



Tolerance of female co-breeders in joint-laying pukeko: the role of egg recognition and peace incentives

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Joint laying, where multiple females contribute eggs to a single nest and provide parental care, is a rare breeding system in the avian world. Currently, little is understood about the fitness consequences that joint laying imposes on all members of a cooperatively breeding group, and this is necessary for understanding the evolution of this unusual breeding system. Here, we combine descriptive and experimental studies to understand the costs of joint laying in the pukeko, *Porphyrio porphyrio melanotus*. Our study shows when total clutch size is large (as a result of two females contributing eggs to a joint clutch), a lower percentage of eggs hatch. As a result, joint-laying females were reproductively compromised relative to females that nested singly. Given this apparent cost of joint laying, it is surprising that females tolerate the eggs of co-breeding females. Thus, in a follow-up study, we tested whether female pukeko restrain from ovicide to avoid the risk of retaliation by the co-breeding female (i.e. the peace incentive hypothesis). Females did not retaliate or cease parental care in response to experimental removal of their eggs from joint nests, and thus, we found no evidence to support the peace incentive hypothesis. However, we suggest that the risk of nest desertion, most likely initiated by male partners, may be an indirect cost preventing the evolution of ovicide. This threat of nest abandonment could force primary laying females to tolerate eggs laid by secondary females.

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Animal societies are rife with elements of both cooperation and conflict. While there are often direct and indirect benefits to social living, there also may be substantial costs that can lead to conflict and competition within groups (Davies 1985, 1989; Cockburn 2004). To understand the basis of altruistic and competitive behaviour in cooperative breeders, it is necessary to examine the fitness consequences of social living for all members of a group. The fitness benefits of a particular social structure are likely to differ between dominant and subordinate individuals and also between the sexes (Cockburn 2004; Vehrencamp & Quinn 2004). Therefore, the reproductive interests of all group members are unlikely to be perfectly aligned in social animals, and selection will favour those individuals that best manipulate group dynamics to maximize their own inclusive fitness, even if such behaviours compromise the fitness of other group members. A comprehensive understanding of the costs and benefits of group living is necessary to explain inter- and intraspecific variation in mating systems and social structure.

In many group-living species, reproductive competition (e.g. mate guarding, intrasexual fights, extragroup copulation) is a prevalent and integral component of the social system, but our current understanding of how reproductive conflicts are resolved is limited (Cockburn 2004). There are surprisingly few species for which we understand the fitness consequences that a dominant incurs from subordinate reproduction, but this is an important consideration for understanding group dynamics since it will largely determine the scope for competition within social groups (Bell 2007). If the reproductive success of dominants is negatively affected by subordinate reproduction, then the allocation of reproduction among individuals will be largely dependent on the ability of dominants to disrupt subordinate reproduction (Beekman et al. 2003) and on the mechanisms by which subordinates can subvert dominant control (Hodge 2009). For example, subordinate reproduction can be subverted by infanticide (e.g. Macedo et al. 2004), but this process will only be effective if dominants do not accidentally kill their own offspring and if subordinates do not retaliate by killing the dominant's offspring (e.g. Young & Clutton-Brock 2006). Understanding the manner in which dominants hold power over subordinates is therefore crucial in understanding the evolutionary stability of a particular social system, yet little research has been performed in this regard (Hodge 2009).

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Joint laying is a rare form of cooperative breeding where multiple females contribute to a single nest and share parental care (Vehrencamp & Quinn 2004). In general, little is known about the fitness consequences of joint laying, but reproductive conflict is evident in a number of these species. For example, in the subfamily Crotophaginae, including ani species (*Crotophaga* spp.) and guira cuckoos, *Guira guira*, group members are reported to bury eggs into the nest structure or toss them out of the nest, most likely in an effort to avoid consequences of asynchrony and nestling competition (Vehrencamp 1977; Macedo 1992; Schmaltz et al. 2008; Riehl 2010). Acorn woodpeckers, *Melanerpes formicivorus*, also toss eggs (Mumme et al. 1983; Koenig et al. 1995), and ostrich, *Struthio camelus*, major hens are known to roll eggs laid by minor hens to the exterior of the nest where they are not incubated (Bertram 1992). Reproductive conflict may be prevalent in joint-laying species because of the diverse parentage of the young (Cockburn 2004). Also, the contribution of multiple females to a single nest probably results in a large total clutch, and since offspring survival is generally low in large avian clutches (Lack 1947; Lessels 1991), joint-laying females may prefer a smaller clutch size than is typically generated. Yet, females in some joint-laying species (e.g. Tasmanian native hens, *Gallinula mortierii*: Goldizen et al. 2000; Taiwan yuhinas, *Yuhina brunneiceps*: Yuan et al. 2004) tolerate eggs laid by co-breeders, and it is currently unknown what produces such wide variation in competitive behaviour.

Here, we combine descriptive and experimental studies to examine joint-laying in the pukeko, *Porphyrio porphyrio melanotus*. While the social structure of pukeko groups is variable, many groups are composed of multiple male and female breeders that mate without exclusivity and all contribute to raising a mixed-clutch incubated in a single nest (joint-nesting plural breeders: Craig & Jamieson 1990; Jamieson 1997). Typically, pukeko groups contain one or two breeding females (Craig & Jamieson 1990), although some groups located in the northern parts of North Island, New Zealand, may have more than two (J. Craig, personal communication), and we differentiate between them by using the term primary and secondary, rather than dominant and subordinate, because social hierarchies are not easily observed between females of this species. Currently, there is no evidence of reproductive conflict in pukeko groups of any size (deliberate egg rejection or destruction), despite the fact that joint clutches are significantly larger than single clutches (Jamieson 1997). Thus, the pukeko provides an excellent contrast to other, more competitive joint layers, to investigate how reproductive conflicts are resolved in cooperative breeders.

First, we present a description of how hatching success varies with group composition. We then present the results of a model egg addition experiment designed to determine whether foreign eggs would be accepted into a clutch with only one breeding female, and what influence experimentally enlarging clutch size would have on hatching success. Together, these studies show that primary females tolerate the eggs laid by co-breeders despite a reproductive cost from the addition of the eggs by a secondary female.

In a follow-up experiment, we provide the first test of the peace incentive hypothesis in a social vertebrate (Reeve & Ratnieks 1993). This hypothesis suggests that individuals tolerate reproduction by co-breeders in order to avoid retaliation. Reeve & Ratnieks (1993) found that when eggs from subordinate paper wasps were experimentally dispatched, the subordinate retaliated physically by attacking the dominant female breeder in the nest. In the present study, we similarly removed all eggs laid by one of two females in joint-clutch nests to test whether the female that lost her eggs would withhold incubation, retaliate by destroying the remaining eggs, or direct aggression towards the mother of the remaining clutch. Although our experiments failed to provide evidence

supporting the peace incentive hypothesis, there were a number of nest desertions in experimentally reduced clutches, suggesting an indirect cost of ovicide that may constrain primary females and allow subordinate reproduction.

METHODS

Study Population

This study was performed at the Otokia Wildlife Reserve (45°56'S, 170°10'E), 30 km south of the city of Dunedin in New Zealand. At this site, pukeko live in nonterritorial flocks during the winter and begin to move onto and defend breeding sites in early spring. Males are larger than females and establish and defend territories singly or in groups (range 1–3; Jamieson 1997). Coalitions of males are composed of unrelated members that establish linear dominance hierarchies (judged by postures and aggressive interactions over food; Jamieson et al. 1994; Jamieson 1997). However, males do not show mate-guarding behaviour, and all males copulate frequently with the female(s) on their territory, resulting in shared paternity (Craig & Jamieson 1990; Jamieson et al. 1994). Unrelated plural breeding females (range 1–2; Jamieson 1997) arrive on the territories with the males, and if two females are present, both lay their eggs in a single nest (Jamieson et al. 1994). When eggs are laid in joint nests, the total clutch size is slightly below twice that of single clutches. Both maternity and paternity are distributed relatively equally among breeding adults, and reproductive skew among both females and males is low (Jamieson 1997). DNA fingerprinting has revealed no cases of extragroup fertilization or conspecific brood parasitism and has also failed to show significant differences in paternity as a function of dominance status (Jamieson et al. 1994; Jamieson & Quinn 1997). Males perform all of the nocturnal incubation (Craig 1980a), while both sexes incubate during the day and provision the chicks (Craig & Jamieson 1990; Jamieson et al. 1994).

Field Methods

Field research was carried out over seven breeding seasons from 1990 to 1995 and 1998 to 1999. Observations of copulations, mapping of territory boundaries and banding of adults commenced in early spring of each year when birds are first establishing territories. Suitable breeding sites are associated with the presence of water (pukeko prefer to build their nest in a clump of grass surrounded by water) and vegetative cover for young chicks to hide from their main predator, Australasian harriers, *Circus approximans* (Craig 1980a; Craig & Jamieson 1990). Individuals were caught using funnel and remote-control traps baited with a mixture of corn, wheat and barley, and marked with unique colour combinations using plastic leg bands. Metal and colour bands (M size) were attached to adult birds according to guidelines of New Zealand Department of Conservation's Banding Office. Disturbance associated with trapping was short term, and captured individuals were released within about 30 min of capture. Traps were set during the day and were checked hourly. Prior to release, we took 200 µl of blood from the brachial vein for genetic analysis. For chicks aged 1–2 days, we took 100 µl of blood from the femoral vein. We marked chicks by attaching small 'mouse eartags' to the patagium when chicks were 1–3 days old. We removed the tags with small 'wire-cut' pliers once the birds were recaptured as adults. Neither method of marking showed evidence of impeding normal behaviour. Detailed methods of blood storage and DNA fingerprinting appear in Jamieson et al. (1994) and Quinn et al. (1999). All surrounding pukeko habitat within a 20 km radius of the study area was surveyed annually to monitor dispersal. Only two of 230

banded adults were ever sighted more than 1 km from the study site (I. G. Jamieson, unpublished data).

Daily observations were performed for 2–3 h after dawn throughout the breeding season from two blinds located on hillsides adjacent to the refuge, and from vehicles parked along raised road beds in the area. We found nests by watching for nesting behaviour and by searching suitable habitat. During nest checks, we weighed, measured and photographed new eggs and marked them with nontoxic indelible ink. We also recorded the identity of the incubating bird as it flushed from the nest. Nests were checked every day through the laying sequence and every 3 days thereafter. We examined hatching success of single- and joint-nesting females found on the main study site plus adjacent areas, excluding groups that were manipulated for other research purposes and ones in which whole clutches were lost because of flooding in the study area. When a nest was found in which all the eggs had disappeared or were destroyed, it was scored as 'depredated' if the previous nest check confirmed the birds' continued incubation (either by the presence of a newly laid egg or by the eggs being warm), or as 'deserted' if the previous nest check suggested no incubation was occurring (cold eggs and no new eggs) (Haselmayer & Jamieson 2001).

Animals were handled with care and released soon after handling. Our field methodologies were approved by the University of Otago Ethics Committee (Permit Numbers 67-92, 64-93, 70-98).

Model Egg Addition Experiment

To test the effect of communal nesting on hatching success, we experimentally increased the clutch size in 16 single-clutch nests in 1995. We painted light brown chicken eggs that were similar in size to pukeko eggs so that they superficially resembled their host's eggs, but differed clearly in background colour, spot pattern and shape. We added one model egg to each nest in which females had initiated laying (i.e. nests with one to three eggs), and then added additional model eggs, one per day, for every egg subsequently laid, to attain a simulated clutch size that was larger, but not more than double the female's own clutch size. Manipulated clutches were, on average, 1.9 times as large as our single clutches, which is similar to the natural difference between single and joint clutches (joint clutches were on average about 1.7 times larger). Four nests were abandoned prior to the completion of the egg additions, but when the adults renested a few days later, we added model eggs to increase the clutches, and they were accepted and incubated in three of the four cases. The three renests were included in the experiment. Nests were checked on the same schedule as previously described. We kept records of eggs that were damaged and/or disappeared during the incubation period. Checking of the nests continued until all eggs had hatched. For each egg that hatched, a model egg was removed; after the last chick hatched, any remaining dummy eggs were removed. Because of the limited number of single-female nests available for experimentation on the study area, we compared hatching success of manipulated nests to hatching success of single-female nests from previous years ($N = 26$).

Egg Removal Experiment

During the breeding season of 1998 and 1999, we conducted egg removal experiments on 21 joint nests from 12 territories. Eggs belonging to individual females have distinctive background colour, spot pattern, size and shape (Craig 1980a; Jamieson & Craig 1987; Haselmayer 2000), which allows eggs from a communal clutch to be separated into two clutches laid by different females. We used multilocus DNA fingerprinting to determine the maternity of 18 eggs from four nests to confirm our field separation (Haselmayer 2000). In all cases, only the eggs of one female were removed, and only the

eggs of one female remained in the nest (J. S. Quinn, unpublished data). Whenever possible, we removed each egg on the same day that it was laid, in the early morning. 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. We were interested in assessing whether the response to the loss of all eggs from one female would include increased aggression towards the other female, or destruction of the remaining eggs to initiate renesting. As such, we watched experimental nests for 2–3 h after the dawn egg removal to ensure that the robbed female would be aware of the loss of her eggs while we were watching. We observed the focal group for female–female aggression, egg destruction by either female, and incubation participation of the two females following egg removals. In two cases, we attempted to place a video camera near the nest to monitor postremoval incubation behaviour. However, both groups subsequently abandoned their nest, and since we could not determine whether abandonment occurred as a response to the clutch manipulation or to the presence of the camera, we excluded these nests from the analysis.

Statistical Analyses

Statistical analyses were performed with JMP (8.0.2, SAS Institute, Cary, NC, U.S.A.) and R (2.12.1, the R Foundation for Statistical Computing, Vienna, Austria) with a level of significance (α) of 0.05. Model residuals were visually examined for normality and heteroscedasticity using quantile–quantile and scale–location plots, respectively. When multivariate analyses were performed, the model residuals were checked for normality. When residuals were non-normally distributed, we used nonparametric analyses or transformed the data, as appropriate. We used two separate linear mixed models (LMM) fit with restriction maximum likelihood variance components (Littell et al. 2006) to investigate how group composition affected male and female fitness. In both models, 'year' and 'territory' were included as random factors to account for these potentially confounding variables. In each model we included the number of breeding males and females, as well as an interaction effect between the number of males and females as fixed effects. All variables were centred and scaled as described in Schielzeth (2010) to allow for comparisons of effect sizes and the interpretation of main effects in the presence of interactions (Engqvist 2005). Total clutch size was not included in the model because of multicollinearity with number of females, the latter being a more important variable for this study. The response variables considered were hatching success per adult male (total hatched per nest divided by number of males in group) and hatching success per breeding female (total hatched per nest divided by number of breeding females in group). These measures should reflect male and female fitness since all males mated with all breeding females and both male and female reproductive skew are low (Jamieson et al. 1994; Jamieson 1997).

RESULTS

Number of Breeding Females, Clutch Size and Hatching Success

Total clutch size was larger in nests where two females laid (mean \pm SE = 9.8 ± 0.64 , $N = 14$) compared to nests where one female laid (5.8 ± 0.16 , $N = 30$; Wilcoxon two-sample test: $Z = 4.86$, $P < 0.0001$). Joint clutches took longer to incubate, on average (30.3 ± 0.68 days, $N = 10$), than single clutches (28.8 ± 0.38 days, $N = 28$), but the difference was not significant ($Z = 1.89$, $P = 0.06$). The total number of eggs hatching from a nest was positively correlated with total clutch size (Spearman rank correlation: $r_s = 0.72$, $P < 0.001$; Fig. 1a), but per-egg hatching success declined with total

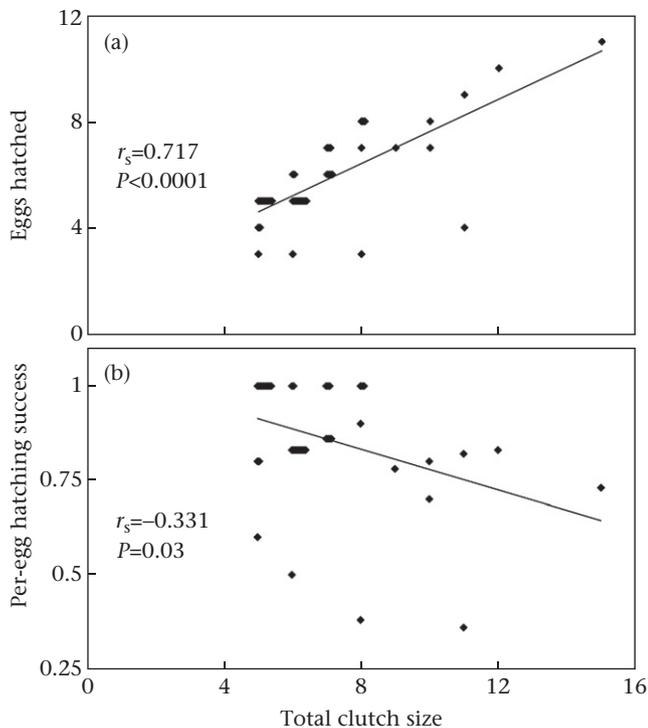


Figure 1. (a) Number of eggs hatched and (b) per-egg hatching success as a function of total clutch size in pukeko nests. Significant correlations, as determined by Spearman rank analysis, are shown with corresponding r_s and P values for each panel. Each data point represents a single nest ($N = 43$). Identical points are offset by 0.05 units on the X axis.

clutch size ($r_s = -0.33$, $P = 0.03$; Fig. 1b). This high percentage of unhatched eggs in joint clutches was primarily the result of eggs being cracked or lost from the nest (67%, N unhatched eggs = 30). As a result of these factors, hatching success was higher (Wilcoxon two-sample test: $Z = 3.21$, $P = 0.001$), but per-egg hatching success tended to be lower ($Z = -1.70$, $P = 0.08$), when joint nests (N total eggs = 130) were compared to single-clutch nests (N total eggs = 174). Hatching success was lower in groups with multiple breeding females (Table 1) but was unaffected by the number of breeding males in the group, and there was no significant interaction effect (Table 1). Conversely, male fitness in the group increased with the number of breeding females (Table 2) and decreased with the number of breeding males (Table 2). Furthermore, there was a significant interaction between the number of male and female breeders on male fitness, with the positive effect of number of females on male fitness being greatest when there were few males.

Model Egg Addition Experiment

To test the relationship between clutch size and hatching success, we experimentally enlarged the clutch size of 16 single-

Table 1
Linear mixed model of factors affecting female fitness (hatching success per female breeder) in pukeko groups

Explanatory variable*	Estimate†	SE	df	F	P
Intercept	-0.07	0.17			
N breeding females	-0.49	0.13	1, 17	15.02	0.001
N breeding males	-0.14	0.12	1, 17	0.82	0.38
Males \times females	-0.16	0.14	1, 17	1.30	0.27

Significant terms are presented in bold.

* Year and territory are included as random effects.

† Parameter estimates are presented with standard errors (SE) and associated F ratios for $N = 43$ nests.

Table 2

Linear mixed model of factors affecting male fitness (hatching success per male breeder) in pukeko groups

Explanatory variable*	Estimate†	SE	df	F	P
Intercept	0.06	0.09			
N breeding females	0.41	0.09	1, 17	6.75	0.02
N breeding males	-0.88	0.09	1, 17	86.46	<0.0001
Males \times females	-0.34	0.10	1, 17	11.54	0.003

Significant terms are presented in bold.

* Year and territory are included as random effects.

† Parameter estimates are presented with standard errors (SE) and associated F ratios for $N = 43$ nests.

clutch nests. Native eggs in experimentally enlarged clutches had substantially lower hatching success compared to unmanipulated single-clutch nests from previous years (mean \pm SE: enlarged clutches: $61 \pm 9\%$, N total eggs = 77; single clutches: $90 \pm 2\%$, N total eggs = 174; Wilcoxon two-sample test: $Z = -2.97$, $P = 0.003$). The introduced model (chicken) eggs were not destroyed or ejected from the experimental nests by the hosts, despite being noticeably different from the native eggs, and did not sustain any cracks or accidental damage (possibly due to their thicker eggshells). By contrast, of the 30 pukeko eggs that did not hatch in experimentally enlarged clutches, 87% ($N = 26$) were cracked/damaged or disappeared. The nature of damage to eggs suggested accidental breakage rather than deliberate destruction. Unhatched eggs of unmanipulated single-female clutches had a much lower percentage of cracked or lost eggs (24%, $N = 17$ eggs; chi-square test: $\chi^2_{1,47} = 18.74$, $P < 0.0001$).

Egg Removal Experiment

Of the 19 joint nests where we removed a single female's clutch, eight groups continued incubating after the egg removals, six were abandoned, with eggs remaining unattended in the nest, and five nests showed signs of predation. In these five latter cases, three showed clear evidence of predation by Australasian harriers (messy nest contents with eggshells scattered) and a harrier was seen at one of those nests eating the eggs. In the remaining two cases, no eggshell fragments remained in the nest; but in one of these nests, a small amount of albumin remained, consistent with predation by mustelids (Moors 1983). Following each experimental egg removal, we saw no behavioural evidence of retaliation (such as egg removal or destruction) by the robbed females or other group members. Considering observations at the nest and this behavioural evidence, we are quite certain that the disappearance of the remaining clutches in these nests was a result of depredation rather than egg destruction by the robbed female.

During 42 h of observations at seven nests that continued incubation (we were unable to observe at the eighth nest), we saw no signs of increased aggression between females and no evidence of either female destroying the remaining eggs. 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. Furthermore, at six of these seven nests, we observed both females incubating the remaining eggs, despite the fact that one female at each nest had no remaining genetic contribution to the clutch. At the remaining nest, we only observed a single incubation bout by one female before the nest was depredated. There was no trend with respect to which female (robbed or nonrobbed) incubated more at the four nests for which we genetically determined which female lost her eggs (mean \pm SE number of incubation bouts: robbed females 8 ± 1.2 ; nonrobbed females 8.25 ± 2.25), although the low sample size precluded statistical analysis.

DISCUSSION

Dominant individuals are expected to evolve a mechanism to control subordinate reproduction if subordinate reproduction is costly to dominants (Bell 2007). However, dominant control of subordinate reproduction may be circumvented if subordinates can respond with retaliatory behaviours (Hodge 2009). When the cost that a dominant incurs from such retaliatory acts exceeds the benefits gained from monopolizing reproduction, a dominant would do better to allow subordinates to reproduce. Thus, the threat of subordinate retaliation can favour the evolution of peace incentives and lead to plural breeding. In our study, the reproductive success of primary female pukeko was lower when a secondary female also contributed eggs to the nest. Furthermore, hatching success was lower in nests in which we experimentally increased the clutch size through the addition of model eggs, suggesting that it is the number of eggs in a nest, rather than any differences in group composition, that is responsible for the low hatching success seen in joint-clutch nests. The majority of unhatched eggs were cracked/damaged or lost during incubation in joint clutches and in experimentally enlarged clutches. Pukeko are known to remove broken eggs from the nest (I. G. Jamieson, personal observation), and when nest predation occurs, the entire clutch is typically depredated; thus, it is likely that eggs noted as lost were also cracked/damaged during incubation. Egg breakage as a result of a large total clutch is probably the primary cost of joint laying to female pukeko.

Since primary females suffer a reproductive cost from the presence of a secondary breeding female, we might expect to see evidence of reproductive competition between co-breeding females. However, deliberate egg tossing or destruction was not observed in this study and appears to be rare, although these behaviours commonly occur in many other joint-laying birds (groove-billed anis, *Crotophaga sulcirostris*: Vehrencamp 1977; acorn woodpeckers: Mumme et al. 1983; guira cuckoos: Macedo 1992; smooth-billed anis, *Crotophaga ani*: Quinn & Startek-Foote 2000; Schmaltz et al. 2008; greater anis, *Crotophaga major*: Riehl 2010; magpie geese, *Anseranas semipalmata*: Frith & Davies 1961; ostriches: Bertram 1992). We investigated whether co-breeding female pukeko refrain from ovicide because they fear physical aggression or retaliatory ovicide by co-breeding females (peace incentives; Reeve & Ratnieks 1993). Our egg removal experiment demonstrated that females do not aggressively retaliate, withhold incubation or destroy the remaining clutch if their clutch is removed. Thus, it seems that primary laying female pukeko do not need to offer peace incentives to avoid direct costs applied by secondary laying females.

Retaliation including egg rejection in response to the loss of a clutch in a joint nest would require the ability to recognize one's own eggs and to distinguish them from the remaining clutch. Researchers are able to recognize differences between eggs and to classify them into clutches from separate laying females (this study; Craig & Jamieson 1990; Haselmayer 2000); therefore, there are sufficient cues for egg recognition. However, pukeko readily accept and incubate foreign eggs (Haselmayer 2000; Dey & O'Connor 2010; this study). Most groups in the egg addition study accepted modified chicken eggs despite the increased risk of breakage to their own eggs. Four groups that initially failed to accept introduced chicken eggs showed no preferential treatment of pukeko versus chicken eggs, but rather abandoned the mixed clutch. In a separate egg addition experiment by Haselmayer (2000), eight single-female clutches were doubled using pukeko eggs from other groups. All eight groups accepted the added eggs and showed no tendency to provide differential positioning of own versus foster eggs within the experimental clutch. Therefore, it

seems that pukeko are unable to recognize their own eggs. This is somewhat surprising given that several confamilial species have evolved egg recognition abilities in response to conspecific brood parasitism (red-knobbed coots, *Fulica cristata*, and lesser moorhens, *Gallinula angulata*: Jamieson et al. 2000; American coots, *Fulica americana*: Lyon 2003, 2007), and joint laying may impose similar selective pressures on pukeko. In fact, only one of the several joint-laying species known to engage in ovicide has been shown to have egg recognition abilities (Bertram 1992) and, therefore, egg recognition is not a necessary pre-adaptation to ovicidal behaviour. While a lack of egg recognition may explain the lack of retaliatory ovicide to the clutch removal experiment in this study, it does not fully explain the lack of ovicide in pukeko. For instance, pukeko females could destroy any eggs that are present in the nest before they start laying their own eggs, although this does not typically occur. Joint clutches are typically laid synchronously (Craig 1980b; Craig & Jamieson 1985), which may allow successful incubation and subsequent care of a large joint clutch laid over a short period while limiting opportunities for egg rejection. Observations of pukeko removing or eating eggs from a nest are rare and typically relate to unincubated eggs. In one case, an egg that was added to an empty nest by a researcher was subsequently destroyed by a female pukeko (I. G. Jamieson, unpublished data). In a second case, two unincubated eggs were destroyed and eaten by a female pukeko 3 days after they were laid (Haselmayer 2000). These are exceptional observations and it appears that deliberate egg destruction is not typical of pukeko behaviour.

Although per-egg hatching success was lower in large clutches in our study, it remains possible that the fitness of female pukeko is not decreased in joint-clutch nests. With the data available, we cannot exclude the possibility that additional parental care provided by a secondary female increases offspring survival in joint-clutch nests; however, there are reasons to believe that this is not the case. Male pukeko perform the majority of incubation and offspring care in pukeko (Craig 1980a), and additional care by females is likely to be of limited importance to chick survival. Furthermore, a previous study on the reproductive success of pukeko noted that pairs fledge a greater percentage of hatched chicks than did groups (Craig 1980a), and thus it seems that additional attending parents fail to increase fledging success. It is also possible that the presence of additional young could dilute the predation risk on the primary female's offspring. Such a predation dilution effect could compensate for a decrease in hatching success if the predation pressure on pukeko chicks is high and the cost of raising additional offspring is low. But given that chicks require diligent parental care to survive, and that starvation and exposure is the main cause of chick death (Craig 1974), it seems unlikely that predation dilution would compensate primary females for the decrease in per-egg hatching success induced by the secondary female.

Primary breeding females apparently are not required to offer peace incentives to secondary breeding females, so why is ovicide not seen in this species? We hypothesize that nest abandonment, which is most likely initiated by incubating male breeders, eliminates the putative benefit gained by females in committing ovicide. In groups with multiple male and female breeders, the additional eggs provided by a secondary breeding female may be required to ensure that each breeding male gains sufficient paternity to invest in parental care (see Hamilton & Heg 2007 for a model of how clutch size might affect male parental care and competition). Also, relatively synchronous laying by two group females, as is typical for joint-nesting pukeko, results in a large clutch that will hatch relatively synchronously, hence reducing complications arising from the need to simultaneously incubate eggs and care for precocial chicks over a prolonged period. Males invest heavily in incubation,

including all nocturnal incubation and chick rearing (Craig 1980a). Since renesting occurs quickly when clutches are lost (I. G. Jamieson, personal observation), males might be selected to abandon reduced clutches that provide low reproductive potential in favour of a replacement joint clutch. Such behaviour by males could eliminate the selective pressure for egg recognition evolution, since even if females could recognize their own eggs, the marginal benefit of ovidice would be overcome by the costs associated with increased risks of nest desertion. A recent experimental study found a decline in incubation constancy and a trend towards increased desertions in joint nests from which secondary clutches were removed (C. Dey, C. M. O'Connor, S. Balshine & J. S. Quinn, unpublished data), providing support for the hypothesis that ovidice is not favoured because of the risk of reduced paternal care.

It is not possible to entirely dismiss the possibility that such abandonments are initiated by the secondary female that lost her clutch. This possibility seems less likely than initiation by breeding males in these groups for a number of reasons. First, females incubate only during the day, so the absence of an incubating female would be detected quickly by other group members. Second, females are responsible for a minority of the incubation and none of the nocturnal incubation; thus, the withdrawal of one female incubator seems unlikely to force desertion of the group. Therefore, it would appear to be unlikely that a single female would be able to initiate desertion without cooperation by the breeding males. Egg destruction would appear a more effective option, but we have not observed this.

The removal of one clutch from a joint nest may initiate nest desertion. This desertion risk would probably exceed expected benefits from increased hatching success in the remaining clutch. Such a risk does not represent the direct costs normally associated with the peace incentive hypothesis (Reeve & Ratnieks 1993) but rather represents indirect costs that may restrain the evolution of selective ovidice.

Conclusions

In pukeko, joint laying seems to impose a fitness cost on primary breeding females due to an increase in accidental egg breakage in large clutches. Despite this cost, intentional egg destruction is not a common behavioural strategy used by females to monopolize group reproduction. Because female pukeko do not distinguish their own eggs from those laid by co-breeders and they do not retaliate when their clutch is removed from a joint nest, it seems that classic peace incentives between co-breeding females are not important in maintaining plural breeding in this species. However, we suggest that the failure to engage in selective ovidice is due to constraints on such a strategy imposed by the threat of reduced care or nest abandonment in response to a reduced total clutch size. Thus, the tolerance of breeding by secondary females is probably driven by the threat of nest abandonment and may represent an incentive paid by the primary breeding female to group males in return for parental investment in the group offspring.

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