Higher reproductive skew among birds than mammals in cooperatively breeding species

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While competition for limited breeding positions is a common feature of group life, species vary widely in the extent to which reproduction is shared among females ('reproductive skew'). In recent years, there has been considerable debate over the mechanisms that generate variation in reproductive skew, with most evidence suggesting that subordinates breed when dominants are unable to prevent them from doing so. Here, we suggest that viviparity reduces the ability of dominant females to control subordinate reproduction and that, as a result, dominant female birds are more able than their mammal counterparts to prevent subordinates from breeding. Empirical data support this assertion. This perspective may increase our understanding of how cooperative groups form and are stabilized in nature.

Keywords: reproductive skew; cooperative breeding; dominance; subordinate; animal societies; sociality

1. INTRODUCTION

In cooperatively breeding species, where individuals receive assistance in the production of young (Brown 1987), reproduction may be shared more or less equitably among the females in a group (Keller & Reeve 1994; Magrath *et al.* 2004). Although several theoretical models providing adaptive explanations for variation in skew have been developed (see Johnstone & Cant 2009 for a review), empirical tests of these models are relatively rare. Moreover, most empirical studies of reproductive skew have focused on testing the predictions of skew models rather than assessing the validity of the underlying assumptions, which is problematic as small perturbations to the assumptions of the model can strongly affect the predicted outcome (Hodge 2009).

Existing reproductive skew models make distinct assumptions regarding the level of control attributed to individuals within the group. Determining which set of assumptions is likely to best reflect reality is crucial in order to interpret empirical data within the most appropriate theoretical framework. Transactional models assume that one individual in the group has

complete control over reproduction but shares reproduction, either to prevent others from leaving (Vehrencamp 1979, 1983) or to prevent others from evicting it (Johnstone & Cant 1999). Compromise models, on the other hand, assume that no individual has full control over reproduction. Instead, the extent of reproductive skew is the outcome of a conflict between dominants and subordinates in which neither is able to enforce their own optimum (Clutton-Brock 1998; Reeve *et al.* 1998). Compromise models were proposed as a more plausible alternative to transactional models, on the grounds that attributing complete control over reproduction to one individual is unrealistic (Clutton-Brock 1998; Nonacs 2007; Johnstone & Cant 2009). However, rigid empirical evidence supporting the key assumption of compromise models—that subordinates are more likely to breed when dominants are unable to prevent them from doing so—is scarce.

Here, we suggest that the ability of dominant females to control subordinates might depend on whether the species is oviparous or viviparous and that this might generate variation in reproductive skew. For example, in birds, a single female could monopolize breeding by preventing other females from accessing the nest during the laying period (e.g. Dickinson *et al.* 1996; Whittingham *et al.* 1997). In contrast, internal gestation in mammals may make it harder for a single female to prevent others from breeding. The extent to which female birds and mammals are able to control subordinate reproduction might then influence the extent of reproductive sharing, with subordinate female mammals being more likely to breed than subordinate female birds. We test this hypothesis using data from 58 cooperatively breeding species.

2. MATERIAL AND METHODS

Data from a total of 58 cooperatively breeding species (37 bird species from 18 families, 21 mammal species from 12 families) were available (see the electronic supplementary material for more information). Reproduction was said to have been monopolized when the dominant female was the mother of more than 95 per cent of offspring born into a group, although the model was also checked using 90 per cent and 99 per cent, respectively, as the threshold values. To control for repeated effects on the distribution of the data, we carried out a linear mixed model (LMM) with 'family' included as a random term. The response term was binary (1 = dominant female monopolizes reproduction; 0 = reproduction shared among more than one female in the group) and the model was fitted to a binomial error distribution with a logit-link function. 'Taxon' (bird/mammal) was included as the sole explanatory term.

3. RESULTS

Dominant female birds are more likely than dominant female mammals to monopolize breeding, by producing more than 95 per cent of the offspring within a group (LMM: $\chi^2_{1,57} = 11.4$, $p = 0.0007$; figure 1). Similar differences are present if the threshold value is increased to 99 per cent (LMM: $\chi^2_{1,57} = 8.96$, $p = 0.003$); or reduced to 90 per cent (LMM: $\chi^2_{1,57} = 4.91$, $p = 0.03$). The significant effect of family was controlled for in all three models (95% threshold: $\chi^2 = 4.25$, $p = 0.039$; 99% threshold: $\chi^2 = 3.93$, $p = 0.047$; 90% threshold: $\chi^2 = 4.34$, $p = 0.037$).

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Figure 1. The mean proportion ($\pm$ s.e.m.) of bird and mammal species in which one female produces >95% of all offspring.

4. DISCUSSION

Models of reproductive skew make distinct assumptions about the extent to which dominants are able to prevent subordinate breeding. Here, using data from 58 cooperatively breeding species, we show that skew among female mammals is lower than among female birds and suggest that this variation may be attributed to asymmetries in control. Specifically, we propose that internal gestation (rather than egg-laying) makes it harder for female mammals to prevent other females from breeding. This finding better supports the assumptions of compromise models (where dominants have limited control over subordinates) than those of transactional models.

There are several reasons why the mode of reproduction might be expected to influence the control that dominant females can exert over subordinates. Oviparity in birds means that females can often prevent subordinates from breeding by defending access to a nest (Dickinson *et al.* 1996; Whittingham *et al.* 1997). Conversely, viviparity in mammals makes it more difficult for a single female to monopolize breeding as she must often police several females rather than defending a single breeding site. This typically involves preventing subordinates from conceiving, evicting pregnant subordinates or killing their offspring (e.g. Creel & Waser 1997; Clutton-Brock *et al.* 1998). A dominant female that evicts a subordinate faces not only energetic costs and the risk of injury but also reduces the pool of available carers to help with her own breeding attempts. This is not the case for birds, where dominant females can remove any eggs she suspects were laid by subordinates without evicting the perpetrators (e.g. Bertram 1979). Although birds risk making recognition errors when tossing eggs, the same risks are also faced by mammals that commit infanticide. Indeed, the cost of inadvertently killing one's own offspring may be substantially increased in mammals compared with birds by increased investment during the gestation period and, in some species, infanticide only occurs when the female can be sure that any pups she kill are not her own (e.g. Digby 1995; Clutton-Brock *et al.* 1998).

Data from bird species where males do the bulk of incubation support the idea that the extent of female control influences reproductive sharing within the group. Where males incubate the clutch, females are

less able to maintain exclusive access to the nest (Haydock & Koenig 2002). As such, joint nesting (where multiple females lay in the same nest) is more common in species with male-biased incubation (Vehrencamp 2000). In some species, subordinate females occasionally breed by laying their eggs in a separate nest to the dominant female (Williams 2004; Berg 2005). Although such plural nesting may be harder for dominant females to prevent, it is relatively rare: just four of the 37 (10.8%) bird species in our dataset were plural-nesting species, while 29.7 per cent were joint-nesting species. The occurrence of plural nesting may be limited by food and habitat availability (Brown 1987; Hatchwell & Komdeur 2000). Furthermore, secondary females' nests are often less successful than those of dominants (Curry 1988; Williams 2004; Berg 2005), perhaps owing to interference by dominants (Curry 1988) and because secondary females commonly receive little or no assistance from auxiliaries (Langen & Vehrencamp 1999). This is not the case for mammals, where evidence suggests that helpers do not preferentially feed the dominant female's offspring (e.g. Clutton-Brock *et al.* 2001).

Although variation in the mode of reproduction seems to be a viable explanation for variation in skew among birds and mammals, there is a plausible alternative. It is possible that dispersal patterns affect the availability of unrelated breeding partners for subordinates and, consequently, the extent to which reproduction is shared among group members. Specifically, female-biased dispersal in birds (Greenwood 1980) might mean that subordinate females rarely have access to unrelated males on the natal territory and so rarely attempt to co-breed alongside the dominant female (see Koenig *et al.* (2009) for a discussion of incest avoidance and reproductive skew). A subordinate female mammal, on the other hand, may regularly encounter and mate with unrelated males that either visit or immigrate into her group (e.g. Young *et al.* 2007). Thus, rather than being harder to control, subordinate female mammals may simply have more opportunities to breed. Although we cannot refute this alternative, we would argue that incest avoidance falls short as an explanation for the variation in skew observed between birds and mammals. Firstly, although inbreeding is typically avoided, this is not universally so (e.g. McRae 1996; Koenig & Haydock 2004; Spottiswoode & Møller 2004). Secondly, female birds may conduct extra-territorial forays to find preferred mates, meaning that they are not constrained to mate only with the males in their home territory (e.g. Double & Cockburn 2000). To conclude, although dispersal patterns and concomitant incest avoidance do not seem to account fully for variation in skew between birds and mammals; more empirical data to assess the link between incest avoidance and reproductive sharing would certainly be useful.

An understanding of the mechanisms that generate skew is essential if we are fully to grasp how cooperative groups form and are maintained in nature. Although variation at the level of the group or species may often be attributed to ecological, social and genetic parameters (Clutton-Brock 1998; Reeve *et al.* 1998; Faulkes & Bennett 2001), higher level taxonomic

variation in reproductive skew may well be explained by differences in reproductive physiology. The extent to which dominant females can control subordinate reproduction might then be expected to have important, broad-scale effects on intra-group conflict, life-history traits and population dynamics in cooperatively breeding birds and mammals.

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