

JOINT NESTING IN THE PUKEKO *PORPHYRIO PORPHYRIO*

By

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Abstract

The primary objective of the study was to determine why established females tolerate new females that join their breeding group and lay eggs in their nest. Previous work on this population has shown that females suffer a cost of joint-nesting in the form of lowered hatching success. Therefore, we would expect female pukeko to attempt to disrupt the reproductive efforts of their co-nesters by ejecting their eggs from the joint nest.

Two hypotheses might explain why this does not happen. The “peace incentive” hypothesis states that females would forego egg destruction to avoid retaliatory behaviour by the other female. Alternatively, females might not destroy the eggs of co-nesters because they cannot discriminate between their own and another female’s eggs. To test between these, we experimentally removed the eggs of one of the females from a number of joint nests. In all seven cases for which we have data on the post-removal behaviour of the females, the robbed female showed no response to the disappearance of her eggs and continued to incubate the clutch.

In addition, we added eggs to eight single female nests. Again, the single females showed no sign that they could distinguish between the foreign eggs and their own. The foreign eggs were not buried, ejected, or destroyed, nor were they moved preferentially to the outer perimeter of the clutch.

To perform the egg removal experiments, I needed to correctly group joint clutches of eggs into maternal sib-groups. I evaluated two methods of doing this, one

relying on qualitative observer assessment and the other on statistical techniques. I determined genetic maternity using DNA fingerprinting. Qualitative assessment was more effective than statistical techniques for identifying the maternity of eggs. Such an approach may be a useful alternative to expensive and time-consuming molecular genetic techniques for measuring reproductive skew in joint-nesting birds.

Predation rates on pukeko nests at our study site during the 1998/99 nesting season were significantly higher than they had been in previous years (1990-1995). In the intervening years, the local rabbit population crashed as the result of two rabbit control measures: poisoning and rabbit haemorrhagic disease (RHD). We hypothesised that the increase in predation rates was due to rabbit specialist predators seeking out alternative prey after the crash in rabbit populations. Such a scenario is of grave concern to wildlife managers in many areas of New Zealand where rabbits are abundant and threatened native bird species are already under extreme pressure from introduced predators.

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Preface

This thesis consists of three multi-authored chapters that are intended for publication. The target journal for Chapter 1 is Behavioral Ecology. The target journal for Chapter 2 is Condor. Chapter 3 has been accepted for publication in New Zealand Journal of Ecology. John Haselmayer conceived and wrote all three chapters and performed all the field work except the collection of predation data prior to 1998. The DNA fingerprinting was performed by Karen Saunders as part of her fourth year thesis project.

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GENERAL INTRODUCTION

Background

The study of animal sociality is one of the most active areas of behavioural ecology. Cooperative breeding is a particularly interesting form of sociality for it involves members of a social group providing care to young that are not their own. Such behaviour stands in direct conflict with Darwinian selectionist thinking. How can one's fitness be improved by expending energy to care for young that are not one's own? Hamilton's (1964) theory of kin selection provided the first theoretical framework within which this question could be addressed. The theory states that an organism's fitness is determined by the number of genes present in the next generation that are identical to its own. Thus, an organism can gain indirect fitness benefits by improving the reproductive success of a close relative.

Upon the base provided by Hamilton's landmark paper, theoretical work on the origin of cooperative breeding continued through the 70's (e.g. Brown 1974, Gaston 1978, Emlen 1982a and b). One set of models which generated much interest are the classical skew models of Vehrencamp (1983a and b) and the extensions thereof by Reeve and Ratnieks (1993) and Keller and Reeve (1994). These models attempt to predict the degree to which reproduction is shared between same sex group members in a cooperatively breeding unit. The short-hand term for the degree of sharing is the reproductive skew. The most widely accepted index of reproductive skew ranges from zero (perfect sharing) to one (complete monopolisation by a single individual; Pamilo and Crozier, 1996).

The skew models assume that dominant group-members can bias the reproductive skew in their favour and will do this to varying degrees depending on

four parameters. (1) Under conditions of strong ecological constraints on solitary breeding (e.g. habitat saturation), skew will increase because subordinates need little incentive to stay in the group. (2) Where the presence of the subordinate greatly increases the fitness of the dominant, skew will decrease because the dominant will offer larger reproductive incentives to keep the subordinate from leaving. (3) Where relatedness between cobreeders is high, skew will increase because the subordinate receives indirect fitness benefits through the dominant's reproduction and therefore requires fewer reproductive incentives to stay. (4) Where the relative fighting abilities of dominants and subordinates are nearly equal and where fighting is potentially costly, skew will decrease because the subordinate will require greater incentives to keep it from fighting for exclusive control of the group's reproductive output.

The pukeko (*Porphyrio porphyrio*) is an ideal study species for testing the predictions of these models because different populations vary with respect to at least two of these parameters: ecological constraints and relatedness of co-breeders. Populations at Shakespeare and Tiritiri Matangi, on the North Island of New Zealand, nest communally in groups of two to three breeding females, two to six breeding males, and up to five non-breeding helpers who are offspring from previous broods. Co-breeders consist of close kin, territories are defended year round, and opportunities for independent breeding are limited by habitat availability. At Otokia, on the South Island, in contrast, groups consist of one to two breeding females, one to three breeding males (monogamy is not uncommon) and non-breeding helpers do not occur. Co-breeders are not close kin, group members disperse and join non-territorial flocks in the non-breeding season, and opportunities for independent breeding are not

limited by habitat availability (Jamieson 1997). These data appear to support the predictions of the classical models.

However, other data on the pukeko raise questions about the assumptions of the classical skew models. In the Otokia population, joint-nesting females have lower per capita reproductive success than females nesting in pairs or polyandrous groups and the reproductive skew between them is low (Jamieson and Quinn, unpublished manuscript). This challenges the basic assumption that groups will form only when it is of benefit to all group members (Emlen 1995). It also challenges the assumption that dominant group members can control the reproductive output of subordinates. My thesis will examine the reasons why dominant pukeko tolerate the presence of subordinates when it apparently decreases their reproductive success.

Study Species

The pukeko, or purple swamphen (*Porphyrio porphyrio*) is a wide-ranging member of the rallidae distributed through southern Europe, Africa, India, Southeast Asia, New Guinea, Melanesia, western Polynesia, Australia, and New Zealand. Thirteen subspecies are recognized. My study population belongs to the subspecies *melanotus*, which breeds in northern and eastern Australia and throughout New Zealand. It is thought that the Pukeko invaded New Zealand from Australia within the past 1000 years (Heather and Robertson 1997).

The pukeko is one of the world's largest rail species, smaller only than the huge flightless rail, the Takahe (*Porphyrio mantelli*), and the large South American coots, *Fulica gigantea* and *F. cornuta*. The subspecies *melanotus* is the largest form of *P. porphyrio*. Mean length of an adult is 51 cm, males weigh an average of 1089

g, and females weigh 881 g on average. Overall coloration of the bird is slate black with bluish-purple underparts and white undertail coverts. The bill and frontal shield are deep scarlet and the legs and feet are orange-red. Sexes can be distinguished in the hand by the male's larger size and longer and deeper bill.

Pukeko are more terrestrial than other rails. Although they virtually always nest over or near water, they spend most of their time foraging on dry land, often hundreds of metres from the nearest body of water. The diet is largely vegetarian, consisting primarily of the soft leaf-bases and pith of aquatic and semi-aquatic vegetation such as *Scirpus* and *Typha*. However, up to 25% of the diet may come from invertebrates, small reptiles and amphibians and their eggs and young, the eggs and young of birds, and carrion (Taylor, 1998). The feeding method of pukeko is unique among rails in that they use their long toes to manipulate and grasp food items through opposition of the hind toe with the three fore toes.

The nest of pukeko is a platform in a clump of grass or reeds which is beaten down to form the base of the nest. Frequently, the surrounding vegetation is pulled together over the nest to create a loose canopy. In our study population, egg laying occurs in August – February with a peak in October. Females typically lay a clutch of four to six eggs; modal clutch size is five. However, because two females sometimes lay in the same nest, clutch size can be as large as twelve. Eggs range in shape from elliptical to long-oval (Harrison 1975), measure 51 x 36 mm, and weigh an average of 36.4 g. The background colour ranges from pale beige to medium brown, sometimes with a greenish hue. The eggs are variably spotted with dark brown blotches that are often concentrated in a ring around the wide end of the egg. The incubation period is about 25 days. Incubation usually does not begin until the third or fourth egg is

layed. The precocial chicks can move around the nest bowl within hours of hatching and frequently leave the nest one or two days after hatching. They begin feeding themselves at 10-14 days and become independent after about 60 days. Both sexes participate in nest building, incubation, and provisioning of young.

Most subspecies of *P. porphyrio* are socially monogamous. However, the subspecies *melanotus* and *poliocephalus* breed in communal groups, the latter only in captivity (Taylor, 1996). The social behaviour and communal mating system of *P. p. melanotus* in New Zealand has been extensively studied by Craig (1977, 1979, 1980a and b), Craig and Jamieson (1990), Jamieson (1997), Jamieson and Craig (1987) and Jamieson et al. (1994). Within co-breeding males, a distinct social hierarchy is evident from interactions at food sources and around the nest. In aggressive postures, the bill is held high, in a position from which a peck can be given. In submissive postures, the bill is held near the ground, or removed from the opponent's view, and frequently the white undertail coverts are presented. Within groups, interactions rarely escalate to fighting. However, fighting is common in territorial disputes, particularly near the beginning of the breeding season when territorial boundaries are less well-defined. Fighting is characterised by much clawing and pecking. Often, fighting birds will fly at one another with feet outstretched and bill open. Within co-breeding females, the social hierarchy is less evident and may be absent in many cases. Co-breeding females appear to be somewhat indifferent to one another and neither submissive nor aggressive postures are taken up when they interact at food sources or near the nest (I. G. Jamieson, pers. comm.). Females also rarely engage in fighting as they do not participate in territorial defence.

Study Site

Our study site was the Otokia Wildlife refuge, located 30 km south-east of Dunedin, South Island, New Zealand. It is an area of semi-flooded pasture with adjacent marshes, ditches, and agricultural land. The habitat is very open, dominated by sedges and grasses, with occasional trees along the ditches. The marshy areas are dominated by cattail (*Typha* spp.). Most pukeko nests were located in the areas of thickest vegetation, usually in a large tussock of grass or cattail, and most often near water. However, the birds regularly foraged in the short grass of the adjacent agricultural lands, allowing for easy observation from two blinds located on nearby hillsides.

Goals of the Study

The primary purpose of this study was to determine why established females tolerate other females joining their group and laying eggs in their nest. Previous work on this population found that females nesting in polyandrous groups have higher reproductive success than females nesting in polygynandrous groups (Jamieson 1997). Two hypotheses might explain why females do not interfere with the reproductive efforts of co-nesters. The first, the “peace incentive” hypothesis (Reeve and Ratnieks, 1993), states that co-breeders might eschew reproductive interference to avoid retaliatory behaviour. The second, the egg-recognition hypothesis, proposes that joint-nesting females that cannot reliably recognise their own eggs would forego interfering with eggs of a co-nester because of the risk of error. In Chapter 1, I describe the egg-removal experiments that I performed to test between these two hypotheses.

One of the critical components of the egg removal experiments was the separation of joint clutches of eggs into maternal sib-groups. To do this, I relied on

my qualitative assessment of intra- versus inter-female variance in external egg morphology. In pukeko, intra-female variability in egg morphology is less than inter-female variability and separation of joint clutches into maternal sib-groups is often possible (Craig, 1980b). This technique is useful not only for performing egg removal experiments but also as a fast and easy method to measure reproductive skew between joint-nesting females. I separated joint clutches in two ways: first, by qualitative assessment in the field; and, second, by multivariate analysis of quantifiable egg morphology variables. I then assessed the efficacy of the two methods against the results of genetic parentage analyses. I describe this evaluation of methodologies in Chapter 2.

The third chapter is dedicated to a discussion of predation rates on nests of pukeko in my study population. Predation rates during the 1998 field season were about ten-fold higher than previous years in which the population had been studied (1990-1994). Coincident with this increase in predation rates, the rabbit population in our area crashed due to the release of rabbit haemorrhagic disease (RHD). Therefore, many predators, especially harriers, ferrets, and stoats, were left without their primary prey species. This final chapter makes a tentative link between the release of RHD and the increase in predation rates on pukeko nests.

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MUTUAL TOLERANCE BY JOINT NESTING FEMALE PUKEKO
(*PORPHYRIO PORPHYRIO*): PEACE INCENTIVE OR LACK OF EGG
RECOGNITION?

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Abstract. Two classes of models which attempt to explain the variation in how reproduction is partitioned among same-sex co-breeders in cooperatively breeding species are the optimal skew models and incomplete control models. Optimal skew models assume that dominants control the reproduction of subordinates and offer reproductive incentives in return for peaceful cooperation. Incomplete control models assume that both dominants and subordinates compete to maximize their own share of the group's reproductive output. Joint-nesting female pukeko (*Porphyrio porphyrio*) have lower per-capita reproductive success than females that nest in pairs. Despite this cost, they do not interfere with the reproductive efforts of co-breeders by destroying or ejecting eggs. The “peace-incentive” hypothesis, aligned conceptually with optimal skew models, states that dominant females might forego destroying the eggs of co-breeders to avoid retaliatory behaviour. The “egg-recognition” hypothesis, aligned conceptually with incomplete control models, states that females cannot recognize their own eggs and therefore cannot destroy the eggs of co-breeders. To test these hypotheses, we experimentally removed all the eggs of one of two females at joint nests. The robbed females did not respond to the removal of their eggs and continued to incubate the remaining eggs. We also experimentally added eggs to the nests of females breeding independently. The host females showed no response to the foreign eggs. We conclude that female pukeko forego egg destruction because they cannot recognize their own eggs. Our results support the assumptions of incomplete control models over those of optimal skew models.

Keywords: cooperative breeding, egg recognition, joint nesting, reproductive skew, sociality

INTRODUCTION

Currently, one of the most active areas of research in behavioral ecology is the study of animal social systems. Since the early 1980's, such research has been based extensively on the framework provided by reproductive skew models (Vehrencamp 1983*a* and *b*, Emlen 1982*a* and *b*, Keller and Reeve 1994). Reproductive skew models attempt to explain the variation in the degree to which reproduction is shared between co-breeders within social groups on the basis of four parameters: 1) ecological constraints on dispersal, 2) the genetic relatedness of group members, 3) the relative fighting abilities of dominants and subordinates, and 4) the degree to which the presence of subordinates enhances group productivity. The models assume that dominants can control the reproduction of subordinates and allocate reproductive "incentives" or "concessions" to subordinates when it is to their benefit. Reeve et al. (1998) distinguish between the above (in their words, "optimal skew models") and incomplete control models. Incomplete control models assume that dominants *cannot* control the reproduction of subordinates but rather, both compete to maximize their share of the group's reproductive output. Both types of models carry the assumption that, as a precondition for group formation, per capita reproductive success must be greater in a group situation than it is for solitary breeders (Emlen, 1995; Vehrencamp, 1983). Recent studies of the pukeko (*Porphyrio porphyrio*) found support for this assumption for co-breeding males but not for co-breeding females (Jamieson and Quinn, unpublished ms).

The pukeko, or purple swamphen (*Porphyrio porphyrio melanotus*) is a communally breeding, joint-nesting gallinule common in marshy areas throughout New Zealand. Populations on both the North and South Islands have been well-

studied (Jamieson 1997; Jamieson et al. 1994; Craig and Jamieson 1990; Jamieson and Craig 1987; Craig 1984, 1980, 1979). Other subspecies occur in Australia, Southern Asia, and Africa. Different populations of pukeko have markedly different social systems. In Shakespeare, on the North Island of New Zealand, breeding groups consist of an average of seven closely related adults, territories are defended year-round, and juveniles remain on their natal territories as helpers. In contrast, breeding groups in Otokia, on the South Island, consist of an average of three unrelated adults, territories are defended only during the breeding season, and juveniles disperse from their natal territories before the next breeding season (Jamieson 1997). Even within a single population, pukeko exhibit a variety of mating systems including monogamy, polygyny, polyandry, and polygynandry (Jamieson et al., 1994). Jamieson and Quinn (unpublished manuscript) found that male pukeko benefit from the presence of other males in their group through enhanced territory defense. They postulated that unmated females may benefit from joining an already established group by gaining access to a high quality territory and high quality males. However, an established female suffers a cost, in the form of lowered hatching success, from another female joining her group, and derives no benefit from the second female's presence since the males perform virtually all the territory defense and most of the incubation and chick care (Craig 1980, Jamieson and Quinn unpublished manuscript).

Jamieson and Quinn (unpublished manuscript) observed that established females behave aggressively toward other females attempting to join their group but that aggression ceases once the new female lays eggs in the joint nest. They concluded that constraints on egg recognition prevent females from ejecting the eggs of co-nesters. This conclusion is similar to that reached by Koenig et al (1995) for

acorn woodpeckers (*Melanerpes formicivorus*) and by Vehrencamp (1977) for groove-billed anis (*Crotophaga sulcirostris*). In both of these species, females destroy the eggs of co-nesters, but only until they themselves have laid an egg in the nest. Ostrich (*Struthio camelus*), on the other hand, despite exhibiting very low inter-female variation in egg morphology, *do* recognize their own eggs and regularly eject the eggs of co-nesters from the nest, even after they themselves have laid (Bertram 1979).

An alternative hypothesis is that female pukeko forego the destruction of their co-nesters' eggs to avoid retaliatory behaviour. For example, a joint-nesting female whose eggs had been ejected by her co-nester could benefit by destroying the rest of the clutch to force a re-nesting. This "peace-incentive" hypothesis (Reeve and Ratnieks, 1993) was tested in *Polistes* wasps by Reeve and Nonacs (1992). They found that beta females significantly increased their aggression toward alpha females when reproductive-destined (but not worker-destined) eggs were removed from the colony. To date, no similar experiments have been performed on social vertebrates.

We tested the peace-incentive hypothesis on joint-nesting female pukeko by removing the eggs of one of the females from joint nests. The hypothesis predicts that the "robbed" female should respond with increased aggression toward the other female in the group or by destroying the remaining eggs to hasten a re-nesting. A lack of response on the part of the "robbed" female would support the hypothesis that constraints on egg recognition prevent female pukeko from destroying one another's eggs. To test further the "egg-recognition constraints" hypothesis, we added the eggs that we removed from joint nests to a number of single female nests. If female pukeko can discriminate between their own eggs and those of other females, we

would predict that they will eject these foreign eggs from their nest, particularly given the high cost to pukeko of incubating an enlarged clutch (Jamieson and Quinn, unpublished ms).

METHODS

Our study site on the Otokia Wildlife Reserve, 30 km south-east of Dunedin, New Zealand, is an area of semi-flooded pasture, adjacent marshes, and agricultural lands. The habitat is heterogeneous, with vegetative cover and amount of standing water varying greatly across the landscape. The highest quality territories (those which are occupied first in the breeding season by the largest breeding groups) are those with the most vegetative cover (Jamieson, 1997). However, even birds from high quality territories regularly forage in open areas of short grass.

We performed daily behavioural observations for two to three hours after dawn throughout the breeding season (August 4, 1998 – January 7, 1999) from two blinds located on hillsides adjacent to the refuge and from raised road beds in the area. We found nests by watching for nesting behaviour and by searching suitable habitat. We checked all nests once per day throughout the laying period. During the incubation period, we checked experimental egg removal nests once every two to three days, and experimental egg addition nests every day. During nest checks, we weighed, measured, and photographed any new eggs and marked them with non-toxic indelible ink. We also recorded the identity of the incubating bird as it flushed from the nest.

We trapped adults in ground traps baited with corn, marked them with colored leg bands for individual recognition in the field, and took 200 μ L of blood from the brachial vein for genetic analysis. We took 100 μ L of blood from the femoral vein of

chicks aged one to two days and marked them with patangial tags. Detailed methods of blood storage and DNA fingerprinting appear in Chapter 2 of this thesis.

We performed egg addition experiments at eight single-female nests. Because we wished to avoid the accidental addition of eggs to a double-female nest, we waited until two days after clutch completion to begin the egg additions so that we could be sure that only one female was laying in that nest. We added as many eggs as the host female had herself laid, once per day shortly after dawn to mimic the rate and time of day of normal laying for this species (Jamieson, unpublished data). Following the egg additions, we checked the nests daily for any sign of destruction or ejection of the foreign eggs. To test whether the incubating female was preferentially moving her own eggs to the center of the clutch, we made daily measurements of the distance from the estimated center of the clutch to each egg in the nest.

We conducted egg removal experiments on 17 joint nests from 8 territories. Joint clutches of pukeko eggs can usually be safely separated into maternal sib-groups by examining aspects of external egg morphology such as size, shape, color, and spot pattern (see Chapter 2). Although we generally did not know which female laid which egg, we were usually confident that we had removed the eggs of only one of the two females from a joint nest. When in doubt, we erred on the side of caution by removing any questionable eggs, thus ensuring that all the eggs remaining in the nest belonged to a single female. We determined the maternity of 18 eggs using DNA fingerprinting to confirm our field separations of joint clutches. Whenever possible, we removed each egg on the same day that it was laid. However, when we discovered a joint clutch containing more than one egg from two females, we removed one egg per day until none of that female's eggs remained. During and

following the egg removals, we observed the focal group for inter-female aggression, egg destruction by either female, and incubation rates of the two females. We supplemented these observations with video cameras placed at the nests throughout the daylight hours for three to four days following the termination of the egg removals.

RESULTS

We conducted experimental egg additions at eight single female nests. If the experimental egg remained in the host nest for three full days following the addition, we considered it to have been accepted by the host. If an egg disappeared at a later time, we assumed that the egg had been broken accidentally and removed by the female or that it had been predated. Except for three experimental eggs that were in a nest that was predated the day after their addition, all experimental eggs were accepted. None of the eight nests was deserted. For each nest, we calculated the average distance from the center of the clutch to native eggs and dummy eggs over all of the daily measurements (Table 1). There was no consistent trend across nests with respect to whether native eggs or experimental eggs were closer to the center of the clutch. The experimental eggs were closer to the center of the clutch in three of the eight nests and the native eggs were closer to the center of the clutch in the remaining five nests. These data were not significant in a t-test for correlated samples ($n = 8$ nests, $t = 1.48$, $p = 0.18$).

Of the 17 experimental egg removal nests, four were predated and six were deserted while we were performing the egg removals and therefore could not be used. We are confident that the four predation events were not actually the result of retaliatory behavior by the robbed female. In one of the four, we observed the

predator, an Australasian Harrier (*Circus approximans*) at the nest. In the other three cases, we have no direct evidence of predation due to video equipment failure.

However, the sign remaining at the nests was identical to that left by harriers at other nests (messy, with many shell fragments and much albumen remaining in the nest).

In the two cases in which we have observed pukeko destroying eggs at a nest, the bird punctured the egg and carried it away, leaving the nest bowl completely clean. At the six nests that were deserted, the eggs remained in the nest but the adults ceased incubating them.

We have data on female behavior and incubation rates following the experimental removals for the remaining seven. Of these seven, two were predated and one was deserted sometime before hatching. We were able to collect blood samples and genetically determine maternity for 16 eggs from the remaining four nests and 2 eggs that had been removed from one of these nests and subsequently hatched as introduced eggs in an experimental egg addition nest. For all 16 samples, the genetically determined maternity confirmed that the eggs that remained in each nest indeed belonged to only one of the females. The two eggs that were removed from one of these nests both belonged to the female with no young in the remaining clutch, as expected. Thus, our in-the-field separations of joint clutches using egg morphology were 100% accurate for the 18 samples we were able to obtain. We therefore have confidence that, at all experimental egg removal nests, the eggs of only one female remained in the nest.

After the experimental egg removals, there was no evidence of retaliatory behavior by either female. During 42 hours of observation at the seven nests, we saw no signs of increased aggression between females and there was no evidence of either

female destroying the remaining eggs. Before, during, and after the egg removal experiments, both females were regularly observed feeding in close proximity to one another and aggressive interactions were never observed.

At six of the seven experimental nests that survived through the egg removal phase, we observed both females incubating the remaining eggs (Table 2). At the seventh (BP2A), we only observed a single incubation bout by one female before the nest was predated. At the four nests for which we determined the identity of the robbed female, there was no consistent trend with respect to which female incubated more. At three of the four, the mother of the remaining eggs was observed performing more incubation bouts and at the fourth, the robbed female was observed performing more incubation bouts.

DISCUSSION

The results of both the egg removal and egg addition experiments support the hypothesis that female pukeko do not discriminate between their own eggs and those of conspecifics. Pukeko nesting in monogamous pairs showed no sign of recognizing the experimental eggs of conspecifics that we added to their clutches. Documented responses to intraspecific brood parasitism include ejection of the parasitic eggs by *Ploceus* weaverbirds (Jackson 1995), burial in the nest material by American Coots (*Fulica americana*; Arnold 1987, Lyon 1993) and Red-knobbed Coots (*Fulica cristata*; Jamieson et al. 2000), Lesser Moorhens (*Gallinula angulata*; Jamieson et al. 2000), and Sora (Sorenson 1995), desertion of the nest by Common Moorhens (*Gallinula chloropus*; McRae and Burke 1996), and movement of the parasitic eggs to the outer perimeter of the clutch by ostriches (*Struthio camelus*; Bertram 1992). Often, these parasitic eggs are moved so far to the periphery that they are not

incubated at all. Hooded Mergansers (*Lophodytes cucullatus*) also move the parasitic eggs of Common Goldeneyes (*Bucephala clangula*) to the outer periphery of their clutches, apparently because ejection out of the nest cavity is difficult and risky (Mallory and Weatherhead 1992). This behaviour should significantly extend the incubation period of the parasitic egg because incubation efficiency decreases with increasing distance from the heat source (Drent 1975).

The pukeko that we experimentally parasitized did not eject, bury or move the experimental eggs to the outer perimeter of the clutch, nor did they abandon their nests. Jamieson (1997) obtained similar results in an egg addition experiment using chicken eggs that he painted to superficially resemble pukeko eggs. Although he did not test whether or not the model eggs were moved to the outside of the clutch, the model eggs were accepted and incubated by the host birds. Furthermore, pukeko have been successfully used in cross-fostering experiments with the eggs of Takahe (*Porphyrio mantelli*), which are similarly patterned but which are almost three times the size of a pukeko egg (Bunin and Jamieson, 1996). It is not surprising that pukeko show no adaptive response to experimental inter- or intra-specific brood parasitism as neither behaviour is reported to occur in this species (e.g. Craig 1980a).

Joint nesting females whose eggs had been experimentally removed from their nest showed no sign of aggression towards the other female and did not destroy the remaining eggs to force a re-nesting. Desertion was one of the major responses to our attempts to set up the experiments (six out of 17 nests). However, when desertion did occur, it was by both females and the males, not just the robbed female, and was presumably the result of perceived predation. For the three nests that were predated during the experimental egg removals, but for which we have no direct evidence of

predation, we cannot completely rule out the possibility that these were not in fact retaliations by the robbed female. However, based on the sign remaining at the nest, we are quite confident that these three nests were indeed predated (see RESULTS).

Not only did robbed females not retaliate, they remained on the territory and incubated clutches that contained none of their own eggs. The only conceivable benefits of this behaviour are those derived through indirect fitness. However, joint-nesting pukeko in our study population are not related (Jamieson et al., 1994). We can therefore conclude that the robbed females, due to constraints on egg recognition, did not know that the clutch contained none of their own eggs.

Joint nesting female pukeko have lower reproductive success than females nesting in pairs (Craig and Jamieson 1990). Given that it would potentially increase their reproductive success, we might expect joint-nesting female pukeko to have evolved better egg-discriminative abilities. One possible explanation is that communal breeding appeared relatively recently in this species and that there has not been sufficient time for pukeko to have evolved this ability. This is in fact plausible for, although communal breeding is known to occur in several gallinule species including the pukeko (Craig, 1980), dusky moorhen (*Gallinula tenebrosa*; Garnett 1980), common moorhen (*Gallinula chloropus*; Gibbons 1986, McRae 1996), and Tasmanian native hens (*Gallinula mortierii*; Goldizen, AW, pers. comm.), it has never been reported from another member of *Porphyrio*. Furthermore, within the pukeko, communal breeding is known to occur in the wild only in the subspecies *P. porphyrio melanotus* from New Zealand.

Alternatively, communal breeding in the pukeko might have evolved first in close kin groups such as those found in populations on the North Island of New

Zealand (Jamieson 1997). In such a situation, the selective force driving the evolution of egg recognition would be weaker due to the inclusive fitness benefits of not destroying the eggs of a closely related co-breeder. In addition, in both pukeko (Jamieson 1997) and common moorhens (*Gallinula chloropus*; McRae 1996), clutch sizes of subordinates nesting jointly with close relatives tend to be suppressed relative to those of the dominant, further reducing the selection pressure for egg recognition.

Female-female competition in other joint nesting birds is well known. Acorn woodpeckers (*Melanerpes formicivorus*; Koenig et al. 1995), groove-billed anis (*Crotophaga sulcirostris*; Koford et al. 1990), and probably common moorhens (*Gallinula chloropus*; McRae 1996) regularly eject the eggs of co-nesters from the nest. Smooth-billed Anis (*Crotophaga ani*) bury the eggs of co-nesters in the nest material (Loflin 1983). However, no female of these species ejects or buries the eggs of a co-nester once she herself has laid in the nest. In these species too, it appears as though females cannot recognize their own eggs.

Similar behaviour may occur infrequently in pukeko. Jamieson (unpublished data) once observed a female pukeko destroy an egg which he had placed in an empty nest on her territory. Haselmayer (unpublished data) observed a joint-nesting female pukeko destroy and eat two eggs that had been laid in a nest on her territory three days earlier but that had not been incubated. We do not know whether the eggs belonged to her or another female. On this same territory, a single egg laid in an otherwise empty nest was gone on the following day with no sign of harrier predation; that is, the nest was completely clean. There was no other active nest on the territory at the time. Haselmayer (unpublished data) has also observed a single egg disappear in a similar fashion from one other multi-female territory. Although

we cannot rule out predation by a mammalian predator that carries eggs away from the nest and therefore leaves no sign remaining in the nest bowl, we have never observed this type of single-egg disappearance to occur at single female nests. This evidence suggests that pukeko, like Acorn Woodpeckers and Groove-billed Anis, occasionally destroy the eggs of co-nesters before they themselves have laid in the nest.

In contrast with other joint-nesting birds, female ostriches (*Struthio camellus*) regularly recognize the eggs of co-nesters and move them to the periphery of the clutch. However, the ostrich mating system more closely resembles a system with very high levels of intra-specific brood parasitism than it does a joint-nesting system as only one female attends any one nest. Established females are remarkably tolerant of newcomers and will even get up from the nest to allow another female to lay. Afterwards, their superior egg-discriminative abilities allow them to push out the foreign egg, although a few foreign eggs usually remain in each clutch (Bertram 1992).

Given that female pukeko suffer a cost of joint-nesting in the form of lowered hatching success (Craig 1980, Jamieson and Quinn unpublished manuscript), we might expect established females to attempt to prevent other females from joining their group. There is some evidence that such behavior does occur. Jamieson and Quinn (unpublished manuscript) and J. Haselmayer (unpublished data) have observed established females aggressively chasing other females from the vicinity of their nest and interrupting copulations between the newcomer and the resident males. In one instance, the newcomer eventually succeeded in copulating with the group males and laid a full clutch of eggs in the nest, after which aggression by the resident female

gradually declined. Faced with the prospect of another female laying in their nest, established female pukeko appear to take an opposite approach to that of female ostriches. Ostriches allow newcomers to lay in their nest, then eject the foreign eggs; pukeko attempt to prevent newcomers from laying, but once they have, are apparently powerless to manipulate the clutch in their favor.

In light of these observations, we propose the “persistent parasite” hypothesis for the evolution and maintenance of joint nesting in the pukeko and perhaps other communally breeding birds. Subordinate or young females may benefit from joining an established female through access to a high-quality territory and high-quality males, as in the Orians-Verner-Willson polygyny threshold models (Verner 1964, Verner and Willson 1966, Orians 1969). Established females suffer a cost of joint nesting, in the case of pukeko, in the form of lowered hatching success. However, the cost of evicting a persistent newcomer may at times be greater than the cost of sharing the nest. An established female can eject foreign eggs from an otherwise empty nest but not from a nest in which she herself has laid. At this point, the best strategy, in the absence of egg recognition, is to cooperate fully in raising the communal brood. This scenario is similar to what Vehrencamp (2000) describes as an evolutionary pathway to female joint-nesting via cooperative polyandry.

Although established females suffer a cost of having another female join the group, the males in the group stand to potentially double their reproductive output if another female joins. Thus, there is a conflict of interest between the sexes that may affect the outcome in a contest between an established female and a newcomer. Although such conflicts of interest may be important in determining both the mating systems that arise within a population and the level of reproductive skew within

cooperative systems, they have not been widely considered in the theoretical literature on cooperative breeding (but see Davies 1989, Davies and Houston 1986). Instead, most work on cooperative breeding theory adopts the framework of a contest between same sex co-breeders.

Recent theoretical work on cooperative breeding has focussed on the variability between and within species in how reproduction is partitioned. A shorthand term for this partitioning is “reproductive skew”. Societies in which reproduction is monopolized by one or a few individuals are said to have high reproductive skew and societies in which reproduction is partitioned equally among all group members are said to have low reproductive skew. The earliest optimal skew models assume (1) that cooperative breeding will arise only when it is of benefit over solitary breeding for all group members and (2) that dominants have some measure of control over the reproduction of subordinates (Vehrencamp 1983a,b). The level of skew is determined by the magnitude of reproductive “staying incentives” offered to the subordinate by the dominant. Staying incentives will be greater (and skew lower) when (1) subordinates greatly enhance the dominant’s fitness, (2) there are few constraints on solitary breeding, and (3) group members are unrelated. Reeve and Ratnieks (1993) extended the early models to include reproductive “peace incentives” which keep the subordinate from fighting for exclusive control over the group’s reproductive output. Peace incentives are greater, and skew lower, when dominants and subordinates are evenly matched and when the cost of fighting is potentially high.

Earlier work on the pukeko (Jamieson 1997) provided support for the predictions of optimal skew models. Populations on the North Island of New Zealand

consist of related group members, experience strong constraints on solitary breeding in the form of access to territories, and exhibit high levels of reproductive skew. Populations on the South Island, in contrast, consist of unrelated group members, experience only weak constraints on solitary breeding, and exhibit low levels of reproductive skew. Our study, however, presents a challenge to the assumptions of optimal skew models. First, the assumption that group breeding will only occur when it is of benefit over solitary breeding for all group members does not hold in that joint-nesting females have lower reproductive success than females nesting in pairs. Second, dominants cannot control the reproductive output of subordinates due to constraints on egg recognition.

The recent “incomplete control” models of reproductive skew produced by Cant (1998) and Reeve et al. (1998) do not depend on this last assumption. In these models, dominants do not control the reproductive output of subordinates but instead both dominants and subordinates compete to maximize their own fitness. In Cant’s model, joint-nesting females produce an optimally-sized brood that strikes a balance between the benefit of producing more of one’s own young and the costs of raising an enlarged clutch. The model predicts that subordinates nesting with close relatives will reduce their clutch size and therefore skew will increase with relatedness. This trend has in fact been demonstrated in many bird species (Jamieson 1999).

The premise of Reeve et al.’s (1998) incomplete control model is that both dominants and subordinates must expend effort to increase their share of reproduction. Both dominants and subordinates, because of indirect fitness benefits, will be less motivated to do this when relatedness is high and therefore skew will decrease with, or be quite insensitive to, increasing relatedness. However, the authors

make an important distinction between symmetrical and asymmetrical relatedness. When relatedness is asymmetrical, as in parent-offspring associations, the subordinate offspring gains more indirect fitness benefits from the dominant parent's reproduction than the parent does from the subordinate offspring's reproduction. In this case, dominants are highly motivated to increase their share of reproduction, but subordinates have no motivation whatsoever because their coefficient of relatedness to the dominant's offspring is the same as to their own. Thus, the model predicts no reproduction by the subordinate; that is, maximal skew with high relatedness.

Testing between optimal skew models and incomplete control models based on their predictions is not easy. Both optimal skew models and Cant's (1998) model predict that skew will increase with increasing relatedness between co-breeders. Reeve et al.'s (1998) incomplete control models, on the other hand, predict that skew will decrease, or be insensitive to, relatedness when relatedness is symmetrical. When relatedness is asymmetrical, as in parent-offspring associations, all three models predict high skew. There is significant overlap in the predictions of the three models. Furthermore, even where the predictions differ, the differences may not be distinguishable by empirical studies. For example, Reeve et al.'s model predicts more equal sharing than the optimal skew models under most conditions but a prediction of a relative difference cannot be evaluated based on an absolute, empirically measured, skew value.

For these reasons, we recommend that the models be evaluated based on their predictions where possible, but also based on their assumptions. The results of this study support the assumptions of incomplete control models. There is no evidence for the "peace incentive" hypothesis: females attempt to prevent others from joining

their breeding groups, and they do not appear to be able to control the reproductive output of co-breeders due to constraints on egg recognition.

The manner in which female pukeko attempt to prevent newcomers from joining their group highlights another problem with the predictions of all types of reproductive skew models. The models predict levels of skew that can range along a continuum from complete monopolization to complete sharing. The case of female pukeko, however, appears to be an all-or-nothing situation. Either the established female succeeds in ejecting the newcomer from the group, in which case she is not a group member and is not included in skew calculations, or the newcomer joins and lays a full clutch of eggs. Thus, measures of reproductive skew in multi-female coalitions in our study population reveal that reproduction is shared equally (Jamieson, 1997). This result should not be interpreted as support for the prediction of optimal skew models that unrelated co-breeders will share reproduction equally. Instead, the low skew results from the fact that only cases where the established female failed to control the reproductive output of a newcomer were included in skew calculations. This is necessarily so because these are the only coalitions that form. The measure of skew in our population would be much higher if the cases in which an established female succeeded in ejecting a newcomer from the group were included. Such cases effectively represent complete monopolization of the group's reproductive output by the established female. In other words, many single-female groups could be thought of as double-female groups with maximal skew, especially if the ejected newcomer fails to find another breeding opportunity. Of course, it would not be practical, nor would it make sense, to include non-breeding females in measures of reproductive skew.

In conclusion, mutual tolerance in joint-nesting female pukeko apparently results not from peace incentives but from constraints on egg recognition. Egg recognition may not have evolved in this population because of the recent appearance of joint-nesting and the lack of intra-specific brood parasitism in this species. It appears that established females attempt to prevent newcomers from joining the group by chasing them off, interrupting copulations, and possibly destroying eggs that are laid in empty nests. When they fail, a multi-female coalition is formed. Thus, our results offer more support for the assumptions of incomplete control models than optimal skew models. Because reproductive skew models in general are difficult to test based on their predictions, we recommend that more studies examine the assumptions of these models as we have done here. Furthermore, the specifics of the cooperative breeding system of pukeko, and perhaps other species, are such that skew is either maximal (the coalition does not form) or nil (equal sharing between all group members). Levels of skew in such systems should not be used as support for any particular type of reproductive skew model.

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Table 1

Mean distance \pm s.d. of eggs from the centre of the clutch in experimental egg addition nests.

| Nest | Mean distance from centre of clutch to native eggs (cm) | Mean distance from centre of clutch to experimental eggs (cm) |
|------|---|---|
| RR4A | 4.7 \pm 1.7 (n = 5, 90) | 4.6 \pm 1.7 (n = 6, 75) |
| E2A | 2.4 \pm 1.6 (n = 4, 4) | 3.1 \pm .05 (n = 3, 3) |
| E2C | 4.7 \pm 1.7 (n = 5, 95) | 4.7 \pm 1.7 (n = 6, 91) |
| W3A | 4.4 \pm 1.8 (n = 6, 92) | 4.7 \pm 1.5 (n = 6, 113) |
| NB5A | 3.9 \pm 1.4 (n = 6, 70) | 3.7 \pm 1.7 (n = 2, 25) |
| BP4A | 3.9 \pm 1.7 (n = 4, 28) | 4.1 \pm 1.1 (n = 4, 22) |
| BP6A | 4.3 \pm 1.5 (n = 6, 66) | 4.2 \pm 1.5 (n = 2, 21) |
| BP9A | 4.5 \pm 1.6 (n = 5, 45) | 4.7 \pm 1.2 (n = 2, 17) |

Means are reported as mean \pm SD. Sample sizes are reported as: n = number of eggs, total number of measurements (distances were measured for each egg on several different days).

Table 2

Observations of incubation by females at joint nests following egg removal experiments.

| Nest | Identity of robbed female [†] | Amount of incubation by both females |
|------|--|--------------------------------------|
| R2I | RA-WR | Unbanded: 8 bouts |
| | | RA-WR: 5 bouts |
| C3B | Undetermined | GA-YY: 4 bouts |
| | | Unbanded: 1 bout |
| W1B | Undetermined | GA-WW: 3 bouts |
| | | WA-RR: 2 bouts |
| W1C | WA-RR | GA-WW: 2 bouts |
| | | WA-RR: 8 bouts |
| NB0B | GA-WB | YA-OY: 12 bouts |
| | | GA-WB: 11 bouts |
| NB4D | OA-RG | BA-RW: 11 bouts |
| | | OA-RG: 8 bouts |
| BP2A | Undetermined | RA-GR: 1 bout |
| | | WA-OGO: none |

A ‘bout’ represents an observation from the blind or on video of the female sitting on the nest for at least fifteen minutes, or an observation of a female flushing from the nest when we approached to perform a nest check. Bouts that we observed from the blind or on video lasted an average of 1.25 hours.

[†]the other female is, by deduction, the mother of the eggs that remained in the nest

USING EGG MORPHOLOGY TO ASSIGN MATERNITY TO THE
EGGS OF A JOINT-NESTING BIRD, THE PUKEKO *PORPHYRIO*
PORPHYRIO

Running head: EGG MORPHOLOGY IN THE PUKEKO

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Abstract. We evaluated two methods of using external egg morphology to assign maternity to the eggs in joint clutches of pukeko (*Porphyrio porphyrio*). We quantified various egg morphology variables, determined which ones exhibited the greatest difference in inter- versus intra-female variance, then used these variables in a cluster analysis. We also assigned maternity to eggs in the field based on our qualitative assessment. We determined true maternity of some of the eggs using DNA fingerprinting. The quantitative statistical technique correctly assigned maternity to 16 out of 18 eggs from four joint clutches. Our qualitative assessments correctly assigned maternity in all 18 cases. Using external egg morphology to assign maternity may be an effective alternative to molecular genetic techniques for measuring reproductive skew between females in some joint-nesting birds.

Key words: cooperative breeding; egg morphology; joint-nesting; reproductive skew

INTRODUCTION

One of the dominant theoretical frameworks for the study of cooperative breeding is provided by optimal skew models, which attempt to predict the degree to which reproduction is shared among same-sex group members (Emlen 1982a, 1982b, Vehrencamp 1983a, 1983b, Keller and Reeve 1994, Reeve et al. 1998). To test the predictions of these models, we need to identify which variables to use as measures of reproductive skew. Genetic parentage of offspring is the most accurate measure of reproductive skew and, for males, may be the only reliable measure available. Molecular genetic techniques such as DNA fingerprinting (Jeffreys et al., 1985) can supply such data with virtual certainty (Westneat 1990, Jamieson et al. 1994, Quinn et al. 1999). However, these techniques are both costly and time-consuming. For joint-nesting female birds, the proportion of eggs laid by each female, as opposed to the proportion of eggs that hatch or chicks that fledge, is thought to be the most direct measure of reproductive skew because it is unlikely to be affected by factors outside the female's control (Jamieson, 1999). In some joint-nesting species, however, many eggs are regularly laid that never hatch (e.g. smooth-billed anis *Crotophaga ani*, Loflin 1983; ostriches *Struthio camelus*, Bertram 1992). In these cases, the number of eggs that hatch or the number of chicks that fledge may be better measures of reproductive skew. We suggest that an analysis of intra- versus inter-female variation in egg morphology can be a useful alternative to molecular genetic techniques for assigning maternity to the eggs of communally breeding, joint-nesting birds.

Numerous studies have employed egg morphology to identify instances of intra-specific brood parasitism (Eadie et al. unpublished manuscript, Yom-Tov et al. 1974, Littlefield 1981, Fetterolf and Blokpoel 1984, Colwell 1986, Gibbons 1986,

Evans 1988, Kendra et al. 1988, Brown and Sherman 1989, Jackson 1992, Lyon 1993a, Lyon 1993b, Sorenson 1995,) and two others (Gibbons 1986, Møller 1987) identified parasitic females by matching odd eggs to those found in neighbouring nests. However, the vast majority of these relied solely on qualitative observer assessment to assign maternity to eggs. Only a handful have performed statistical analyses comparing intra- and inter-female variance in quantifiable egg morphology variables (Eadie et al. unpublished manuscript, Fetterolf and Blokpoel 1984, Brown and Sherman 1989, Jackson 1992) and only Eadie et al. (unpublished manuscript) and McCrae (1997) have tested the accuracy of assigning maternity to eggs using morphology against results obtained from DNA fingerprinting. Both authors caution against relying heavily on egg morphology to identify instances of brood parasitism, but for opposite reasons. Eadie et al. (unpublished manuscript) conclude that, for goldeneye, the technique is conservative but offers a minimum estimate of the frequency of intraspecific brood parasitism. McCrae (1997), on the other hand, found that the last laid egg in the moorhen (*Gallinula chloropus*) was frequently odd-looking and tended to be misidentified as parasitic. She concludes that relying only on egg morphology would result in over-estimating the frequency of brood parasitism and recommends combining egg morphology with data on laying sequence.

A few investigators have used egg morphology to divide joint clutches of eggs into maternal sib-groups as a measure of reproductive skew (Vehrencamp, 1977, Craig 1980, Koenig et al. 1995, McCrae 1996, Jamieson 1997). However, none have quantified aspects of egg morphology, compared variances between and within females, or verified the accuracy of their methods using molecular genetic techniques.

In this study, we do all three of these for a communally breeding, joint-nesting gallinule, the pukeko (*Porphyrio porphyrio*).

METHODS

We performed the present study during the 1998 breeding season as part of an investigation of the co-operative breeding system of the pukeko in which we conducted egg removal experiments. To perform the egg removals, it was important that we be able to separate the joint-clutches into maternal sib-groups. That need brought about this evaluation of two methods of doing so using external egg morphology.

The pukeko (or purple swamphen) is a wide-ranging gallinule common in wetlands throughout New Zealand, Australia, South Asia and Africa. Our study site was the Otokia Wildlife Refuge, 30 km south-east of Dunedin, New Zealand, and adjacent wetlands. Pukeko at Otokia exhibit a variable mating system, with monogamy, polyandry, polygyny, and polygynandry all occurring regularly (Jamieson et al., 1994). We found nests by watching for nesting behavior from two blinds located on a hillside above the refuge and by searching suitable habitat. We checked all nests daily during the laying period and marked the eggs with non-toxic indelible ink. New eggs were photographed, weighed, and their lengths and widths measured. We subsequently weighed all eggs approximately every five days to determine an average rate of water loss. This rate was then used to adjust the mass of eggs that were first weighed after the onset of incubation so that they could be compared to eggs that were weighed on the day they were laid.

In addition to the three egg morphology variables measured in the field, we used the University of Texas Health Sciences Centre in San Antonio Image Tool,

version 2.00 (UTHSCSA 1995) to measure other aspects of egg morphology from the photographs taken in the field. We collected data on spot pattern separately for the top and bottom hemisphere of each egg because spotting was typically more concentrated on the bottom hemisphere. We considered only primary spots (those in the outermost layer of pigment) in our analysis because secondary spots (those with at least one layer of pigment on top of them) could not be consistently distinguished from the background. We measured neither the colour of spots nor the background colour of the egg because such a measurement would have been too greatly affected by the type of film used, the lighting conditions and the scanning process. The complete list of variables measured for each egg is as follows: mass at laying (some masses adjusted using known rate of water loss); length; width; sphericity (l/w ; Lyon, 1993); volume ($0.498 * l * w^2$; Spaw and Rowher, 1987); pointedness ($[\text{width at } \frac{1}{4} \text{ length}] / [\text{width at } \frac{3}{4} \text{ length}]$); number of spots_{top hemisphere}; number of spots_{bottom hemisphere}; mean size of spots_{top hemisphere}; mean size of spots_{bottom hemisphere}; percent cover of spots_{top hemisphere}; percent cover of spots_{bottom hemisphere}; percent cover of spots_{bottom hemisphere} / percent cover of spots_{top hemisphere}; overall percent cover of spots; overall mean size of spots. Although many of these variables correlate with one another, we follow Sokal and Sneath (1963) in including them all in our preliminary analysis.

As part of the egg-removal experiment at joint nests, we divided joint clutches into maternal sib-groups in the field then removed what we considered to be all the eggs of one of the two females. To do this, we used our qualitative assessment of which eggs looked most similar to one another. We considered all aspects of egg morphology, including size, shape, colour, and spot pattern. Although we had no

systematic method of doing this, we relied more heavily on size and shape than on spot pattern or colour.

To determine genetic maternity at joint nests, we took up to 200 μ L of blood from the brachial vein of adults during banding and a maximum of 100 μ L from the femoral vein of chicks at 1-2 days of age. Maternity was assumed at single nests because a previous long-term study of this population using genetically-determined parentage revealed no cases of brood parasitism (Quinn and Jamieson, unpublished manuscript).

DNA Fingerprinting

Blood was stored in 1 X lysis buffer (4.0 M Urea, 0.2 M NaCl, 0.1 M Tris-HCl, pH 8.00, 0.5% n-laurylarcosine, 0.1 M 1,2-cyclohexanediamine) (Seutin et al. 1991) at 4°C until the time of DNA extraction. DNA was extracted from the whole blood using a salt extraction procedure (Miller et al. 1988). Once DNA concentration of each extracted sample was determined, 15 μ g of DNA was digested with the Hae III restriction enzyme. Five micrograms of digested extract for each sample and 18 ng of a lambda in-lane marker were run on a 0.8% agarose gel at a rate of 2 V/cm for 48 hrs to size fractionate the DNA fragments. The DNA was then transferred from the gel to a membrane by Southern blotting. The blots were sequentially probed with three multi-locus minisatellite DNA probes radio-labelled with [α -³²P]dCTP. Jefferys 33.6 (Jeffery et al. 1985), PER (Shin et al. 1985) and a lambda probe were used to hybridize to the blotted DNA. Exposure of probed membranes to X-ray film resulted in autoradiographed DNA fingerprints. These DNA fingerprints were scored to determine parentage of pukeko nestlings by comparing banding patterns of putative parents' digested DNA to that of the nestlings.

Samples were arranged in families on each blot. All families examined contained one non-sampled adult. Banding patterns of nestling DNA were first examined to determine if a parent was one of the non-sampled individuals. This was done by examining unexplained bands in a chick's DNA banding pattern. If the DNA banding pattern of a nestling contained two or more unexplainable bands and/or contained a band present in two or more nestlings but not in any of the parents scored it was assumed that this nestling was of the non-sampled (unbanded) individual. This assumption was made based on the greater probability that the non-sampled individual was a parent compared to the probability of one nestling having two or more mutations or a mutation arising in the stem cell that gave rise to the gametocytes of a parent, respectively. If a non-sampled individual was assumed to be a parent of a nestling then the DNA banding patterns of opposite-sex individuals, compared to the non-sampled individual, were examined to see which shared the greatest number of bands. The individual sharing the greater number of bands was considered to be the other parent. If it was determined that the non-sampled individual was not a parent then parents were decided by finding the two individuals whose DNA banding patterns could explain all bands present in the nestling's DNA banding pattern. Parentage was verified by examining two DNA fingerprints (J33.6 and PER) for concurring results.

Statistical Analyses

The first step in the analysis of egg morphology was to use the clutches of single females (known maternity) to perform a Kruskal-Wallis analysis of variance on all variables. We used the Kruskal-Wallis test because many of the variables violated the assumptions of normality and homoscedasticity required for ANOVA. Those

variables that showed a significant effect of female were then used to separate joint clutches using a cluster analysis. Cluster analysis groups multivariate data points into a specific number of clusters in such a way as to minimise intra-cluster variance and maximise inter-cluster variance. We used Statistica® software for all the statistical analyses.

RESULTS

We measured the length, width, and mass of 63 eggs from eight single-female clutches and 264 eggs from 48 joint clutches in the field. However, because many nests failed due to desertion and predation, we only photographed and collected pattern data for 58 eggs from seven single-female clutches and 88 eggs from 9 joint clutches. Of these 83, 18 hatched and were blood sampled for genetic analysis. The other 70 did not hatch either because they were predated or because they were removed as part of an egg-removal experiment and not placed in a foster nest.

The results of the Kruskal-Wallis test on single-female clutches indicate that a subset of the variables do indeed show significantly higher inter- than intra-female variance (Table 1). Overall, size and shape variables appear to be more consistent within females than pattern variables.

We tested the accuracy of the cluster analysis technique with dyads of single-female clutches. We therefore had *a priori* knowledge of how the eggs should cluster. We used all possible dyads of clutches. Therefore, the total number of “eggs” used for this analysis is 228 for those variables which required photographs and 301 for those that did not (i.e. variables that we measured in the field). However, these numbers are not sample sizes because they include the duplication that results from every clutch being compared with every other. Therefore, we did not use these

data in any statistical tests. For this analysis, we standardised all variables by subtracting the mean and dividing by the standard deviation.

When we used all of the variables, 7.9% (18/228) of eggs were misclassified. With only those variables that we measured in the field without photographs (mass, length, width, sphericity, volume; all of which yielded significant results in the Kruskal-Wallis test), 14.3% (43/301) of eggs were misclassified. When we selected only and all those variables that had yielded significant results in the Kruskal-Wallis test (in italics in Table 1), only 6.6% (15/228) of eggs were misclassified. Using this subset of variables produces the most correct classification.

When we applied the cluster analysis to the 18 eggs from four joint clutches for which maternity had been determined genetically, we used this same subset of variables that had yielded significant results in the Kruskal-Wallis test (in italics in Table 1). Two out of 18 eggs (11%) were misclassified. Our qualitative assessments in the field performed better than our quantitative statistical analysis; maternity was assigned correctly in every case that was tested with genetic data. Although the difference between the two methods is not significant (Fisher's exact test; $p > 0.1$), sample size is small, and the power of the test is therefore weak. Our results suggest that assigning egg maternity in the field based on the observer's qualitative assessment is at least as accurate as using quantifiable variables and statistical techniques to do the same.

DISCUSSION

External egg morphology can successfully be used to separate joint clutches of pukeko eggs into maternal sib-groups. Many egg morphology variables exhibit significantly greater inter- than intra-female variance. Those variables that exhibit the

greatest difference should be most heavily relied upon in assigning maternity to eggs. In pukeko, the most useful variables are those that relate to the size and shape of the egg. The number of spots and percent cover of spotting on the bottom hemisphere of the egg also showed significantly greater inter- than intra-female variance, but to a lesser extent. These can also be used as clues to the maternity of eggs, but they should be secondary to variables relating to size and shape.

That the size and shape of the egg should have significantly higher variance among than within females makes sense in light of what we know about egg formation. The size and shape of an egg is determined during mineralization, which occurs in the shell gland pouch, a portion of the oviduct, approximately 4.5 hours after ovulation (Board, 1982). Mineralization occurs while the egg is still plumping; that is, while the albumen is still absorbing water. The precise size and shape of the egg therefore depend on the balance between the expansive plumping forces and the resistance from the walls of the shell gland pouch at all points on the egg. Thus, there is a close relationship between the size and shape of an individual female's shell gland pouch and the ultimate size and shape of her eggs.

Note, however, that there is still room for variation, at least in egg size, within a single female's clutch of eggs. Variation in egg size with laying sequence is well-documented in many bird species including Herring Gulls (*Larus argentatus*; Parsons 1976), Canada Geese (*Branta canadensis*; Leblanc 1987), Pied-billed Grebes (*Podilymbus podiceps*; Forbes and Ankney 1988), and American Coots (*Fulica americana*; Arnold 1991). In particular, last laid eggs are often significantly smaller than the rest of the clutch (Gochfield 1977, Baerends and Hogan-Warburg 1982, McRae 1997). Investigators attempting to assign maternity based on egg morphology

should be aware of the extent of this variability in their study species and be especially cautious in assigning maternity to last-laid eggs.

Spot pattern results from the deposition of small granules of a brown pigment, ooporphyrin, which are imbedded in the calcite crystals of the egg shell (Tyler, 1969). If they are on the surface, the spots appear brown, but the deeper they are in the shell, the paler they appear. The deepest spots are invisible from the outside of the egg. The ultimate pattern of the spotting depends on the distribution of pigment in all shell layers. Thus, there are stochastic elements that determine the ultimate pattern of spotting on the egg. There can therefore be significant variability in spot pattern within a clutch of eggs from a single female. For example, the last laid egg of the House Sparrow (*Passer domesticus*) is known to have consistently less spotting than other eggs in the clutch, possibly due to physiological changes at the onset of incubation that affect the functioning of the pigment glands (Lowther 1988). Although intraclutch variability in spot pattern is less well-documented than intraclutch variability in egg size, the phenomenon of particularly distinct last-laid eggs may be quite widespread. Here again, researchers should be cautious in assigning maternity of last laid eggs based on spot pattern.

Our qualitative field assessments of egg maternity were more accurate than the quantitative statistical techniques that we used. The most likely explanation is that, in the field, we used several morphological characteristics that we did not quantify and therefore could not use for the cluster analyses. The most obvious of these are the background and spot colour (not pattern) of the eggs. We think it unlikely that spot colour could be used to distinguish between the eggs of different females as it appears to be quite uniform across all females. The outer spots were

consistently coloured a rich, reddish brown. Background colour, on the other hand, did appear to vary significantly between females. While some clutches were pale grey, others were brown, and still others had a distinct greenish hue to them.

However, we recommend caution in using background colour as a clue to maternity of eggs as it can change over time. Fresh pukeko eggs tend to be pale and greenish and to become darker and browner as they age, either through the degradation of some pigments or the accumulation of dust and dirt. Nevertheless, colour can be a helpful clue to the maternity of an egg. Further, colour can be quantified in the field or through photographs if care is taken to control lighting conditions and if the effects of ageing are accounted for.

Although colour can potentially be used in quantitative statistical analyses, there are elements of shape that almost certainly cannot. The two shape variables that we used, sphericity (length/width) and pointedness (width at $\frac{1}{4}$ length/width at $\frac{3}{4}$ length), capture certain aspects of shape, but there are many subtleties which they do not. For example, two eggs with equal pointedness might differ in whether the narrow pole is sharply pointed or more rounded, or whether the egg is long and tapered or short and more bluntly pointed. We found that we often relied on a qualitative assessment of shape (football-shaped versus watermelon-shaped, etc.) as the primary characteristic for separating joint clutches into maternal sib-groups. Preston and Preston (1953) developed a method of making thorough quantitative descriptions of egg shape using length, width and the radii of both poles to specify three parameters: elongation, asymmetry, and bicone. However, lack of a spherometer precluded the use of their method in this study. There are subtle aspects of spot pattern which also could not be incorporated into our quantitative analysis but

which could be used in a qualitative field assessment. For example, a ring of spots around the bottom hemisphere of an egg would be quantified in the same way as a concentration of spotting on the bottom hemisphere. To a human observer, however, these two patterns would be considered to be different.

Which morphological characteristics are best relied upon will naturally vary widely between species. For example, the eggs of the northern masked weaver (*Ploceus taeniopterus*) and other species of *Ploceus* weaverbird, exhibit dramatic inter-female variability in background colour (Jackson, 1995). One female's eggs may be red, another's blue and another's orange. The coloration of Barrow's Goldeneye (*Bucephala islandica*) eggs, on the other hand, is almost completely uniform. Nevertheless, approximately 86 percent of parasitic eggs can be accurately identified using size and shape variables alone (Eadie et al., unpublished manuscript). Bertram (1992) has even suggested that the pattern of pores may allow for discrimination between the eggs of different female ostriches (*Struthio camelus*).

This study has demonstrated that external egg morphology can be used to separate joint clutches of pukeko eggs into maternal sib-groups. Qualitative human assessment is at least as accurate, and probably more accurate, than statistical techniques. As imaging technologies improve, statistical techniques will become more and more reliable. However, they may never surpass the accuracy of qualitative assessments as these rely on the brain's simultaneous consideration of many interacting characteristics. Likely, this method is also applicable to other joint-nesting birds and can be used as a surrogate for molecular genetic techniques for measuring reproductive skew between joint-nesting females. However, we strongly recommend that, before this method is applied, researchers first perform an

examination of the level of intra- and inter-female variance in egg morphology using known-maternity eggs.

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Table 1

Results of the Kruskal-Wallis analysis of variance using eggs from single females.

Variables in italics are those in which inter-females variance is significantly higher than intra-female variance.

| <u>Variable</u> | H | p |
|--|----------|----------|
| <i>Mass (adjusted for water loss)*</i> | 48.56 | < 0.001 |
| <i>Length*</i> | 36.62 | < 0.001 |
| <i>Width*</i> | 31.35 | < 0.001 |
| <i>Sphericity*</i> | 23.54 | < 0.01 |
| <i>Volume*</i> | 36.99 | < 0.001 |
| Number of spots (top hemisphere)† | 12.38 | > 0.05 |
| Percent cover of spots (top hemisphere)† | 9.64 | > 0.05 |
| Mean spot size (top hemisphere)† | 9.70 | > 0.05 |
| <i>Pointedness†</i> | 28.73 | < 0.001 |
| <i>Number of spots (bottom hemisphere)†</i> | 20.32 | < 0.01 |
| <i>Percent cover of spots (bottom hemisphere)†</i> | 21.57 | < 0.01 |
| Mean spot size (bottom hemisphere)† | 15.44 | > 0.05 |
| Total percent cover of spots† | 11.56 | > 0.05 |
| Percent cover top : bottom† | 10.43 | > 0.05 |
| Number of spots top : bottom† | 7.31 | > 0.05 |
| Overall mean spot size† | 11.30 | > 0.05 |

* n = 63 eggs from 8 females

† n = 58 eggs from 7 females

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SHORT COMMUNICATION

INCREASED PREDATION ON PUKEKO EGGS AFTER THE APPLICATION OF RABBIT CONTROL MEASURES.

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Summary: We have been studying the social behaviour and ecology of pukeko (*Porphyrio porphyrio*) for over five years at a study site in the Lower Taieri River, Otago New Zealand. After an application of rabbit poison in 1995 and the illegal release of RHD in New Zealand in 1997, there was strong circumstantial evidence that rabbit (*Oryctolagus cuniculus*) abundance on and around our study site had been substantially reduced. In a retrospective analysis, we compared predation rates on the eggs of pukeko (*Porphyrio porphyrio*) over a four-year period (1991-1994) before the application of these measures and one year (1998) after their application.

Significantly more nests were predated in 1998 than in previous years. While we recognise a number of explanations for this result, we suggest that the most plausible reason for the increase in predation rates is a shift in diet by the rabbit specialist predator, the Australasian harrier (*Circus approximans*).

Keywords: nest predation; rabbit control; RHD; conservation; New Zealand.

INTRODUCTION

Rabbit haemorrhagic disease (RHD) was illegally introduced into Central Otago in the spring of 1997 as a means of controlling rabbit (*Oryctolagus cuniculus* L.) abundance. Its short-term effects on rabbit populations were highly variable, with kills ranging from over 95% to almost nil (Parkes et al., 1999). Little is known of the longer term effects of RHD on rabbit populations or the indirect effects of declines in rabbit abundance on other species in the community.

One of the concerns regarding the introduction of RHD to New Zealand is the possibility that rabbit-specialist predators (e.g. ferrets (*Mustela furo* L.), cats (*Felis catus* L.), stoats (*Mustela erminea* L.), and Australasian harriers (*Circus approximans* Peale) will shift their diet to native prey in the absence of rabbits (Norbury and Murphy, 1996; Norbury, 1999). A few studies from New Zealand and overseas have shown an increase in native prey in the diets of predators after experimentally-induced declines in rabbit abundance (reviewed by Norbury, 1999). In New Zealand, these studies have focussed on semi-arid tussock grassland of Central Otago, an area that supports very high rabbit populations and several vulnerable native bird species. The purpose of this paper is to report on an increase in predation on pukeko (*Porphyrio porphyrio* L.) eggs after an RHD outbreak in an area outside of Central Otago.

STUDY SPECIES BACKGROUND

The pukeko (or purple swamphen) is a large gallinule native to New Zealand, as well as much of Australasia, India, southern Africa and the Iberian Peninsula. They build a large, shallow cup nest woven from grasses and reeds, which is typically placed in the centre of a clump of reeds or in raupo (*Typha spp.*) over shallow water or within

about one meter of the water's edge. Both sexes incubate the eggs, which hatch asynchronously after 23-27 days. The precocial chicks are capable of leaving the nest within hours of hatching but often remain in the nest for two or three days.

METHODS

We collected the data incidentally to a study of the breeding behaviour of pukeko (Jamieson *et al*, 1994; Jamieson, 1997; Haselmayer, unpubl, data), carried out over five breeding seasons (September – January): 1991-1994 inclusive and 1998. Our main study site was the Otokia Wildlife Reserve, an 11.2 ha area of reclaimed wetland and semi-flooded pasture, and adjacent paddocks and swampy areas 30 km south of Dunedin.

We found nests by observing pukeko from hides located on an adjacent hillside and from vehicles on elevated roadways and flood banks then searching areas where we observed nesting behaviour. We subsequently checked all nests every 1-2 days throughout the incubation and hatching periods. We scored each nest as belonging to one of three categories. A nest from which all the eggs disappeared or were destroyed was scored as “predated” if the previous nest check had confirmed the birds’ continued attendance at the nest (by either the presence of a newly laid egg or by the eggs’ being warm). If the previous nest check failed to confirm the birds’ continued attendance at the nest (cold eggs, and no new eggs), it was scored as “deserted.” If at least one egg from a nest hatched successfully, the nest was scored as “hatched.” For all predation events in 1998, we made descriptive notes of the sign left by the predator but made no concerted efforts (e.g. video) to identify the nest predators.

We compared predation rates in 1998 (post-RHD) with previous years. Our behavioural studies concentrated on finding nests early in the egg-laying period. We did come across a few nests that were in the later stages of the incubation period and the inclusion of these could have effected the probability of observing a predation event. Because our sample sizes were relatively large, we therefore included in our analysis only those nests that were found during the egg-laying period. In addition, because we manipulated nests in 1998 by adding eggs to some nests during the laying period, we report results that both include and exclude manipulated nests.

RESULTS

Over the five field seasons, we found a total of 112 nests during the laying period of which 50 hatched, 28 were predated, and 17 were deserted. The mean number of territories per year in the study area was 16.8 ± 2.3 SE. In any one year, a single territory generated from one to ten nests (1.8 ± 0.3 SE) as a result of renesting after predation or desertion. The 1998 season was different from other years in that, due to greater search effort, we found more territories with active nests (24 in 1998 compared with 16, 12, 16, and 16 for 1991-1994 respectively), and thus more nests during the egg-laying period (45 in 1998 compared with 16, 18, 16, and 17 in 1991-1994, respectively). The distribution of hatched, predated, and deserted nests over the five years is given in Figure 1.

To compare predation rates between 1998 and previous years, we pooled the data from the three years 1992-94 to generate expected values in a contingency analysis. The pooling of these data is justified by the lack of significant heterogeneity in the predation rates from the three years ($G_H = 3.27$; $df = 2$; $p > 0.10$). However, we excluded the 1991 data from the analysis because a G-test did show evidence of

heterogeneity among the predation rates from all four years 1991-1994 ($G_H = 8.68$; $df = 3$; $p < 0.05$). Because 1991 is the year that is most dissimilar to 1998 in terms of nest predation (none of our observed nests were predated or deserted in that year), its exclusion will, if anything, underestimate the implied predation response. Predation rates in 1998 were significantly greater than in previous years (manipulated nests included: $\chi^2 = 19.12$, $df = 1$, $p < 0.001$; manipulated nests excluded: $\chi^2 = 28.95$, $df = 1$, $p < 0.001$).

To compare desertion rates between 1998 and previous years, we pooled the data from all four years 1991-94 because a G-test showed no evidence of heterogeneity among them ($G_H = 3.23$; $df = 3$; $p > 0.10$). Desertion rates in 1998 were much higher than in previous years (manipulated nests included: $\chi^2 = 35.96$, $df = 1$, $p < 0.001$; manipulated nests excluded: $\chi^2 = 9.04$, $df = 1$, $p < 0.005$).

We were able to directly observe only three predation events in 1998; all involved Australasian harriers. At all three, the sign left by the predator was very messy, with many shell fragments and a few half-eaten eggs remaining in the nest. Fourteen of the 20 predations in 1998 involved similar sign. The remaining six left very clean sign, the eggs having simply disappeared. Data on sign were not collected in 1991-1994.

DISCUSSION

Efforts at rabbit control in New Zealand and the attendant studies of the ecological effects of such control have naturally focussed on areas of extreme rabbit abundance, such as the semi-arid high country of Central Otago (Norbury and Heyward, 1997; Norbury and McGlinchy, 1996; Pierce, 1987). Unfortunately, this means that rabbit

count data are lacking for areas of lower rabbit abundance, such as our study site in the Lower Taieri River valley. Without these data, we cannot make a numerical correlation between rabbit numbers and predation rates on pukeko nests. However, we know that RHD was released in our study area in the summer of 1997, shortly after its release in Central Otago, and that rabbit poison was applied to our study area in 1995. One adjacent landowner informed us that, before 1995, rabbits were common on his land, that their abundance decreased after the 1995 poisoning, and that he has not seen a single rabbit in the area since the release of RHD in the summer of 1997. Though not quantitative, this anecdote strongly suggests that, between 1994 and 1998, there was a significant decrease in the rabbit population on our study site that coincided with a marked increase in predation rates (and possibly predation-related desertions; see below) of pukeko nests.

We suggest that the increase in predation rates in 1998 was the result of the crash in rabbit populations following the 1995 poisoning and the 1997 RHD epidemic; i.e rabbit specialist predators in the area responded to a decrease in rabbit abundance by seeking out alternative prey, including pukeko eggs. This response has been documented for harriers (Pierce and Maloney, 1989; Pierce 1987), ferrets (Norbury and Heyward, 1997; Pierce, 1987), and cats (Pierce, 1987) in New Zealand as well as for foxes and stoats in England (Sumption and Flowerdew, 1985).

It is possible that predators from nearby areas of previously high rabbit abundance (e.g. Central Otago) may have dispersed into our study site when rabbit populations there crashed during the 1997 epidemic of RHD. However, most dispersing predators presumably would not have remained in our study area given the lack of rabbits and the relatively small population of pukeko and their eggs as

alternative prey. Furthermore, we did not notice any obvious increase in harrier numbers between 1994 and 1998.

Other than the decline in rabbit populations, there are several alternative explanations that could account for the observed increase in predation rates in 1998. First, it is possible that our activities at the nests in 1998 caused greater disturbance than in previous years and that predators took advantage of the window during which the adults were away from the nest. Certainly, the fact that we also see a significant increase in desertion rates in 1998 suggests that this could have been the case. However, we made similar numbers of visits in all years, and, although our visits were longer (and therefore disturbance higher) at *manipulated* nests in 1998, we still see markedly higher predation and desertion rates in 1998 when these nests are removed from the analysis. Furthermore, after each nest visit, we watched the nest area from a safe distance for 15 min to ensure that no harriers approached the nest during this time. It is much more likely that both increased predation *and* desertion were caused by increased pressure by predators.

Second, more of the 1998 nests may have been in marginal habitats where they are more susceptible to predation. Indeed, we found more territories in 1998 largely because we expanded our study site into surrounding paddocks where the nests are much less concealed than on the main site. However, out of sixteen nests in 1998 from “new” marginal territories, only one was predated – markedly fewer than the 64% of nests predated on non-marginal territories that year.

In 1998, the three months leading up to pukeko breeding season were exceptionally dry in the area of our study site. Only 61.4 mm of precipitation fell between June and August, 1998 compared with a mean of 143.6 ± 28.8 SE for the

same months in 1991 – 1994. Thus, large areas of our study site, which would normally have been under at least a few centimeters of water, were completely dry. This would allow greater access to nests for terrestrial predators, particularly mustelids (Craig, 1980). However, only six of the 20 predation events in 1998 showed the “clean” sign typical of mustelid predation (Moors, 1983). The other fourteen showed “messy” sign similar to the three harrier predations that we observed directly but that could also be attributed to ship rats (*Rattus rattus* L.). It should be noted here that Brown et al. (1998) question the utility of sign for identifying nest predators, at least for passerines. Nevertheless, we suspect that harriers were the main predators at our nests both because of sign and because we frequently saw harriers hunting directly over the study site. However, in the absence of conclusive data on the identity of the predators, we cannot be certain of the importance of water levels for driving predation rates on pukeko nests.

Finally, our result may have been caused by something as simple as one or two harriers in our area that adopted a search image for pukeko nests. Because this was not a planned experiment designed to investigate predation, we are unable to make a conclusive statement about the cause of the increase in predation in 1998. It is most plausible, however, that this increase was the result of rabbit-specialist predators seeking out alternative prey as rabbit numbers declined after the 1995 poisoning and 1997 RHD outbreak. We feel that even the possibility that RHD could cause such a dramatic increase in predation at the nests of a native bird species should be of concern to managers and conservationists. More extensive studies are needed to adequately document and quantify this effect and we hope that this note will spur

further investigations into the broader ecological implications, both positive and negative, of RHD in New Zealand.

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Figure 1: *Absolute numbers of hatched, predated and deserted nests by year. None of the nests we observed in 1991 were predated or deserted, so absence of columns does not indicate a lack of data.*

