

Testing reproductive skew models in a communally breeding bird, the pukeko, *Porphyrio porphyrio*

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SUMMARY

Recent attempts to explain variation among social species in the degree to which reproduction is shared among group members have focused on what are known as reproductive skew models. Reproduction within social groups can vary from an even distribution among all adults (i.e. low skew) to complete monopolization by a dominant individual (high skew). Three critical predictions derived from these models have remained largely untested: (1) reduced chances of independent breeding due to strong ecological constraints results in high reproductive skew; (2) the lower the genetic relatedness within social groups the lower the skew; and, counter-intuitively, (3) dominance-related aggression will be more prevalent in social groups composed of close kin where reproductive skew is predicted to be high. Here I test these predictions by comparing two populations of the communally breeding pukeko (*Porphyrio porphyrio*), which show extremes in social organization, namely social groups consisting of close kin versus groups made up of unrelated breeders. I report evidence from both cobreeding males and females in support of the above predictions. The results also indicate that low reproductive skew among unrelated group members may be prevalent in social species that possess weapons that can inflict serious injury in situations where reproductive competition may escalate to fighting. The consistency between these results and those from studies of social insects suggests that reproductive skew models may represent a unifying framework for understanding the factors shaping complex animal societies.

1. INTRODUCTION

A fundamental feature that differentiates complex animal societies is the degree to which reproduction is shared among group members. Reproduction within social groups can vary from an even distribution among all adults (i.e. low skew) to complete monopolization by a single individual (high skew). Attempts to explain the variation in the degree to which reproduction is shared have focused on what are known as reproductive skew models that have as their basic assumption that dominant individuals control the reproduction of subordinates (Emlen 1982*a*; Vehrencamp 1983; Keller & Vargo 1993; Reeve & Ratnieks 1993; Keller & Reeve 1994). The models identify several parameters, such as the intensity of ecological constraints on the opportunity to disperse and breed independently and relatedness of group members, that affect the degree to which reproduction will be skewed within social groups. For example, a dominant gains leverage over a subordinate within its group with increasing ecological constraints on successful dispersal. The subordinate still obtains inclusive fitness benefits if it is closely related to the breeders in its group, but if it is not related then a larger reproductive inducement will be required by the subordinate to either remain in the group or stop it from engaging the dominant in a fight for reproductive control of the group. Therefore, the models predict that reproductive skew should be highest where

ecological constraints on dispersal are greatest and social groups are comprised of close relatives, and lowest where ecological constraints are minimal and social groups are comprised of unrelated breeders (Vehrencamp 1983; Keller & Reeve 1994; Emlen 1996).

Reproductive skew models also predict that the dominance-related interactions should be more common in high-skew societies where the greater disparity in relative breeding success should make subordinates more likely to challenge the dominant, resulting in the dominant exerting more effort in suppressing the subordinates. When skew is low, the reproductive reward for challenging the dominant and winning his position is smaller, thus interactions between cobreeders are expected to be fewer. Therefore, dominance-related aggression is expected to be more prevalent in social groups that are under strong ecological constraints and, counter-intuitively, comprise close relatives (Keller & Vargo 1993; Reeve & Ratnieks 1993; Bourke & Heinze 1994; Keller & Reeve 1994).

Recent interest in reproductive skew models has come primarily from researchers working on polygynous social insects, with the aim of explaining variation in skew across species (e.g. Bourke & Heinze 1994; Heinze 1995; Reeve & Keller 1995). Social vertebrates are of particular interest to reproductive skew models because they often exhibit intraspecific variation in sociality, and groups can be composed of

Table 1. *Comparison of group size and composition for the Otokia and Shakespear populations*(Values are means \pm s.e. with ranges given in brackets.)

	Otokia (<i>n</i> = 46 group-years)	Shakespear (<i>n</i> = 28 group-years)
average group size	2.9 \pm 0.14 (2–5)	7.1 \pm 0.49 (3–12)
average number of males and females in each group		
breeding males	1.5 \pm 0.10 (1–3)	3.3 \pm 0.23 (2–7)
breeding females	1.3 \pm 0.07 (1–2)	1.8 \pm 0.08 (1–2)
helper males	0	0.6 \pm 0.12 (0–2)
helper females	0.09 \pm 0.06 (0–2)	1.3 \pm 0.26 (0–5)
percentage of various breeding units		
monogamous pairs	41	0
polygynous trios	13	0
polyandrous trios	33	21
polygynandrous groups	13	79

both multiple-female and multiple-male breeders. Such social systems allow questions to be asked about whether males and females are affected differently by the ecological and behavioural factors affecting reproductive skew.

This study attempts to test reproductive skew models using a socially variable, communally breeding bird. The purple swamphen, or pukeko (the New Zealand Maori name), is a large gallinule common to marshy areas throughout south-east Asia, Africa, Australia and New Zealand. In New Zealand, where they have been studied most extensively, pukeko exhibit a variable mating system but commonly live in communal groups consisting of two breeding females that share a single nest with several breeding males as well as non-breeding helpers of both sexes (Craig & Jamieson 1990). A long-term study of one population at Shakespear Park, located on the North Island of New Zealand, found that territories were occupied and defended by large social groups of 6–9 birds comprised of two breeding females, 3–4 breeding males and 1–3 helpers, all of which were close kin (Craig & Jamieson 1988, 1990). Another long-term study recently completed at Otokia on the South Island of New Zealand has revealed a very different pattern of social organization in the pukeko. In this population, monogamous pairs were common along with small social groups consisting of 1–2 breeding female and 2–3 breeding males with almost no helpers (table 1); in this case, group members were non-kin (Jamieson *et al.* 1994).

These two populations represent extremes in a continuum of social organization and therefore are ideal for testing predictions from reproductive skew models. In particular, they should allow us to identify the ecological and life history conditions under which reproduction becomes either more or less skewed

among social group members. In this respect, the models predict that reproductive skew should be much less in the Otokia population where groups comprise unrelated breeders only and ecological constraints are considered to be moderate to weak (see §3). Skew should be much greater in the Shakespear population where the greater degree of habitat saturation has led to low levels of dispersal and the formation of kin groups with non-breeding helpers.

However, a higher skew at Shakespear would be expected simply because groups are larger and contain non-reproductive helpers. If helpers are excluded and a difference in reproductive skew among breeders is still evident between the two populations, this would suggest that overall differences in skew between these two extremes in social organization is not simply due to the presence or absence of non-breeding helpers. Comparisons between these two study populations should, therefore, provide a strong test of the versatility of reproductive skew models as a framework for explaining the nature of diverse social organizations in the pukeko as well as other social vertebrates.

2. STUDY AREA AND METHODS

A population of pukeko located at Shakespear Regional Park, approximately 25 km north of Auckland on the northern half of the North Island of New Zealand, was studied over seven breeding seasons between 1979 and 1985. A second population at Otokia Wildlife Reserve, located 30 km south of the city of Dunedin on the southern part of the South Island of New Zealand, was studied over five breeding seasons from 1990 to 1994. Detailed descriptions of these study sites and the methods used to capture, mark and observe birds, and to determine dominance status are published elsewhere (Jamieson & Craig 1987a; Craig & Jamieson 1988, 1990; Jamieson *et al.* 1994).

Unless otherwise noted, data were analysed on a group-year basis. Group membership changed substantially from year to year at Otokia (Jamieson *et al.* 1994), but was much more stable at Shakespear, although overall group composition changed through mortality and the recruitment of juvenile and yearling helpers to breeders (see below). Where same-sex individuals within a group remained the same from one year to the next, data were averaged over those group-years.

Keller & Vargo (1993) and Reeve & Ratnieks (1993) developed an index to quantify the degree of reproductive skew which varied from 0 (reproduction is evenly distributed among all group members) to 1 (reproduction is monopolized by a single individual). However, Pamilo & Crozier (1996) showed that the formula used to estimate skew had statistical characteristics inherent in it that led to discontinuities in an otherwise linear relationship. To address this problem, they derived a new formula for reproductive skew (*S*):

$$S = (N_T - Q_E) / (N_T - 1),$$

where N_T is the total number of potential breeders and Q_E is the 'effective number' of breeders defined as $Q_E = 1 / \sum p_i^2$, where p_i is the reproductive contribution of the *i*th breeder. I use this formula to calculate the reproductive skew of each group-year and average these values to derive a population estimate. I defined 'potential' breeders as any male or female two years of age or older (Craig & Jamieson 1990).

Female reproductive skew was estimated in both populations based on the number of eggs laid by each female in a communal clutch. Nests were checked on a daily basis during the laying period and new eggs were numbered as they were laid. Eggs belonging to individual females have distinctive background colours and spot patterns, as well as sizes and shapes, that allows eggs in communal nests to be assigned to one female or another (Craig 1980; Jamieson & Craig 1987a; I. Jamieson, unpublished data). Male reproductive skew in Otokia was calculated based on the number of offspring fathered by each male as determined by DNA fingerprinting (for details of methods see Jamieson *et al.* (1994)). The study at Shakespear was completed before molecular techniques to determine paternity had been developed. John Craig, Dave Lambert and their associates from Auckland University initiated a molecular parentage study on pukeko in 1989, but had to conduct it on Tiritiri Matangi Island (about 1 km from Shakespear) because the Shakespear population had crashed for unknown reasons. The Tiritiri Matangi population exhibits comparable group structure and composition to that of Shakespear (I. Jamieson, unpublished data) and molecular analyses showed group members to be related (Lambert *et al.* 1994). Therefore, for this paper, male reproductive skew (S) for pukeko breeding in groups comprised of closely related individuals was estimated from the paternity and group composition data presented in Lambert *et al.* (1994).

Means and standard errors are given throughout the paper and statistical analyses follow that of Zar (1984).

3. RESULTS

(a) Comparison between populations of extent of ecological constraints on dispersal

The Shakespear population showed all the signs of 'habitat saturation' (Emlen 1982b; Brown 1987), whereas Otokia did not. At Shakespear, the number of adults per territorial group per year was significantly greater than Otokia (7.1 ± 0.35 , $n = 7$ years versus 3.0 ± 0.19 , $n = 5$; t -test, $t = -8.4$, $p < 0.001$), marginal habitat was occupied by territorial groups and territories were defended all year round (Craig & Jamieson 1990). Both male and female juveniles remain on their natal territory as helpers, and eventually become breeders within their group, resulting in unusually high levels of relatedness among breeders (Craig & Jamieson 1988; Lambert *et al.* 1994). In contrast, birds were resident throughout the year at Otokia but form non-territorial flocks over winter. Unrelated males and females come together to form small groups and establish breeding territories each spring. A few areas within the main study site remained unoccupied in some years, although territories with dense vegetative cover (high quality sites) were always occupied and defended by groups with 2–3 males. Juveniles disperse from their natal territory before breeding commences the following season and some birds breed as yearlings (Jamieson *et al.* 1994). Annual survival of territorial adults peaks at two years of age at Otokia compared to over five years at Shakespear (I. Jamieson, unpublished data), resulting in a significantly higher annual turnover of resident territorial adults at Otokia ($35.5\% \pm 6.3$, $n = 4$ years) than at Shakespear ($12.3\% \pm 4.4$, $n = 6$) ($t = 2.8$ (arcsine transformation), $p < 0.05$). Thus ecological con-

straints on dispersal were considered to be strong for Shakespear and weak to moderate for Otokia. These differences in adult mortality rates between the two populations are presumably caused by the harsher climatic conditions over winter at Otokia (I. Jamieson, unpublished work).

(b) Reproductive skew in multi-male and multi-female groups

According to reproductive skew models, the Otokia population, with its weaker ecological constraints and unrelated group members, should show the lowest reproductive skew. At Otokia, 96 offspring from 15 broods were fingerprinted, and all broods were fathered by resident breeding males (see Jamieson *et al.* 1994). Similarly, all six broods with 31 offspring were fathered by resident males at Tiritiri Matangi (Lambert *et al.* 1994). The average skew index for unrelated males at Otokia was less than half of the value for kin groups at Tiritiri Matangi, but the difference was not significant although sample size was small for the latter population (table 2). The higher skew value for Tiritiri Matangi results in part from a portion of the potential breeders being non-reproductive helpers. If helpers are excluded from the calculation, the skew index for Tiritiri Matangi is reduced but is still higher than the index for Otokia (table 2).

Skew is very low for group-breeding females at Otokia (0.04) and significantly lower than group-breeding females at Shakespear (0.42) (table 2). The skew index is reduced substantially for females at Shakespear if non-copulating helpers are excluded, but the difference between the two study populations is still significant (table 2). Although it was generally not known which female (dominant or subordinate) laid which eggs, further analysis revealed that the average proportion of eggs of the female that laid the most eggs in each communal clutch was significantly lower at Otokia (0.56 ± 0.01 , $n = 14$) than at Shakespear (0.61 ± 0.02 , $n = 15$) (Mann–Whitney U -test; $U = 159$; $p < 0.05$), but the average total clutch size of communal nests was much larger at Otokia (9.8 ± 0.68 , $n = 14$) than at Shakespear (6.6 ± 0.58 , $n = 13$) ($U = 152.5$, $p < 0.005$). Communal clutches were, on average, 1.8 times as large as single female clutches in Otokia but only 1.4 times as large for related females at Shakespear. In over 35% of the communal nests at Otokia, each female laid more eggs than the median clutch size of single females. This suggests that unrelated communally nesting females at Otokia may have been competing by trying to outlay each other, while at Shakespear maximum egg production by one of the females, presumably the subordinate, appears to have been suppressed.

(c) Comparison between populations of dominance-related behaviour

Reproductive skew models also predict that dominance-related interactions should be more frequent in high-skew societies where the subordinate has more to gain and the dominant more to lose relative to low-skew societies (Keller & Reeve 1994). Thus we

Table 2. *Comparison of reproductive skew indices for the Otokia and Shakespear (including Tiritiri Matangi) populations*

(Formula for calculating skew index is given in §2. Paternity data for the Shakespear population were unavailable and thus data from an adjacent population at Tiritiri Matangi are used to calculate the skew indices for males (in square brackets). These data are taken from Lambert *et al.*'s (1994) House Group (figure 4) and Upper Dam Group (figure 6), which were each sampled over three years, with the following modifications: the alpha male in the House Group achieved the highest percentage of copulations (out of a total of four adult males) but fathered 0/14 offspring over a three-year period. Similarly, the beta male in the Upper Dam Group (total of three adult males) copulated frequently but fathered 0/17 offspring over three years. In both cases the chances of fathering no offspring over three years is extremely low and thus the males were possibly sterile. Including these two males would have increased the skew for the Shakespear population and therefore they were omitted from the calculations. Values are means \pm s.e. and were compared statistically using the Mann–Whitney *U*-test.)

	Otokia	Shakespear [Tiritiri Matangi]	<i>p</i> values
reproductive skew in multi-male and multi-female groups			
males	0.25 \pm 0.08 (12)	[0.58 \pm 0.12 (6)] ^a	> 0.10
females	0.04 \pm 0.01 (14)	0.42 \pm 0.09 (18)	< 0.001
reproductive skew excluding helpers			
males	0.25 \pm 0.08 (12)	[0.39 \pm 0.13 (6)] ^a	> 0.10
females	0.04 \pm 0.01 (14)	0.17 \pm 0.09 (16)	< 0.05

^a Averaging the skew indices over three years for each of the two groups produced similar results.

should expect behaviour by which the dominant individual suppresses subordinates to be more prevalent at Shakespear than at Otokia. Alpha males are highly tolerant of mating behaviour by other breeding males within their group at Shakespear and at Otokia (Jamieson & Craig 1987*a*; Jamieson *et al.* 1994), perhaps reflecting the low reproductive skew among breeding males in both populations (see above). However, at Shakespear 11 dominant males interrupted copulations of subordinate males while only one subordinate did the same to a dominant (binomial test ($p_0 = 0.5$), $p < 0.05$). At Otokia, by contrast, seven dominant males interrupted copulations of subordinate males and five subordinates interrupted copulations involving dominant males ($p > 0.10$). Moreover, the dominant and subordinate males within groups at Otokia were more likely not to interrupt a copulation than they were to interrupt it (Wilcoxon paired-sample test, $T_+ = 27$, $n = 7$ groups, $p < 0.05$), although when they did, there was no significant difference between dominant and subordinate males in the proportion of interrupted copulations (Fisher's exact tests, $p > 0.10$ for seven groups).

Another more subtle form of interference by alpha males occurred within groups at Shakespear. An alpha male would sometimes redirect subordinate males away from a receptive female by exhibiting a female receptive posture in front of the males and allowing one to mount and copulate with him (Jamieson & Craig 1987*b*); such behaviour was never observed at Otokia.

Differences between the two populations in female dominance-related behaviour were much the same as for males. Communally laying females did not interrupt each other's copulations in either population. At Shakespear, however, alpha females asserted their dominance by mounting and copulating with beta females, a behaviour they exhibited only during the egg laying period (see Jamieson & Craig 1987*b*). Similar female–female mounting behaviour was never observed at Otokia and dominance interactions between communal females were extremely rare (I.

Jamieson, personal observation). Egg ejection from communal nests did not occur in either population, and despite females having distinctly coloured eggs, recent model egg experiments on single female nests indicate that once a female initiates laying she does not distinguish her own eggs from those added by another female (I. Jamieson, unpublished data).

4. DISCUSSION

A basic premise of reproductive skew models is that if subordinate group members could have higher reproductive success by breeding solitarily, then they should disperse. Therefore, the models explain the extent to which dominant group members skew reproduction in their favour in terms of the ecological constraints on subordinates breeding independently, the relatedness of subordinates to the dominant breeder and their relative fighting abilities (Vehrencamp 1983; Keller & Reeve 1994; Emlen 1996). Reproductive skew was greater, as predicted, in kin groups of pukeko that were under strong ecological constraints and previous studies had indicated that alpha females generally lay more eggs than beta females (Craig 1980; Jamieson & Craig 1987*a*). However, available fingerprinting data for estimating skew among males in the Tiritiri Matangi population were too few (two groups' samples over three years) and incomplete to determine whether reproduction was skewed in favour of alpha males; this aspect needs further study in the pukeko. Nevertheless, a related prediction that relatively large same-sex coalitions can form only when groups are comprised of close kin because large groups have inherently higher variance in mating success (Packer *et al.* 1991) was upheld. Non-kin groups at Otokia never had more than three breeding males whereas kin groups at Shakespear often had four or more reproductively active males (table 1).

Reproductive skew models also predict that dominance interactions should be more prevalent in high-skew societies because of the greater disparity in

relative breeding success (Keller & Reeve 1994). I had no quantitative data to compare the rates of dominance interactions between the two populations, but alpha males and females appeared to assert their dominance more readily at Shakespear, and dominant and subordinate individuals seemed to be more evenly matched at Otokia. However, the wording of Keller and Reeve's prediction suggests that in groups with high skew, subordinates are expected to physically challenge or test dominant individuals more often, and dominants are expected to react with suppressive behaviour. Alpha males and females asserting their dominance over subordinate individuals was observed in the Shakespear population, but challenges or testing behaviour by subordinates were not. Dominance assertion in itself could lead to higher skew rather than being a consequence of high skew. This distinction needs to be examined more closely in the future when testing the predictions of skew models dealing with dominance interactions.

The low level of dominance interactions among group-breeding males at Otokia may arise because high quality territories are codefended by high quality males (I. Jamieson, unpublished data), which are presumably of similar age and fighting ability. Although a dominance hierarchy is established, the alpha male may be unwilling to risk injury by confronting the beta male. Males do the majority of territorial defence in pukekos (Craig & Jamieson 1990) and have extremely powerful beaks and legs and sharp claws that they use in fighting. Fights between territorial groups can sometimes become protracted with participants incurring serious injury (I. Jamieson, personal observation). Thus mutual breeding tolerance among unrelated males within a group could be seen as a form of 'peace incentive' (Keller & Reeve 1994) resulting in low reproductive skew; competition for paternity of offspring taking on more subtle forms such as high frequencies of copulation (Jamieson *et al.* 1994). Shared reproduction among unrelated individuals may be prevalent in social species such as lions (*Panthera leo*) (Packer *et al.* 1991), Galapagos hawks (*Buteo galapagoensis*) (Faaborg *et al.* 1995) and several social insects (Keller & Reeve 1994), all of which possess weapons that can inflict serious injury in situations where reproductive competition can escalate to fighting.

In the females' case, the lack of response by the alpha to the beta's eggs in her nest may partly be a result of constraints on egg recognition rather than any form of peace incentive. In *Polistes* wasps, for example, enhanced aggression by the subordinate toward the dominant queen when the subordinate's eggs are experimentally removed from a nest indicates that females can recognize their own eggs and may explain why natural egg removal by dominant queens is rare in such species (Reeve & Novacs 1992). In the pukeko, however, once an unrelated beta female gains access to the alpha female's mates and nest site, the alpha female would have few options but to share her nest. Estimates of lifetime reproductive success at Otokia indicate that the net benefits of group breeding are much lower for females than for males, and therefore different factors

are influencing the tendency for dominants of either sex to share reproduction with subordinates (I. Jamieson, unpublished data).

In conclusion, reproductive skew models have been widely heralded as providing a general unifying framework for investigating factors shaping complex societies in both vertebrates and invertebrates (Vehrencamp 1983; Bourke & Heinze 1994; Keller & Reeve 1994; Emlen 1996). However, most of the interest in using these models has come from those aiming to explain inter-species variation in queen number and related social behaviour among Hymenoptera insects. This application of the models to explain inter-population variation in social structure and behaviour in a vertebrate should not only help bridge the gap between these two groups of researchers, but also illustrates that within-species variability in social behaviour is predictable based on skew models.

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