Observations on the breeding behaviour of the Takahe (*Porphyrio mantelli*) on Mana Island

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ABSTRACT

The establishment since 1984 of small populations of Takahe (*Porphyrio mantelli*) on four predator-free islands has been an important component of the conservation strategy for the birds. However, initial productivity of birds in these habitats has been lower than expected due largely to low hatching success of early clutches. This study aims to describe behaviour associated with courtship, incubation and post-hatch care to assess possible behavioural causes of low productivity in Takahe on islands. No unusual behaviour associated with breeding was observed that might result in low productivity, although only two complete copulations were observed during the study. One incomplete copulation involving a yearling male was also observed. Territorial behaviour was recorded to compare with later years when densities of island populations increase. Six territorial interactions between neighbouring pairs were observed, three when pairs were between nesting attempts and ranging widely, and three when two pairs nested in close proximity. Monitoring of aggressive behaviour may be important as it may interfere with successful reproduction.

KEYWORDS: Takahe, breeding behaviour, territoriality

INTRODUCTION

Takahe (*Porphyrio mantelli*), a large flightless rail once thought to be extinct in New Zealand, persist in low numbers (approximately 130) in the Murchison Mountains, Fiordland (J. Maxwell, pers. comm.). Since their rediscovery in 1948 (Crouchley 1994), research into the habitat, predators, competitors, population ecology and breeding biology of Takahe in Fiordland has been carried out (for example William's 1960, Mills 1975, Mills *et al.* 1989, see also Crouchley 1994 and references therein), providing a substantial and valuable resource for making management decisions. In addition, techniques for captive-rearing and translocation have been developed. Since 1984, small populations have been established on four predator-free offshore islands: Maud, Kapiti, Tiritiri Matangi and Mana. Island populations provide an excellent opportunity to study the behaviour of Takahe in detail. Most of what is known about Takahe behaviour is from captive birds at Mt Bruce Wildlife Centre (see Morris 1977, Reid 1978, Williams 1960) as field conditions in Fiordland make detailed behavioural observations difficult. In addition, a recent study found that while adult survival was high on islands, hatching and fledging

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success was lower than in Fiordland, due largely to poor success in early clutches (Bunin *et al.* 1997). This study therefore aims to describe courtship, incubation and post-hatch care patterns of Takahe on Mana Island in order to assess possible behavioural causes of low hatching and fledging success in island Takahe. Descriptions of behaviour, especially territorial interactions, at the current low densities on islands may be important for comparing with behaviour in later years when density increases.

STUDY AREA AND METHODS

Mana Island (41°15'S,174°47'E), 217 ha in area, is situated approximately 4 km off the western coast of the North Island, New Zealand, 21 km north of Wellington. As a consequence of a long farming history the vegetation is highly modified, being predominantly native and introduced grasses (70 % cover). The rest of the island, except for one established section of native bush, is at various stages of revegetation with native shrubs and trees (for a full vegetation description see Timmins *et al.* 1987). The cover for Takahe therefore ranges from rank grass and newly planted trees (0.5 m) to established trees (3 - 4 m). Mana Island is one of the few in the New Zealand region to be declared free of introduced mammals, following removal of cattle in 1986 and eradication of mice in 1991 and is therefore of significant value for conservation.

Takahe have been established on Mana since 1988, when three pairs were transferred there. Additional translocations of birds from the Burwood Bush Captiverearing Centre in Te Anau and other islands have occurred in subsequent years. Observations for the present study of four breeding pairs and one trio consisting of two females and one male were conducted over one breeding season, between 1 September 1994 and 13 February 1995. At the time the study began, one pair (Terri and Ernie) was already incubating their first clutch and one pair (Rima and Lucky) was not yet formed. The remaining two pairs and one trio had not yet begun nesting. All Takahe on Mana are colour banded for easy identification. Observations were made both with and without hides as the mobile nature of the Takahe often made constant viewing from a hide impossible. However, the birds were judged to be accustomed enough to people to allow undisturbed observation without a hide. Observations were spread throughout the day between 06:00 h and 19:00 h, and directed at one to three pairs per day. Length of observation sessions ranged from 15 min to 3 h, often determined by the activity and visibility of the birds. All activities and behaviours of the focal birds were recorded continuously during the observation session using a time-activity budget and it was usually possible to record the activities of both Takahe in a pair at the same time. Takahe on Mana are actively managed to maximise productivity, thus when eggs are infertile or embryos die during incubation, they are removed and nests destroyed to promote re-nesting.

Incubation and post-hatch care data on one pair (Terri and Ernie) were collected by Phil Todd and Tina Wyatt, the island managers, as this pair lived and nested around their house. These data were collected in an opportunistic way, with observations being recorded by the managers when the birds were present outside their house. As there was no guarantee that the recording of observations was consistent with my own, data collected by the managers were included in the results but no comparisons were made with my data.

RESULTS AND DISCUSSION

Although 113 h were spent in the field observing Takahe on Mana Island during the 1994/95 breeding season, only 47 h (42 %) resulted in actually seeing the birds. This was due to the time birds spent out of sight in vegetation, either amongst shrubs or long grass. In addition, some of the Takahe pairs were particularly mobile, requiring a large amount of time to locate the pairs before observation could begin.

All breeding pairs on Mana laid at least one clutch during the 1994/95 breeding season; one pair laid one clutch, two pairs laid two clutches, and two pairs laid three clutches. Re-laying intervals varied between 4.5 and 8.5 weeks (average = 6.8 weeks). Nests were usually built in flax (*Phormium tenax*) or giant umbrella sedge (*Cyperus ustulatus*). No nest-building behaviour was observed, except one instance where a female (Mataku) went into some flax bushes with dry grass in her bill. Nest-building is, however, thought to be shared by both sexes (Morris 1977, Williams 1960). All pairs built one or more trial nests before laying a clutch which is also common in Takahe in Fiordland (Williams 1960).

Courtship and copulation behaviour

Obvious courtship patterns were seen in one pair only (see below), although a small amount of allopreening was observed, often preceded by soft calling between members of a pair. Two copulations were seen during the course of the study. On the first occasion (06:17 h, 13 September 1994) the sequence may have started before observation began. Toni (female) was moving away from the feeding station towards a trial nest under a poroporo bush (*Solanum aviculare*). Alec (male) mounted Toni for about 5 sec making cloacal contact, then they turned to face each other and 'fronted up' (see description later) before Toni moved out of sight. This occurred three days after the first egg of two (both were fertile) in the first clutch had been laid.

On the second occasion (10:43 h, 13 September 1994), 12 days before their first clutch of two eggs (one of which was infertile) was laid, Redleft (female) and Tuarua (male) were feeding close together (1-8 m apart) and allopreening occasionally for almost an hour. Tuarua made clicking noises as Redleft was approaching him, then Tuarua mounted Redleft for about 5 sec with his wings flapping for balance. Tuarua dismounted after making cloacal contact, they pecked beaks, then Tuarua moved 1 m away. Both birds preened and resumed feeding. Before this interaction, Lucky (their juvenile from the previous year) was seen approaching Redleft. They appeared to peck each other's beaks, then both ran out of view and some rapid calling was heard, similar to that heard in confrontational situations and also during courtship. Two days earlier Lucky had been seen away from this territory for the first time, and three days later he formed a bond with Rima and did not return to his parents' territory.

TABLE 1 - Number of times male and female Takahe were seen on the nest at different times of the day.

Sex	Individual	Daytime ¹	Early morning / evening ¹	
Males	Ernie	1	6	
	Tuarua	1	1	
	Snow	0	2	
	Alec	0	1	
	Lucky	0 _	3	
Average	·	0.4	2.6	
Females	Terri	3	0	
	Redleft	12	0	
	Matuku	6	0	•
	Toni/Tilly	13	5	
	Rima	4	0	
Average		7.6	1.0	,

¹ Daytime: 08:30 - 17:00 h; early morning/evening: 06:00-08:30 and after 17:00 h Relative differences in day- and nighttime incubation for males and females were significant; sign test, N = 9, P < 0.05.

Only one pair, Rima (female) and Lucky (male yearling) showed distinctive courtship patterns. This pair formed while the study was under way. Their assumed first encounter involved Lucky wandering into Rima's home range; Rima approached Lucky, and he ran off a short distance. Rima half-raised her wings and tail and stalked after him. Several minutes later, after Rima had been preening, she moved towards Lucky, then chased him until they were out of sight. Duetting was heard and about an hour later, Rima was feeding and Lucky was close by. Over the next 15 min, they 'fronted up' (see explanation following) several times in between feeding, this time with Lucky following Rima.

Rima and Lucky were seen together for the remainder of the study, and provided information on courtship patterns. A courtship sequence involved several behaviours, not all of which were always present. A full sequence would be as follows: duetting (calling alternately to each other), running together, 'fronting up' (facing each other close together and standing with necks stretched upwards), neck-pecking (circling each other and pecking each other's necks), soliciting (a posture where the female turns her back to the male, spreads her wings and puts her head down), allopreening and copulation (cloacal contact). Of the thirty-two courtship sequences seen of this pair, seven resulted in copulation being solicited by Rima and only one of those resulted in an attempted copulation. This occurred eight days after Rimahad laid an infertile egg and two days after the egg was removed. On the occasion (06:00 h, 19 November 1994), loud calling was heard from Rima and Lucky's nest area and Alec, the male from the neighbouring trio, chased Rima a short distance (this had been seen twice before while Rima was incubating on this nest). About 5 - 10 min later, Rima solicited Lucky as he came out of nearby bushes. He put his foot up on her back, mounted for about 5 sec, then climbed off without making cloacal contact. Rima solicited again, but Lucky started feeding and she stopped soliciting.

Lucky's age and/or inexperience may have hindered successful breeding for this pair; few one-year olds have been known to breed (Williams 1960, D. Eason pers. comm.) Although perhaps physiologically mature, one-year old birds may lack the social or behavioural maturity necessary for successful reproduction. Studies of the closely related Pukeko (P. porphyrio) show that, in newly formed pairs in particular, copulation rates can be low and breeding cycles asynchronous resulting in infertile eggs (I. Jamieson, pers. comm.). Studies of other species have shown that age and/or experience can affect breeding success (e.g. in Adélie Penguin Pygoscelis adeliae: Ainley et al. 1983, Richdale 1954, 1957; Red-billed Gull Larus novaehollandiae: Mills 1973; Wandering Albatross Diomedea exulans: Croxall et al. 1992) through either physiological or behavioural effects. Ainley (1978) reports a higher prevalence of incomplete sex acts in young than old Adélie Penguins. Lucky has since successfully raised one chick (during the 1995/96 breeding season) and assuming he was the father, this suggests that his failure to breed in his first year was indeed related to his age and/or experience rather than other genetic or environmental factors.

Other than Rima and Lucky, too few copulation attempts were seen to determine whether some aspect of mating behaviour was related to the high rates of infertility on islands. It is possible that low copulation frequency itself may be contributing to high rates of infertility, however, without data on copulation rates in Fiordland with which to compare results of the present study, few conclusions can be reached. The sperm devaluation hypothesis (Birkhead & Møller 1992) predicts that copulation rates will be high where the risk of extra-pair copulations is also high and where mate-guarding cannot take place (e.g. in colonial species) because sperm from frequent copulations may displace or devalue the sperm of possible competitors. For example, male Pukeko living in polyandrous groups (i.e. two or three males) have significantly higher copulation rates than lone males living in polygynous groups (I. Jamieson, unpublished data). Takahe currently live at low (but increasing) densities and thus the risk of extra-pair copulations should be low. They might, therefore, be expected to have a relatively low copulation rate. If this hypothesis was correct, we would expect to see an increase in the copulation rate of Takahe on islands as population densities, and therefore the risk of extra-pair copulations, increase.

Incubation behaviour

Two birds of a pair were never seen at the same time during incubation, so it was assumed that one bird was always on the nest. In contrast, when pairs were not incubating they were generally seen in close proximity to each other. Females incubated significantly more during the day and males more at night (Table 1). Change-overs took place at approximately 17:00 -18:00 h in the evening and 07:00 h in the morning, based on times that males and females were seen on and off nests. One pair observed in captivity at the Mt Bruce Wildlife Centre was recorded changing over several times during the day (Morris 1977); this was very rarely seen on Mana, except in the trio. The two females in the trio did not seem to have a regular

TABLE 2 - Post-hatch care patterns of two pairs and one trio of breeding Takahe on Mana Island during 1994/95 breeding season.

Bird		Total time				
	Sex	Observations (h)	Birds in view (min)	Birds feeding chick (min)	% time feeding ¹	
Mataku	F	3.7 ²	55	33	60	
Snow	М		166	118	71	
Terri	F	8.7^{3}	484	66	14	
Ernie	M		492	75	15	
Toni	F	5.8^{3}	71	22	31	
Filly	F		101	22	22	
Alec	М		52	2	4	

¹ Time feeding chick/ time in view

pattern of incubation. Both females incubated during all three clutches and it appeared from the pigment pattern that eggs in at least two of the three clutches were laid by different females. Both were seen on the nest during the mornings and the afternoons on different days and both were seen incubating in early morning and evening when the male would normally incubate. Communally nesting female Pukeko take turns incubating during the day along with the male, but normally only the male incubates at night (Craig 1980).

Overall, there were no unusual or abnormal incubation patterns observed in any of the pairs that would account for the low hatching success seen on Mana and in other island populations (Bunin *et al.* 1997).

Post-hatch care

Of 19 eggs laid on Mana, only nine hatched (five were infertile, four embryos died and one egg disappeared). Of the nine chicks, five survived less than 2 weeks. One chick had pneumonia prior to its death but it was not determined whether this was the actual cause of death, another had a deformed neck and spine, and the remaining three died of unknown causes; too few observations were obtained to ascertain whether these deaths were related to their parents' behaviour. Of the four chicks that survived, one was cross-fostered to a Pukeko nest (see Bunin & Jamieson 1996 for more details), leaving three with their Takahe parents. In two of the pairs, both sexes spent similar amounts of time feeding the chicks, although samples sizes were too small to make a statistical comparison (Table 2). However, in the trio, the two females were seen doing most of the feeding (Table 2). Differences between pairs in the total time spent feeding chicks (Table 2) are largely due to the varying ages of their chicks when observations took place. Chicks were fed predominantly grass stems, but insects (beetles and larvae) and supplementary pellets were also included regularly in small amounts, particularly in the first few weeks after hatching. Adults were attentive and were never far away from the

² chick 0-2 weeks old

³ data collected by Phil Todd and Tina Wyatt, chick 4-10 weeks old

chicks, calling frequently to maintain contact. When disturbed, adults gave an alarm call ("oomp") and chicks usually hid in long grass or under shrubs. Few data on chick-rearing in Fiordland are available due to the difficulty in observing chicks in thick cover (Williams 1957). In Pukeko, both males and females spend similar amounts of time caring for the chick (Craig 1980).

All three Takahe chicks surviving on Mana Island were still with their parents at the end of the study, ranging in age from 4 to 12 weeks. In Fiordland, juveniles are known to stay with their parents until at least the beginning of the following breeding season (Williams 1960) and some juveniles stay on and help raise the chicks from that season (Lavers & Mills 1984). This is also known to occur on Mana and Tiritiri Matangi islands (J. Christensen & B. Walter pers. comm.).

Territorial behaviour

Home ranges of Takahe varied in size from 1.2 - 4.9 ha (mean = 2.8 ha, N = 4) and birds were more concentrated in the moist lowland part of the island. Six inter-territorial confrontations were seen during the study. Five of these occurred between Rima and Lucky and the trio (Toni, Tilly and Alec) which lived in an adjacent territory in the lowland area of the island. The other occurred between Terri and Ernie and Rima and Lucky, who also had neighbouring territories. Three of the six incidents occurred while pairs were between nesting attempts and ranging more widely then they do during other parts of the breeding cycle. The others occurred while the trio was incubating their second clutch and Rima and Lucky were incubating their first clutch. These nests were located within 100 m of each other and all incidents involved Alec coming to Rima's nest area and chasing her. Rima and Alec had been penned together prior to the beginning of the breeding season in the hope that they would form a pair bond. However, when they were released from the enclosure, Alec immediately formed a trio with Toni and Tilly. This may have resulted in additional aggression between Alec and Rima.

There are many references to Takahe in Fiordland being highly territorial (Williams 1960, Mills 1975, Lavers & Mills 1984, Crouchley 1994) and aggressive behaviour of Takahe in captivity at the Mt Bruce Wildlife Centre has been extensively described (Reid 1978). In fact, the extent to which Takahe were territorial at Mt Bruce is thought to have prevented them breeding through the effects of stress (Reid 1978). Reproduction is a complex process relying on neuroendocrine control and thus is highly sensitive to the effects of stress which may upset this control (Moberg 1985). With populations on islands growing steadily the frequency of social and territorial interactions between Takahe is likely to increase and may impact on reproductive success. Monitoring territorial behaviour will therefore be of even greater importance as these changes take place.

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