

Kinship and Incest Avoidance Drive Patterns of Reproductive Skew in Cooperatively Breeding Birds

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ABSTRACT: Social animals vary in how reproduction is divided among group members, ranging from monopolization by a dominant pair (high skew) to equal sharing by cobreeders (low skew). Despite many theoretical models, the ecological and life-history factors that generate this variation are still debated. Here I analyze data from 83 species of cooperatively breeding birds, finding that kinship within the breeding group is a powerful predictor of reproductive sharing across species. Societies composed of nuclear families have significantly higher skew than those that contain unrelated members, a pattern that holds for both multimale and multifemale groups. Within-species studies confirm this, showing that unrelated subordinates of both sexes are more likely to breed than related subordinates are. Crucially, subordinates in cooperative groups are more likely to breed if they are unrelated to the opposite-sex dominant, whereas relatedness to the same-sex dominant has no effect. This suggests that incest avoidance, rather than suppression by dominant breeders, may be an important proximate mechanism limiting reproduction by subordinates. Overall, these results support the ultimate evolutionary logic behind concessions models of skew—namely, that related subordinates gain indirect fitness benefits from helping at the nests of kin, so a lower direct reproductive share is required for selection to favor helping over dispersal—but not the proximate mechanism of dominant control assumed by these models.

Keywords: dominance, genetic relatedness, inbreeding, kin selection, reproductive bias, social evolution.

Introduction

Cooperatively breeding animals live in social groups in which several individuals provide parental care to a single brood of young (Brown 1987; Cockburn 1998). Across species, breeding groups vary widely in the extent to which reproduction is shared among group members. At one end of the continuum are groups in which a few individuals reproduce, assisted by nonreproductive group members (high

skew); at the other end are groups in which most or all group members reproduce and cooperatively provide parental care (low skew). In birds, high-skew societies contain one breeding pair and nonbreeding “helpers” that provide alloparental care to the pair’s nestlings, whereas low-skew societies contain several adult breeders that produce young in a shared nest and cooperatively provide care to the mixed clutch of nestlings (Magrath and Heinsohn 2000; Vehrencamp 2000). Intermediate between these two extremes are cooperative groups in which reproduction is unequally shared among cobreeders—for example, in which an ostensibly nonreproductive helper male sires a minority of nestlings in a dominant’s nest or a helper female lays a minority of eggs. Understanding the sources of variation in reproduction among group members is crucial to understanding why animals live in social groups and remains a central focus of studies of the evolution of cooperative breeding (Raihani and Clutton-Brock 2010; Alberts 2012; Green et al. 2014; Chak et al. 2017).

Many theoretical models have been developed to provide adaptive explanations for variation in reproductive skew within and across species. Skew models attempt to optimize the fitness payoffs to a group member as a function of several life-history variables, including the effect of cooperation on the group’s productivity, options for independent breeding outside the social group, genetic relatedness to other group members, and competitive ability (reviewed in Johnstone 2000; Magrath et al. 2004; Buston et al. 2007; Reeve and Shen 2013). These models, as well as their attendant tests, typically refer to breeding individuals as “dominants” and nonreproductive individuals as “subordinates” for the sake of simplicity, even though behavioral dominance interactions may not be obvious in all cases. Different types of models differ primarily in their assumptions about how dominants and subordinates interact, variously assuming that (1) dominants have complete control over subordinate reproduction (“concessions” models; Vehrencamp 1983*a*, 1983*b*), (2) dominants cannot prevent subordinates from reproducing but can evict them from the social group (“restraint”

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models; Johnstone and Cant 1999), or (3) dominants and subordinates directly compete for reproduction and their respective shares are primarily determined by competitive ability (“compromise” models; Clutton-Brock 1998; Reeve et al. 1998). The goal of these models is to understand how reproduction is divided among group members of the same sex—for example, under what circumstances two males might sire offspring in the same brood and the optimal reproductive share that maximizes the inclusive fitness of each.

Empirical tests of skew models have largely focused on predicted correlations between reproductive skew and genetic relatedness within a single species, partly because genetic relatedness is relatively easy to quantify in natural populations and partly because different submodels of skew theory make contrasting predictions regarding the effect of relatedness on reproductive skew. Concessions models, inspired by Vehrencamp’s (1983*a*, 1983*b*) original optimal skew model, predict that reproductive skew should increase with relatedness of the dominant to the subordinate: since related subordinates gain indirect fitness benefits by helping kin, they should require a relatively smaller direct fitness benefit to remain with the social group than unrelated subordinates do. By contrast, restraint models predict that reproductive skew should decrease with increasing relatedness within the social group since dominants should gain greater inclusive fitness by sharing reproduction with relatives than with nonkin (Johnstone and Cant 1999). Compromise models predict variable correlations between relatedness and reproductive skew, depending on the assumptions of the specific model and the degree of relatedness being considered (Johnstone 2000); however, all else being equal compromise models generally predict that skew should either not vary with kinship or decrease with increasing relatedness (Reeve et al. 1998; Nonacs 2007).

Within-species tests of these predictions have yielded conflicting results. In social insects, some studies have found positive correlations between genetic relatedness and reproductive skew, which have been interpreted as support for concessions models (Keller and Reeve 1994; Reeve and Keller 1995; reviewed in Reeve and Keller 2001), whereas others have found either no correlation between skew and relatedness or a negative correlation (Field et al. 1998; Seppä et al. 2002; Sumner et al. 2002; Langer et al. 2004; Hammond et al. 2006). In social vertebrates, very few studies have found support for concessions models (but see Jamieson et al. 1997), whereas there is widespread evidence that group members compete directly for reproduction, consistent with compromise models (Clutton-Brock et al. 2001; Haydock and Koenig 2003; Widdig et al. 2004; Heg et al. 2006; Cant et al. 2014). Because it is difficult to quantify and compare the other parameters that are essential to reproductive skew models, such as the severity of ecological constraints on independent breeding, it is not clear whether this diversity poses a

challenge to current theory or simply represents the range of outcomes predicted by existing models.

Current skew models share two assumptions, both of which have been widely criticized (Magrath and Heinsohn 2000; Cant and Reeve 2002; Nonacs and Hager 2011). The first is that the division of reproduction is solely determined by interactions between same-sex group members, even though some studies have found that opposite-sex group members can also influence reproductive share (e.g., via female control of paternity; Williams 2004; Ostner et al. 2008). The second is that inbreeding avoidance does not influence mating decisions within social groups—a potentially unrealistic assumption since many cooperatively breeding animals breed in family groups (Emlen 1995, 1996; Koenig and Haydock 2004). If the availability of unrelated mates limits reproduction by subordinates, then incest avoidance could drive patterns of reproductive skew similar to those predicted by concessions models (e.g., Cooney and Bennett 2000). In birds, for example, if a male helper is genetically related to the only female breeder in a cooperative group, that male cannot sire young in the nest unless he mates incestuously with his relative. If selection favors inbreeding avoidance, high levels of relatedness in social groups could lead to high reproductive skew regardless of whether the dominant can actively control subordinate reproduction.

To date, the only interspecific analysis to examine correlations between reproductive skew and genetic relatedness across social vertebrates was performed by Koenig et al. (2009), who found that reproductive skew for both males and females in cooperatively breeding groups of birds tended to be higher when cobreeders were closely related. This result is consistent with concessions models, which predict that reproductive skew should increase with relatedness of the dominant to the subordinate. However, because Koenig et al. (2009) included several variables other than genetic relatedness, this analysis was based on a small sample size (14 species), and it is not known whether this correlation holds across cooperatively breeding birds. Furthermore, it is unclear whether the proximate mechanism limiting reproduction by related subordinates is suppression by the dominant breeder, as assumed by concessions models, or incest avoidance, which could lead to the same pattern.

My goal in this study was to build on Koenig et al.’s (2009) analysis, examining the relationship between relatedness and reproductive skew in all 83 cooperatively breeding species for which genetic information is available. I used data from the published literature to ask three questions. First, across species, is reproductive sharing more or less common in groups that contain nonrelatives compared with those that are family based? Second, within species, are unrelated subordinates more or less likely to gain parentage in the clutch than are related subordinates? Third,

is subordinate reproduction primarily influenced by kinship with the opposite-sex dominant or the same-sex dominant? If patterns of reproductive skew are driven largely by incest avoidance, then subordinates should be less likely to breed when they are related to the opposite-sex dominant. By contrast, if skew is driven primarily by competition over reproduction, then subordinate reproduction should be influenced by kinship with the same-sex dominant.

Methods

Data from a total of 83 cooperatively breeding bird species from 42 families were included in the analyses (table A1; tables A1, S1–S6 are available online). Genetic data on both kinship within the cooperative group and reproductive skew were required for inclusion, with three exceptions: white-winged trumpeters (*Psophia leucoptera*), for which information on reproductive activity was obtained from direct laparotomy (Sherman 1995); greater rheas (*Rhea americana*), for which reproductive sharing by females was confirmed by the appearance of multiple eggs in the same nest on the same day (Fernandez and Rebores 1998); and dusky moorhens (*Gallinula tenebrosa*), for which recently fledged offspring act as helpers and are presumed to be reproductively immature (Putland and Goldizen 2001). Species were drawn from Riehl's (2013) global review of cooperative breeding in birds, and accounts were updated to include additional genetic information published since 2013.

Following Raihani and Clutton-Brock (2010), reproduction within the social group was considered to be monopolized when a single group member was the father or mother of at least 95% of offspring in a clutch. Following Riehl (2013), cooperative groups were considered to be kin based when more than 80% of groups in the population were composed of nuclear families or when more than 80% of helpers or cobreeders in the population were genetic relatives of the breeding pair. Cooperative groups were considered to have a mixed kin structure when at least 20% of subordinates were unrelated to any of the other breeders in the social group and at least 20% of subordinates were first-order kin of one of the breeders in the social group, such that groups in the study area commonly included both related and unrelated subordinates. Finally, groups were considered to be composed of nonrelatives when more than 80% of subordinates (or cobreeders) were unrelated to other breeders in the social group, such that a minority of group members were genetic relatives.

The first set of analyses examined whether genetic relatedness within the social group predicts reproductive skew across species. To control for phylogenetic effects, I constructed mixed effects logistic regression models with family included as a random term. The response term (repro-

ductive skew) was binary (1 = reproduction monopolized by a single individual; 0 = reproduction shared by multiple group members), and the sole explanatory term (kinship) was also binary (1 = kin-based cooperation; 0 = nonkin-based or mixed kin structure, as defined above). Separate analyses were run to predict reproductive skew in multimale groups (79 species in 38 families) and in multifemale groups (49 species in 30 families).

The second set of analyses examined whether within a species genetic relatedness between a subordinate and the breeding pair influences the likelihood that the subordinate shares parentage in the clutch. To answer this question, I used a subset of 26 species that breed in cooperative groups containing both related and unrelated subordinates (groups with a mixed kin structure, as defined above). Such an analysis would ideally quantify the proportion of young produced by related and unrelated subordinates in each group or the population-wide proportion of subordinates that are reproductively active, but these data are available for very few species. Therefore, I instead asked whether related or unrelated subordinates are more likely to achieve parentage within the social group by using mixed effects logistic regression models with breeding status as the binary response variable (0 = nonbreeding, 1 = reproductive) and subordinate sex (male or female) and relatedness to either member of the breeding pair as explanatory variables. Species was included as a random effect (with subordinate sex, relatedness, and breeding status nested within species), but family was not included as a random effect in this analysis because the 26 species were drawn from phylogenetically diverse clades (20 families).

Finally, the third set of analyses investigated whether a subordinate's likelihood of reproducing is differentially influenced by its genetic relationship to the same-sex breeder or to the opposite-sex breeder. If subordinate reproduction is primarily constrained by competition with other group members, then relatedness to the same-sex dominant should be a significant predictor of whether the subordinate breeds, whereas the opposite pattern is predicted if subordinate reproduction is constrained by incest avoidance. To distinguish between these alternatives, I used mixed effects logistic regression models to ask whether a subordinate's breeding status (0 = nonbreeding, 1 = reproductive) is significantly influenced by its relatedness to the same-sex breeder, to the opposite-sex breeder, or to either breeder. Binary predictors included subordinate sex, kinship to same-sex breeder, kinship to opposite-sex breeder, and kinship to either breeder. The full data set of 83 species was used for this analysis. Species was included as a random effect in all models because for many societies with mixed kin structures data were available on the breeding status for both male and female subordinates or for subordinate breeding status with both related and unrelated opposite-

sex and same-sex breeders. Best-fit models were selected using a “best-subsets” approach in which initial models included all terms and were compared with all possible models using subsets of the terms. Models were evaluated with Akaike’s information criterion corrected for finite sample size (AIC_c; Burnham and Anderson 2002). Models within two AIC_c units of the top model ($\Delta AIC_c = 0$) were candidates of potential explanatory value; however, models within two AIC_c units of the top model that differed from a higher-ranking model by the addition of one parameter were rejected as uninformative, as recommended by Arnold (2010). Analyses were conducted in STATA 14, and statistical significance was set at $\alpha = .05$.

Results

Reproductive Skew across Species

Across species, a single dominant individual is more likely to monopolize reproduction in social groups composed of nuclear families than in those that include nonrelatives (fig. 1a). Mixed effects logistic regression models revealed a significant effect of kinship on reproductive skew for both males ($z = 4.52, P < .0001; n = 79$ species) and females ($z = 2.03, P = .04; n = 49$ species; table 1). Both models had high overall statistical significance, indicating that kinship alone is a significant predictor of reproductive skew (male skew: Wald $\chi^2 = 20.46, P < .0001$; female skew: Wald $\chi^2 = 4.14, P = .042$). The random effect of family was sig-

nificant in the model predicting female skew (likelihood ratio $\chi^2 = 3.87, P = .02$) but was not significant in the model predicting male skew (likelihood ratio $\chi^2 = 0.42, P = .26$). Rerunning the model for male skew as a simple logistic regression (excluding family) led to qualitatively identical results: reproductive monopolization by a single male is significantly more likely in kin-based groups ($z = 5.20, P < .0001$). Overall significance for this model was also high (likelihood ratio $\chi^2 = 42.25, P < .0001$). Full model details are presented in tables S1–S3.

Reproduction by Related and Unrelated Subordinates within Species

Data were available for 26 species in which breeding pairs are regularly attended by both related and unrelated subordinates (male-only subordinates in six species and subordinates of both sexes in 20 species). Within species, unrelated subordinates were more likely to gain parentage in the clutch than were related subordinates ($z = -3.01, P = .003$; table 2). Initial models included subordinate sex as a predictor of breeding status, but this variable was not significant ($z = 0.92, P = .36$) and was dropped from the final model. Therefore, when groups contain female subordinates they are as likely to gain parentage in cooperative groups as male subordinates are, and unrelated subordinates of either sex are more likely to reproduce than related subordinates are. Full model details are presented in tables S4 and S5.

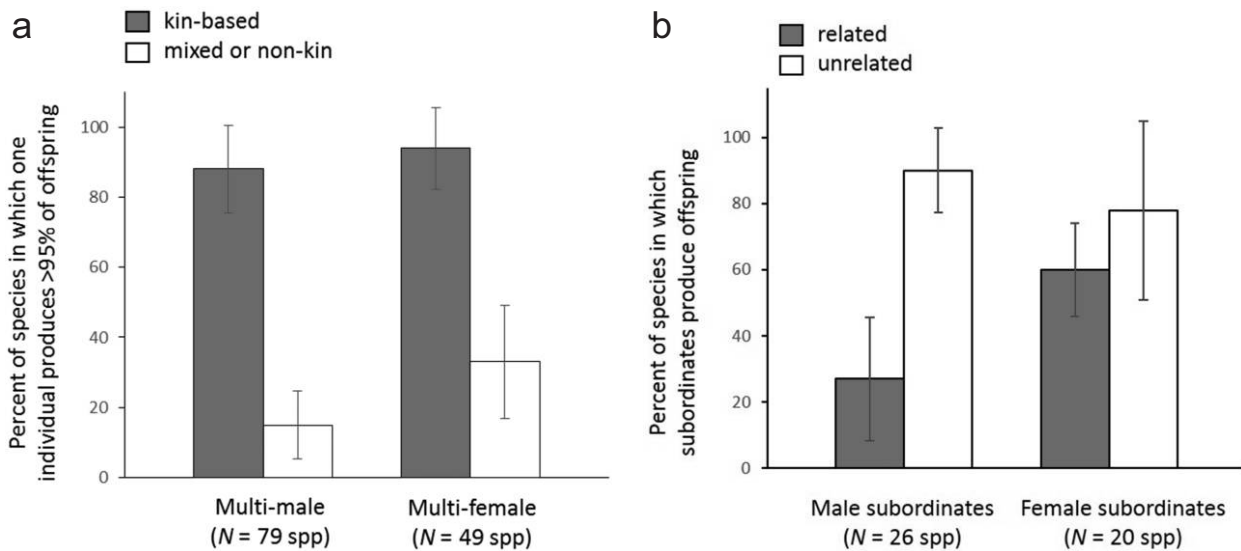


Figure 1: a, Percentage ($\pm 95\%$ confidence interval) of species in which one individual monopolizes reproduction by producing $\geq 95\%$ of offspring in the clutch, for males in multimale social groups and for females in multifemale social groups. b, Percentage ($\pm 95\%$ confidence interval) of species in which male and female subordinates produce offspring with respect to the subordinate’s genetic relatedness to the dominant breeder of the opposite sex.

Table 1: Mixed effects logistic regression models to determine whether kinship predicts reproductive skew among males in multimale groups and among females in multifemale groups

	Coefficient	SE	<i>z</i>	<i>P</i>	95% CI
Male reproductive skew					
Fixed effects:					
Kinship	4.01	.88	4.52	.000	2.27 to 5.76
Intercept	-1.87	.49	-3.78	.000	-2.85 to -.91
Random effects:					
Family	.43	.80			.011 to 16.37
Female reproductive skew					
Fixed effects:					
Kinship	5.12	2.51	2.03	.04	.186 to 10.06
Intercept	-.91	.87	-1.04	.30	-2.61 to .806
Random effects:					
Family	6.52	8.63			.487 to 87.20

Note: CI = confidence interval.

Subordinate Relatedness to Same-Sex Breeder and Opposite-Sex Breeder

Using the full data set of 83 species, subordinate group members were significantly less likely to reproduce when genetically related to the opposite-sex dominant breeder (fig. 1*b*). The best-fit model predicting a subordinate's breeding status contained kinship to the opposite-sex dominant as the sole predictor (table 3; $AIC_c = 138.2$). Candidate models with kinship to the same-sex dominant or to either dominant as the sole predictor were rejected ($AIC_c = 170.7$ and 161.4 , respectively). Furthermore, including both kinship to the same-sex dominant and kinship to the opposite-sex dominant did not improve model fit ($AIC_c = 137.0$), and kinship to the same-sex dominant was not a significant predictor in this model ($P = .126$). Similarly, candidate models containing subordinate sex and/or the interaction between subordinate sex and kinship to the opposite-sex group members did not improve model fit, and these variables were dropped from the final best-fit model. Therefore, both male and female subordinates are less likely to reproduce when related to the opposite-sex dominant breeder, but genetic relatedness to the same-sex breeder

has no significant effect. Full model details and model selection are presented in table S6.

Discussion

Although a rich body of theory has been developed to predict the partitioning of reproduction in animal societies, surprisingly few empirical analyses have examined large-scale patterns that emerge across species. Using data from 83 cooperatively breeding bird species, I show that reproductive skew is significantly higher in species that breed in nuclear family groups than in those with mixed kin structures and that unrelated subordinates are more likely to gain parentage in the cooperative clutch than are related subordinates (regardless of subordinate sex). Genetic relatedness between the subordinate and the opposite-sex breeder appears to be the primary driver of this pattern, not relatedness between the subordinate and the same-sex breeder. These findings confirm and extend the preliminary analysis of Koenig et al. (2009), who also found a positive correlation between genetic relatedness and reproductive skew in avian cooperative breeders, and they

Table 2: Final mixed effects logistic regression model to determine whether a subordinate's relatedness to the breeding pair predicts likelihood of gaining parentage in the clutch for species in which a dominant breeding pair is regularly assisted by both related and unrelated subordinates

Subordinate breeding status	Coefficient	SE	<i>z</i>	<i>P</i>	95% CI
Fixed effects:					
Relatedness to breeding pair	-2.57	.86	-3.01	.003	-4.25 to -.90
Intercept	2.03	.71	2.86	.004	.64 to 3.41
Random effects:					
Species	.33	.98			.00 to 116.2

Note: CI = confidence interval.

Table 3: Final mixed effects logistic regression model to determine whether a subordinate's relatedness to the opposite-sex breeder in the social group predicts likelihood of gaining parentage in the clutch

Subordinate breeding status	Coefficient	SE	<i>z</i>	<i>P</i>	95% CI
Fixed effects:					
Relatedness to opposite-sex breeder	-4.55	1.13	-4.03	.000	-6.76 to -2.33
Intercept	2.44	.72	3.37	.001	1.02 to 3.85
Random effects:					
Species	4.50	3.10			1.17 to 17.39

Note: Including subordinate sex, relatedness to same-sex breeder, and/or the interaction between subordinate sex and relatedness with the opposite-sex breeder did not improve model fit and were dropped from the final model. CI = confidence interval.

suggest that incest avoidance may be an important proximate mechanism limiting subordinate reproduction.

With respect to theoretical models of reproductive skew, these data support the predictions of early concessions models of skew—that reproductive skew should increase with relatedness in the social group—but not the assumption that dominant control is the proximate mechanism enforcing this pattern. At the ultimate level, concessions models and their variants predict that, when related subordinates are unable to breed independently (due to ecological constraints or a lack of reproductive opportunities), helping at the nest of a relative is a best-of-a-bad-job strategy. The subordinate gains some indirect fitness benefits by raising relatives, so helping is favored over dispersal even if the helper does not breed directly. But why shouldn't the subordinate maximize its inclusive fitness by attempting to reproduce in the same clutch along with its relatives? Skew theory essentially assumes that subordinates would reproduce if the same-sex dominants let them, so egg ejection by females and interference in mating attempts by males have been invoked as potential behaviors by which dominants could suppress subordinate reproduction. Incest avoidance is, potentially, a more parsimonious explanation for the same pattern: raising full siblings instead of one's own offspring are equivalent strategies from an inclusive fitness perspective, but raising inbred offspring should be costly for both subordinate and dominant members. Subordinate reproduction should therefore not be favored by natural selection, and physical suppression or domination is not necessary. Regardless of the mechanism by which subordinate reproduction is limited, the key predictions of skew theory (and kin selection) still hold: related subordinates gain indirect fitness from helping at the nests of kin, so helping is favored over dispersal when independent breeding opportunities are limited.

The results of this analysis suggest two additional questions relevant to understanding the division of reproduction in cooperative groups and the evolutionary stability of these groups. First, how should theoretical models incorporate incest avoidance to better predict the reproductive opportunities of group members? Second, given the widespread occurrence of alternative reproductive strategies in

birds, such as extragroup mating, how can theoretical models of reproductive skew more accurately capture the total inclusive fitness of group members?

Incest Avoidance

Although many empirical studies have now documented incest avoidance and called for its incorporation into models of reproductive skew (e.g., Cooney and Bennett 2000; Blackmore and Heinsohn 2008; Nelson-Flower et al. 2012; Van Dijk et al. 2015), opinions differ on whether avoidance of incest should be considered separately or included in skew models. Models of skew have thus far assumed that there is no constraint on incest (mating with first-order kin) or inbreeding (mating with more distant kin; Koenig and Haydock 2004), here collectively referred to as incest. Magrath et al. (2004) suggested two potential ways in which current models could be modified to incorporate incest. First, the effects of inbreeding depression on the realized fitness of group members could be directly incorporated into current skew models by assuming that inbred young have lower prospects of survival and/or reproduction. This would lower the realized reproductive output of subordinates that mate incestuously, leading to the paradoxical expectation that skew should actually be lower when cobreeders are related and mating with one another. However, this situation seems to occur only rarely in birds. Of the limited set of cooperatively breeding species in which subordinates breed despite being related to the opposite-sex group member, incest is a regular occurrence in only three species, and there is direct or indirect evidence for negative fitness consequences in all three (table 4).

Alternatively—and more realistically—related subordinates might avoid incest altogether. There is now substantial empirical evidence for learned kin recognition in birds, with many studies finding that individuals appear to gauge genetic relatedness by a simple rule of thumb: nestlings learn to recognize caregivers in early life and subsequently avoid mating with them regardless of actual genetic relationships (reviewed in Riehl and Stern 2015). In cooperative breeders that form nuclear family groups, group mem-

Table 4: Cooperatively breeding bird species in which subordinates routinely reproduce in the group's clutch despite being genetically related to the opposite-sex dominant breeder

Species	Subordinate sex	Incest/inbreeding?	Fitness cost?	Source(s)
<i>Acrocephalus seychellensis</i>	Female	Yes (5%); subordinates mate with male relatives; reduced by extragroup mating	Indirect; lower output by inbred females	Richardson et al. 2004
<i>Gallinula chloropus</i>	Female	Yes (22%); subordinates mate with fathers	Yes; lower survival of nestlings	McRae 1996
<i>Gymnorhina tibicen</i>	Female	No; female subordinates mate with extragroup males	NA	Durrant and Hughes 2005
<i>Calocitta formosa</i>	Female	No; female subordinates mate with extragroup males	NA	Berg 2005
<i>Cracticus nigrogularis</i>	Female	No; female subordinates mate with extragroup males	NA	Robinson 1994
<i>Corvus brachyrhynchos</i>	Male	Yes (2%); male subordinates mate with mothers	Yes; higher disease risk	Townsend et al. 2009a, 2009b
<i>Monias benschi</i>	Male	Possible, not confirmed	Indirect; lower output by inbred males	Seddon et al. 2004, 2005

Note: In instances where incest (mating with first-order kin) or inbreeding (mating with more distant kin) was documented, percentages represent the percentage of offspring genotyped that were the product of such pairings. NA = not available.

bership serves as a proxy for kinship. It is therefore likely that subordinates are capable of assessing their relatedness to dominant breeders—at least the crude judgement of “family” versus “not family”—and that this assessment influences mate choice. Since this type of incest avoidance appears to evolve readily in birds, in family-based societies there may be little selective pressure for costly mechanisms of reproductive suppression, such as physical domination or physiological suppression.

There is similarly strong evidence that individuals generally do not mate with close relatives even when their overall reproductive success would be higher by producing inbred young than by failing to reproduce altogether (Koenig et al. 1998). In many species included in the data set presented here, subordinate males fail to reproduce when related to the breeding female, but the same individuals will breed if the relative is replaced by an unrelated female (Rabenold et al. 1990; Mullner 2004; Webster et al. 2004; Brouwer et al. 2011). This again suggests that suppression by the same-sex breeder (in this case, the breeding male) is relatively less important than the availability of unrelated mates. By contrast, related female subordinates could avoid incest and contribute eggs to a clutch by mating with an unrelated extragroup male, but this situation appears to be relatively uncommon (table 4). To a first approximation, therefore, excluding related subordinates as potential breeders does a reasonably good job of predicting patterns of reproductive skew in birds,

although incest and extragroup mating pose complications in a subset of species.

Reproductive Skew and Inclusive Fitness

By definition, reproductive skew models assume that the reproductive output of each group member is limited to the group's shared brood. This assumption, like the assumption that incest avoidance can safely be ignored, is more likely to hold in some taxa than others. In birds, both males and females can increase their direct fitness by contributing offspring to other groups—females by laying parasitically in extragroup nests, and males by extragroup fertilizations (Koenig et al. 2009). Both strategies (especially the latter) are widespread in birds, and in some cooperative species included in this data set they significantly increase the direct fitness of subordinates (Robinson 1994; Hughes et al. 2003; Berg 2005; Brouwer et al. 2011).

The ability to produce young outside the social group could be incorporated into reproductive skew models as a potential benefit to subordinates, similar to other direct fitness benefits of group membership (such as increased survival) that are not captured by measures of reproductive skew but that still may favor group formation. Kokko and Johnstone (1999), for example, considered the possibility that subordinates gain future reproductive benefits through group membership (via territory or dominance inheri-

tance) rather than solely the inclusive fitness of the current brood. Their dynamic model, which incorporated the probability that the subordinate would live to the next breeding season and subsequently inherit the dominant's breeding position, found that the possibility of future fitness benefits greatly increased the range of conditions in which high reproductive skew was evolutionarily stable: subordinates were more likely to stay with groups even when unable to reproduce. Incorporating the possibility that subordinates might gain access to mating opportunities outside the social group should, similarly, predict higher levels of reproductive skew within the social group.

In conclusion, this analysis suggests that interspecific analyses of patterns of reproductive skew across species can be useful not only in identifying correlations between factors such as relatedness and skew but also in testing hypotheses for the proximate mechanisms driving these correlations. An interspecific approach might also prove fruitful across taxa, including cooperatively breeding mammals and social insects. These groups vary widely in mechanisms of reproductive suppression, genetic structuring, and group size, providing fertile ground for broad-scale meta-analyses.

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A communal nest of greater anis (*Crotophaga major*) containing 10 eggs laid by three unrelated females. Photo credit: Christina Riehl.