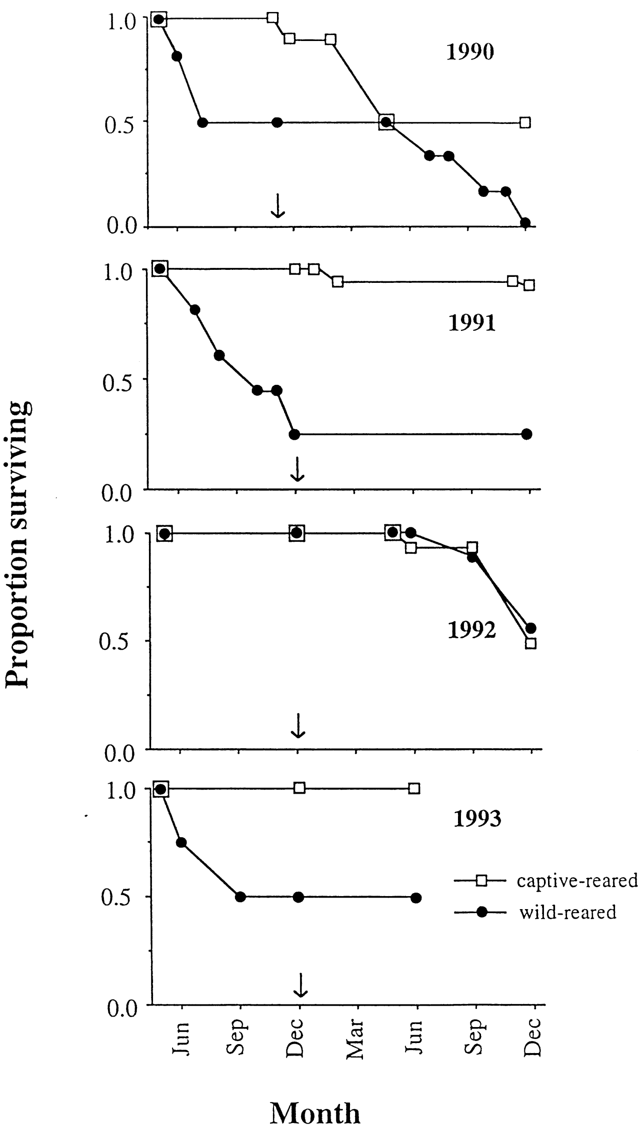

Figure 2. Observed survival rates of radio-tagged captive-reared and wild-reared Takahe between age 6 months and 2 years for four cohorts (1990–1994). The total number of birds that were followed varied at different times of the study primarily because of loss of transmitters; the proportions alive at various stages are given in the text. The arrow indicates release of captive-reared birds at approximately 1 year of age.

was only statistically different from the proportion of WR birds surviving in 1991 ($p < 0.05$) (Fig. 2).

For the post-release period (from 1 to 2 years of age), there was no significant difference in the proportion of CR versus WR birds that survived. For the 1990 cohort 3 of 6 (50%) CR birds survived versus 0 of 2 WR (0%) birds ($p = 0.46$); for the 1991 cohort 7 of 8 (88%) CR versus 1 of 1 (100%) WR ($p = 1.0$); and for the 1992 cohort 5 of 10 (50%) CR versus 3 of 5 (60%) WR ($p = 0.56$). For the 1993–1994 cohort 7 of 7 (100%) CR had survived to age 18 months versus 4 of 4 (100%) of WR birds ($p = 1.0$).

Causes of Mortality

Twelve radio-tagged birds (4 CR and 8 WR) that died during the study were recovered. Two birds (both WR) that were scavenged by a stoat were found mid-winter 1991 with too much of the carcasses removed to say whether or not they had actually been killed by the stoats. Accidental death including entrapment in a large boulder pile, falling through snow into a stream, and being washed down a stream was suspected in three cases (1 CR and 2 WR). Three CR birds died of no obvious cause in the summer of their release. The gut of one of these birds was examined and found to contain none of the tussock grasses that normally form the major part of the diet. Instead it had mainly a species of sedge of low nutrient quality (Mills et al. 1978) that is taken in small amounts by CR and WR birds alike (J. Maxwell, unpublished data). Four WR birds died of no obvious cause late in the winter of 1992. Their deaths came after the coldest part of the winter had passed, although snow still covered the tussock above treeline. Three weighed 59% (±5.3 g) of their autumn weights (the fourth was too decomposed to weigh) and probably died of starvation, the lack of food being exacerbated by cold temperatures and the late onset of the spring thaw. However, other complicating factors cannot be ruled out particularly for birds in poor condition.

Environmental Factors and Population Fluctuations

The apparent differences in environmental conditions between years of this study raise the question of whether or not these years were typical of trends overall. To investigate the relationship between environmental conditions and changes in the Takahe population, climate data taken since 1981 were compared with annual changes in the number of birds.

The winters of 1991 and 1992 were exceptionally cold and are likely to have reduced the survival rate of birds in the wild. Meteorological data have been recorded by the New Zealand Department of Conservation at Takahe Valley in the Murchison Mountains since 1973. Daily minima and maxima were averaged to provide daily medians and these were then averaged to provide monthly means. Mean winter temperatures of −1.6 and −2.6°C in 1991 and 1992 respectively were the two coldest winters in the past 20 on record and were well below normal (mean of −0.3°C ± 0.8).

To test the hypothesis that Takahe survivorship is affected by winter cold, relative changes in Takahe numbers (change in numbers from year t to year $[t+1]$ as a percentage of the population size in year t) were compared with the mean temperature for the preceding winter, determined using mean temperatures for the 3 coldest months of each year. There was a significant positive relationship between winter temperatures and relative changes in Takahe numbers in the following summer (correlation coefficient $r = +0.63$, $p = 0.01$; Fig. 3). Thus, Takahe survivorship in the wild, particularly that of young birds, would presumably have been adversely affected during the particularly cold winters of 1991 and 1992, whereas birds in captivity would have avoided these harsh conditions.

Movement and Habitat Selection and Foraging

Using the minimum convex polygon method, the size of area used by CR birds (mean = 617 ha ± 619 SD, range 32–1677, $n = 9$) was significantly larger and more variable than that of WR birds (mean = 69 ha ± 43, range 28–140, $n = 7$), (t test, $p < 0.01$). The distances between observations method revealed CR birds moved significantly further distances than WR birds in spring (t test, $p < 0.001$) and summer ($p < 0.05$) with similar but non-significant trends in winter ($0.1 > p > 0.05$) and autumn ($p > 0.10$; Fig. 4).

In winter CR and WR birds could be found in tussock grassland on average 43% ± 7.8 and 52% ± 7.3 of the time respectively, with the remaining time spent in either alpine scrub, forest, or forest clearing (ANOVA, $F = 0.59$, df = 47, $p > 0.10$). In summer, however, WR birds spent almost all of their time (97% ± 12) in tussock grassland whereas CR birds were found in tussock grassland (67% ± 5.0) as well as the other habitats (scrub, forest, or forest clearings) ($F = 7.43$, df = 31, $p < 0.01$).

Both CR and WR Takahe were selective feeders and seemed to share similar patterns in their choice of food species. In both summer and winter there was a significant positive relationship between the proportion of CR birds selecting 22 different food species and the proportion of wild birds selecting the same species ($r = +0.67$, $p < 0.001$ and $+0.74$, $p < 0.001$ for summer and winter, respectively; Fig. 5).

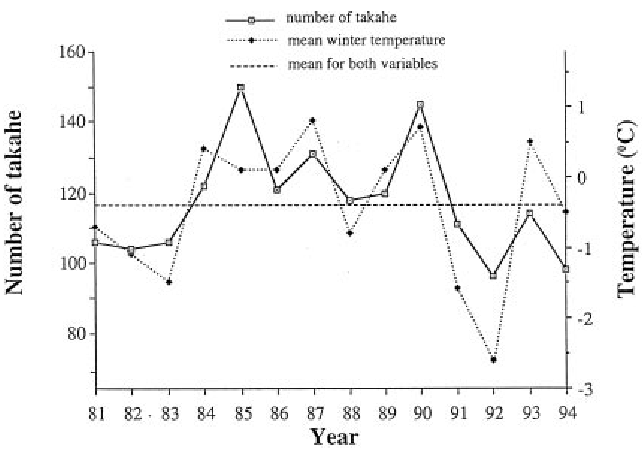

Figure 3. Changes in adult Takahe population size (excluding captive-reared birds) and mean temperature over the 3 coldest months of winter for the Murchison Mountains between 1981 and 1994.

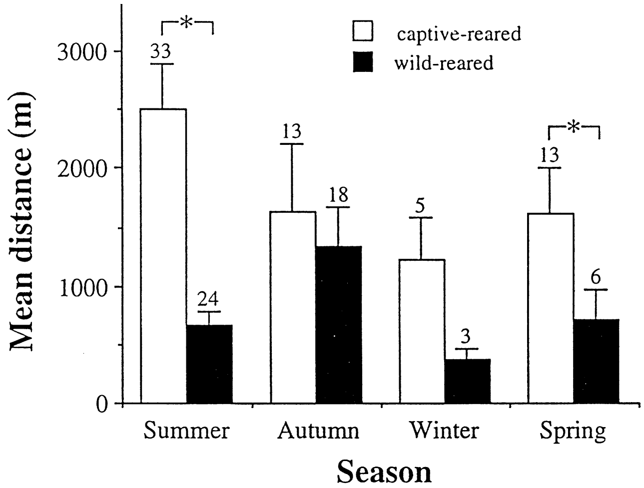

Figure 4. Mean minimum distances moved within each season by captive-reared and wild-reared Takahe over 2-month periods. Vertical bars indicate standard errors, numbers above bars are sample sizes, and asterisk indicates significant differences between groups.

Recruitment and Breeding

Each of the four releases into the Murchison Mountains involved near equal numbers of CR birds of each sex. Although there was a trend towards higher female survival, there was no significant difference in overall survivorship between males and females (Fisher's exact test, $p > 0.10$; Table 1). However, eight of nine (89%) CR females that still had transmitters intact paired versus only two of eight (25%) males (Fisher's exact test, $p < 0.05$); in addition, four CR females that lost their transmitters also paired. In one case, a trio was formed by two CR females sharing a wild male. This happened despite the fact that the two females were released together with two CR males. This was also surprising in that all known breeders in the wild are monogamous.

Of the paired CR females, 6 of 10 (60%) nested the summer following their release (Table 2). Two CR females raised a chick to at least 6 months of age. Several of the others have hatched chicks that died at a very young age although eggs taken from the same pairs have been successfully raised in captivity (D. Eason, personal communication). Low reproductive success rate for inexperienced, first-time breeders is not uncommon in Takahe (D. Eason, personal communication).

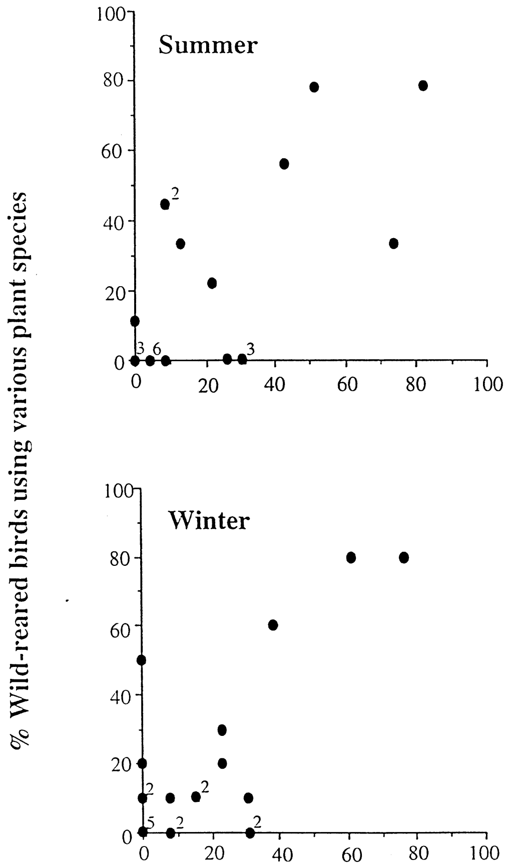

Figure 5. The proportion of captive-reared birds (n = 23 in summer, 13 in winter) selecting 22 food species and the proportion of wild-reared birds (n = 9 summer, 10 winter) selecting the same species of plant. The 22 food species represent all plant species that captive-reared and wild-reared Takahe were observed feeding on during the study. Values on the graph indicate the number of overlaid datum points.

All WR birds from 1990 and 1991 cohorts are now either dead or have lost their transmitters. All WR birds surviving from the 1992 cohort stayed with their parents at least until the end of their second summer (aged 1 year 3 months), and all five survivors of the 1993 cohort are still with parents at age 1 year 7 months. Therefore while the CR birds were independent and available for pairing, WR birds of the same age were not.

Discussion

Environmental factors were extreme in two cohorts of wild birds in this study and survivorship in any other season could not be expected to be much worse. Captive rearing is clearly beneficial to survivorship in these situations. However, in seasons of more typical environmental conditions, captive rearing did not improve survivorship from age 6 months over that of WR birds. The benefit of captive rearing in such seasons lies in the significant improvement (up to 60%) in survivorship of viable eggs between hatching and age 6 months (Eason 1992). This study indicates that Takahe raised in captivity are capable of surviving in the wild as well as WR birds which implies that the CR birds are able to cope with their unaccustomed environment after release. Moreover, CR females formed pair-bonds rapidly with WR males and, in a few instances, attempted breeding.

The differences in both habitat selection and amount of movement between CR and WR birds reflect differences in social behavior. Differences were unlikely to have been influenced by the choice of sites where CR were released as these were typical of habitat used by WR birds for that time of year. Yearlings in the wild remained sedentary with their territorial parents, whereas CR birds wandered more widely either alone or with new mates. The choice of habitat by those CR birds that paired with wild birds may have been influenced by that of their mate, but overall differences in movement and habitat selection with WR birds did not have any negative effect on the survival rate of CR birds.

Although the two groups may use different habitats, they fed on a similar range of plant species. Thus, although CR birds are not exposed to all the food species present in the Murchison Mountains during their time in captivity, they were able to use suitable foods when re-

Table 1. Proportion of captive-reared radio-tagged female and male Takahe surviving after their release as of February 1995.[a]

Release	*Female*	*Male*
1991	0/1 (2/3)[b]	1/3
1992	3/3 (5/5)[b]	1/2 (4/5?)[b]
1993	3/4	2/6
1994	3/3	4/4
Total	9/11 (13/15)	8/15 (11/18)

[a] Proportions in brackets include birds that have lost their transmitters.
[b] All four females that lost their transmitters have paired and settled on territories and thus are known to be alive. Three males released in 1992 have also lost their transmitters but they have not settled on territories and thus their fate is unknown.

Table 2. Proportion of captive-reared females that are paired and are known to have nested.

Release date	*Release summer*	*2nd summer*	*3rd summer*	*4th summer*
1991	0/2	1/2	2/2	1/2
1992	0/5	4/5	4/5	—
1993	0/3	1/3	—	—
1994	0/2	—	—	—
Total	0/12	6/10	6/7	1/2

leased into the wild. Only a few plant species are common to both the rearing pens and the wild environment, but many of the foods in the wild are of similar growth form (sedges, small grasses, and large tussock-forming grasses) to those with which the CR birds are familiar (J. Maxwell, pers. obs.). Mills et al. (1991) have shown that wild Takahe can select both within and between species for plants with high nutrient content and that within a species, birds sample widely before feeding intensively on certain plants.

The difference in pairing success between male and female CR birds may have been due to a lack of females in the wild population. The slightly smaller mean body weight of females (Mills 1978) combined with the extra stress of egg-laying could potentially contribute to a higher mortality rate for breeding females. If this apparent imbalance is real, the effective population size is smaller than that suggested by census figures which assume an equal sex ratio (sexes cannot be distinguished by sight). Census figures for the past 14 years indicate that, on average, 84% (±4.1) of individuals in the wild population (including CR birds) are paired. The remaining 15% may not have much chance of pairing if a high proportion of them are male.

Low pairing success of CR males could also be a reflection of their young age or lower social status. Because the wild birds of the corresponding cohorts are either dead or still with their parents and not competing for mates, the released males in this sample presumably had to compete against birds that were at least 1–2 years older than themselves. In addition, CR males may differ from WR males as a result of their early upbringing in groups without adults, in that they may be less dominant than WR males. This latter scenario has been reported by Marshall and Black (1992) in captive-reared Hawaiian Geese (*Branta sandvicensis*); parent-reared goslings were more dominant, more vigilant, and integrated earlier into the adult flock than those reared in gosling-only groups. The CR male Takahe have formed successful pair bonds at Burwood Bush Rearing Unit and on island reserves but in these areas they are not in competition with WR males for mates.

The lack of pairing by yearling WR birds that stayed with their parents may not be a disadvantage to them in the long term. Although they have missed one potential pair-forming season, it is possible that remaining with parents and in some cases helping to raise their younger siblings (Crouchley 1994) has given them experience that will be advantageous later. It is assumed at this point that breeding success of CR birds will be similar to that of WR birds, but it is important to confirm whether this assumption is correct by continuing to monitor both CR and WR birds.

We conclude that captive-rearing of Takahe for release back into the wild was successful in increasing recruitment of juveniles into the population. The encouraging results of the Takahe Recovery Program to date suggest that there is a place for the careful use of captive-rearing and release techniques in endangered species management. Our study has shown that although there are many potential problems in captive rearing (Derrickson & Snyder 1992; Snyder et al. 1996), these should not be over generalized.

The success of the Takahe Recovery Program may be attributable to many features. Early ecological research identified factors limiting the population and the life history stages most at risk in the wild. Management followed to improve habitat suitability and to instigate captive rearing and release to reduce risks of mortality to eggs and juveniles. Use of a single species rearing unit located close to the source population lowered the risk of disease. Efforts were made to improve hatching success, manage hatchlings to minimize human imprinting, and provide an environment as similar to the natural habitat as possible. Characteristics of the species that make it relatively tolerant to nest manipulation and captivity also helped.

However, the Takahe captive-rearing and release program is not without its critics (Clout & Craig 1995), and it is labor intensive and costly to maintain. In addition, the initial attempt to introduce CR Takahe to their former range in the Stuart Mountains has been deemed unsuccessful. With the subsequent change in management policy of returning CR birds to their parent population in the Murchison Mountains, we should start to see an increase in the rate of population growth that would not otherwise be possible without captive rearing. This should improve the stability of the Murchison Mountains population in the face of adverse environmental fluctuations (such as unusually harsh winters) that could force a smaller population to dangerously low levels. Although the importance of thorough monitoring of any group of captive-reared animals that have been released into the wild is illustrated by the Takahe Recovery Program, more information on pairing and breeding success of CR and WR birds is still needed to ensure the successful management of this highly endangered species.

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