Patterns of Reproductive Skew in the Polygynandrous Acorn Woodpecker

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ABSTRACT: We compared observed levels of reproductive skew in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*) with those predicted by two alternative transactional models. "Concession" models predict the degree to which parentage is shared assuming that a single dominant is in complete control of reproduction. Alternatively, "restraint" models predict reproductive sharing assuming that the dominant controls only whether subordinates remain in the group but does not control its share of reproduction. Reproductive skew is high among males: on average, the most successful male sires more than three times as many offspring as the next most successful male. Females share parentage equally and have lower constraints on dispersal and lower survival rates compared with males, which is consistent with predictions from the concessions model. Also as predicted by the concessions model, yearly variation in opportunities for dispersal before the breeding season correlates positively with skew. However, in contrast to concessions but consistent with the restraint model, skew decreases with relatedness. Thus, neither model consistently predicts patterns of reproductive skew in this species. We suggest that models of reproductive skew will need to include competitive interactions among potential breeders and mate choice before they will adequately predict patterns of reproductive partitioning in most vertebrate societies.

Keywords: acorn woodpecker, *Melanerpes*, cooperative breeding, parentage, inclusive fitness, reproductive skew.

Reproductive skew is low when breeding success is similar among group members of the same sex, whereas high skew

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results when a single individual parents most or all of the offspring in a group. Explaining the adaptive significance of variation in reproductive skew within social groups is currently a focus of empirical research and theoretical modeling on eusocial species (Emlen 1996; Cant 1998; Clutton-Brock 1998; Reeve et al. 1998; Vehrencamp 2000; Clutton-Brock et al. 2001; Reeve and Keller 2001).

Most recent skew models as well as the original conceptualization of reproductive skew (Vehrencamp 1979, 1983*a*, 1983*b*) assume that a single dominant is in complete control of reproduction and that dominants induce subordinates to stay in the group by offering them reproductive concessions. These models have been variously referred to as "concessions," "incentives," "optimal skew," or "complete control" models. In contrast, alternative "restraint" models suggest that dominants have limited or incomplete control (Cant 1998; Clutton-Brock 1998; Reeve et al. 1998; Johnstone 2000) in that they only have the ability to evict a subordinate from the group if the subordinate garners too large a share of reproduction. Both types of models consider constraints imposed by group stability since they attempt to explain the amount of subordinate reproduction that is predicted to preclude the subordinate from dispersing and breeding independently (Johnstone 2000). The concessions-based models predict that the dominant's inclusive fitness is increased above what would be obtained if the subordinate left the group and that the subordinate's inclusive fitness would be just greater than what could be obtained by independent breeding. In restraint models, the dominant is expected to do only just better than he or she could by evicting the subordinate, and the subordinate is predicted to reproduce to the level that is just below the "eviction threshold." Thus, in the concessions model, incentives given by the dominant maintain group stability, whereas in the restraint model, groups are maintained because the subordinate restrains its own reproduction, thus avoiding eviction.

The concessions and restraint models represent two extremes of reproductive skew necessary to promote group stability, with qualitatively differing predictions. Most models of both types have considered only two potential

breeders. However, models that consider three individuals have been developed, with generally similar predictions assuming decreasing benefits of additional cobreeders (Johnstone et al. 1999).

Concessions models always predict that reproductive success of dominants should be higher and, thus, that there will be greater skew than in restraint models. Fitness benefits for dominants and subordinates are calculated in relation to ecological constraints on independent breeding, the benefits of group living, the genetic relatedness of the subordinates to the dominant, and the relative fighting ability of the potential breeders (Vehrencamp 1979, 1983*a*, 1983*b*; Reeve and Ratnieks 1993; Reeve et al. 1998).

Acorn woodpeckers (*Melanerpes formicivorus*) offer one of the best opportunities to test alternative models of reproductive skew among vertebrates. In contrast to many cooperative breeders in which groups consist of monogamous pairs along with their adult offspring, acorn woodpeckers have a polygynandrous mating system in which several potential breeders of each sex can contribute genetically to the communal nest. There is variation in the level of relatedness among potential breeders and differences in the benefits of group living between the males and females. Furthermore, ecological constraints on dispersal vary both among years and between males and females, providing yet another means to test alternative models of reproductive skew.

Here we determine reproductive skew based on 6 yr of molecular data (Haydock et al. 2001) and qualitatively contrast observed patterns with those predicted by skew theory based on group stability. Elsewhere (Haydock and Koenig 2002), we have quantitatively tested these models for groups limited to two breeders of either sex. Here our goal is to qualitatively test these models using our complete data set including groups with three or more potential breeders. Specifically, we examine whether the concessions model or the restraint model better predicts intrapopulation differences in reproductive skew between segments of the population experiencing different levels of kinship and ecological constraints.

Methods

Study Population

Acorn woodpeckers have been studied continuously since 1972 at the Hastings Natural History Reservation located in central coastal California (MacRoberts and MacRoberts 1976; Koenig and Mumme 1987; Koenig et al. 1998). More than 3,500 individuals have been marked with individually identifiable color leg bands; currently, the study population consists of about 40 groups and 200 adults. Social groups of acorn woodpeckers range from genetically monoga-

mous pairs (Dickinson et al. 1995) to cooperatively polygynandrous groups with cobreeding males, joint-nesting females, and nonreproductive helpers (Haydock et al. 2001). Mean $\pm$ SE group size is 4.4 ± 0.1 individuals, but groups can have as many as 15 adults during the breeding season, including up to seven males and three females with breeding status (Koenig and Mumme 1987). Regardless of the number of breeders in a group, there is only one active nest on a territory, except in rare cases when a second nest is initiated just before fledging of an earlier nest. In addition, females that share breeding status will sometimes simultaneously lay eggs in two cavities, but eventually one of these nests invariably is abandoned, and both females will subsequently lay jointly in a single cavity.

Our classification of breeder status versus helper status is based on genetically confirmed incest avoidance (Koenig et al. 1998; Haydock et al. 2001). Among breeders, we recognize two categories of individuals, both of which may be present in a single group: single-sex coalitions of siblings that have immigrated into a territory following a reproductive vacancy (Hannon et al. 1985) and helpers that have ascended to breeding status on their natal territory, following an opposite-sex reproductive vacancy. In the latter case, all adult helpers present in a group and of the opposite sex than the vacancy ascend to become potential breeders, along with their same-sex parent and/or same-sex parent's relative. Helpers of the same sex as the coalition of recent immigrants normally leave after the new breeders have become established, presumably because of reduced fitness benefits and possibly reproductive competition (Koenig et al. 1998). All progeny produced on a territory by the breeders are assigned helper status and normally do not attain breeder status until an opposite-sex reproductive vacancy and subsequent replacement has taken place.

Up to three males or females have been shown to share parentage at a single nest (Haydock et al. 2001), and up to four males have shared breeding when combining consecutive nests produced during one or more years by the same set of males (J. Haydock, unpublished data). It is more common for groups to have more than one male with breeding status (46.5% of 797 group years) than to have more than one female with breeding status (21.5% of 797 group years). Joint-nesting females engage in competitive reciprocal destruction of each others' eggs, a behavior that ensures synchrony in egg laying (Mumme et al. 1983*b*; Koenig et al. 1995). Cobreeding males participate in intensive mate guarding before egg laying, a behavior that is conspicuously reduced from groups with only one breeding male (Mumme et al. 1983*a*).

Assignment of Parentage

Parentage is based on multilocus DNA fingerprinting for 381 offspring (Haydock et al. 2001) and on intensive observations during egg laying for 82 offspring produced by joint-nesting females. Observationally determined parentage involved continuous observations during periods on and near egg laying and nest checks immediately after females visited cavities, as described in Koenig et al. 1995. The accuracy of such observations was supported by our molecular determination of parentage for additional groups that had joint-nesting females (Haydock et al. 2001). A more detailed protocol of our fingerprinting and assignment methods can be found elsewhere (Dickinson et al. 1995; Haydock et al. 1996, 2001).

Calculation and Statistical Analysis of Reproductive Skew

Reproductive skew was calculated according to indices proposed by Reeve and Keller (1995) and by Pamilo and Crozier (1996), but we only present the former since results were similar in all cases. We calculated reproductive skew values by considering only individuals that had been assigned breeding status, excluding all helpers, which we have never detected parenting offspring successfully in groups having a male and female with breeder status (Haydock et al. 2001). In other words, inbreeding depression appears strong enough to prevent helpers from attempting to breed regardless of their competitive abilities with the same-sex breeders in the group. Including helpers would involve adding the cost of incest as an additional variable into the model. However, the new variable would have to be sufficiently high so that breeding by helpers would never be predicted to occur, effectively reducing the analysis to one excluding helpers.

A problem with both skew indices is that they are affected by differences in reproductive output (Kokko and Lindström 1997; Tsuji and Tsuji 1998; Tsuji and Kasuya 2001). The reason for this is that reproductive output, or sample size, affects sample variance, and parentage cannot necessarily be divided exactly as hypothesized among potential breeders. For example, parentage in a brood of three cannot be divided evenly between two breeders. To compensate for this and to obtain confidence intervals for skew values, we ran two types of computer simulations. In the first type, we determined whether our observed index value for skew was significantly different from the value that would be expected based on assigning parentage randomly to breeders of each sex for each offspring. As discussed above, only birds with breeding status were included as potential parents. We determined means and confidence intervals for each index value from 5,000 runs of each simulation. For clarity of presentation of our randomization tests, we only provide estimates of the significance level rather than listing confidence intervals for each value.

In the second set of simulations, we approximated confidence intervals for our observed skew values by performing a simulation that produced a mean skew value equal to the observed value. This type of simulation was able to determine whether confidence intervals overlapped each other and thus was used to determine significant differences between data sets. When the simulated skew value based on randomly assigning parentage was less than the observed value, each offspring was assigned to a breeder based on a linearly decreasing probability of parentage for each potential breeder in the group. The rate of decrease was chosen using a series of simulations differing in the rate of decrease and then interpolating the rate necessary to achieve the observed mean skew value for the data set. When the actual skew was less than the simulated skew, offspring from some nests were assigned deterministically by giving each potential breeder, as closely as possible, an equal number of offspring. Remaining offspring were assigned randomly with an equal probability of parenting offspring by each breeder. The proportion that had to be assigned deterministically was found by running a series of simulations and then interpolating to find the proportion necessary to achieve the observed skew value. After determining the necessary rate of decrease or proportion parented deterministically, confidence intervals were generated from 5,000 trials. In the text, a reported significance level of $P < .05$ indicates that neither of the randomly generated confidence intervals overlapped the mean of the other data set using 95% confidence intervals.

Survival and Reproductive Success

The predictions of reproductive skew theory depend on the independent influence of cobreeding and joint nesting on the breeder's survival and reproductive success, controlling for social and ecological factors. To control for variation in territory quality both across the study site and between years, we included a dichotomous variable that indicated whether acorn stores remained into the breeding season in the group's granary. This provided an index of both the acorn crop on each territory during the previous winter and the relative granary size or number of holes for storing the acorns harvested. We determined whether breeder age, dominance rank as indexed by relative age, experience, or turnover since the previous breeding season influenced breeder survival or reproductive success. In addition, we examined whether the number of helpers was an important explanatory variable. The sample unit for reproductive success was group year, and the sample unit for survival was individual year.

Annual survival was measured from September 1 to August 31 of the following year by asking whether an individual survived the yearlong period or died (assumed because the bird was never again seen). These dates were chosen because they come as close as possible to encompassing a single breeding season and the acorn crop cycle (harvest through depletion of stored acorns). We used the maximum likelihood method for logistic regression (Stokes et al. 1995) and report Wald χ^2 estimates and associated probabilities. Values for all explanatory variables were determined on September 1 in order to minimize bias due to overall ecological conditions, most notably acorn production. For example, if the acorn crop is poor in the fall, group size will tend to be smaller the following spring, and using a spring value of group size for the explanatory variable in the analysis will tend to correlate with low survival not because of group size but rather because of the continued low availability of acorns.

Reproductive success of the group was estimated by determining the number of nestlings surviving to 21 d old, the age at which they are usually banded. Nearly all nestlings surviving to an age of 21 d successfully fledge. We combined nests for groups that produced two successful nests (13% of successful nests), but we only included nests initiated during the spring and summer (March 1 through July 31). We excluded fall nests from the analysis (5% of known nests) because field observations during this period were not as intensive. Reproductive success was analyzed using ANCOVA, and we report Type III partial sums of squares and associated probabilities. In addition to the explanatory (independent) variables, year was also included as a covariate. Our analyses included data from all territories that were regularly monitored for group membership and nesting success between 1975 and 1999.

Ecological Constraints on Dispersal

We estimated overall dispersal constraints on males versus females by determining the number of individuals of each sex that obtained breeding positions compared with the number of adult helpers of each sex present in the study site. We assumed that all adult helpers at least 8 mo old actively seek breeding positions and that they will attempt to fill any vacancies in existing territories (Hannon et al. 1985). To determine the number of breeding positions acquired, we combined the number of individuals of each sex that took breeding positions within the study population with the estimated number of individuals of each sex that obtained breeding positions outside the population, estimated assuming that the number of individuals obtaining positions outside the study population is equal to the number of immigrants inside the study population. Fledglings were considered adult helpers on February 1 of

the year following fledging when they were about 8 mo old. Sometimes breeders compete for breeding vacancies in other groups, but this is unusual, and we did not include breeders in our estimates. Including such birds would slightly increase constraints on males relative to females because cobreeding among males is more common than joint nesting by females and thus would not alter the general results.

For cobreeding males only, we estimated yearly variation in ecological constraints by two methods. First, we determined the number of vacancies filled within and outside the population within 3 mo before the date the last egg was laid for each nest. Ecological constraints were then estimated as the mean number of vacancies for nests with parentage data for the breeding season. This effectively weights the abundance of vacancies relative to our parentage data set and to the associated nesting dates, which can vary considerably (eggs are laid from March to June). Second, we divided the number of vacancies by the number of individuals that were potentially competing for these positions. In addition to including helpers as potential competitors, we included all breeders beyond a pair in each group, since such "excess" breeders could in theory be competing for independent breeding opportunities. For each nest with parentage data, we calculated the daily mean number of helpers and "excess" breeders across all groups in the population within 3 mo before the date the last egg was laid. We then calculated the mean of the means for all nests with parentage data in each breeding season and divided the number of vacancies by the number of potential competitors to obtain an estimate of relative ecological constraints for that year. Because joint-nesting females share parentage nearly equally, these analyses were performed for cobreeder males only.

Results

Benefits of Group Living and Ecological Constraints on Independent Breeding

After controlling for the various factors affecting reproduction, success increases with the number of breeder males and females up to three individuals, but additional breeders have little effect or even decrease reproductive success (table 1; fig. 1a). Significantly more offspring were produced in groups with two or three breeders versus one breeder for both males and females (1 vs. 2: males: $N_1 = 366$ group years, $N_2 = 204$, $P < .002$; females: $N_1 = 538$, $N_2 = 136$, $P < .01$; 1 vs. 3: males: $N_1 = 366$, $N_3 = 81$, $P < .001$; females: $N_1 = 538$, $N_3 = 18$, $P < .05$). However, groups with three cobreeding males or three joint-nesting females do not produce significantly more offspring than groups with only two breeders (males:

Table 1: Factors influencing reproductive success in acorn woodpeckers

Source	df	Type III SS	F	P
Number of breeding males	4	59	5.2	.0004
Number of breeding females	3	25	2.9	.0334
Number of helpers	9	90	3.5	.0001
Breeder turnover	1	57	20.2	.0003
Acorn stores in breeding season	1	98	34.4	.0001
Year	25	506	7.1	.0001

Note: ANCOVA, full model: $F = 11.11$, df $= 43,620$, $R^2 = 0.44$, $P < .001$, $N = 664$ group years, 1975–1998.

$N_2 = 204$ group years, $N_3 = 81$, $P > .1$; females: $N_2 = 136$, $N_3 = 18$, $P > .2$). Assuming equal success for each breeder, reproductive success per breeder peaks for singletons and decreases with each additional bird for both males and females (fig. 1*b*).

Overall, male breeders have a higher probability of survival on a yearly basis (75%) than do female breeders (69%), but in contrast to reproductive success, relatively few confounding factors appear to influence breeder survival. Survival of both male and female breeders is affected by whether or not acorns remain in the granary during the breeding season but not by age, the number of male breeders, or number of helpers in the group (table 2). Comparing survival of male and female breeders, the only difference was in relation to the number of breeders in the group: female survivorship decreases as the number of joint-nesting females increases, but survival of cobreeding males is unaffected by the number of breeders of either sex (table 3). We also examined whether the number of young fledged during the previous breeding season, the number of years of breeding experience, or an opposite-sex breeder turnover during the year had an influence on probability of survival for either sex of breeders, but none of these factors was significant ($P > .1$ in all cases after controlling for the significant effects of acorn stores and number of female breeders).

Estimating dispersal constraints on breeders is problematic because it is impossible to determine whether birds in breeding positions are "attempting" to disperse. A few apparently are: nearly 10% of individuals that have held cobreeding or joint-nesting status for at least 60 d during the breeding season abandon their position in favor of breeding positions in other groups (J. Haydock, unpublished data). In contrast, about one-third of male helpers and one-half of female helpers obtain a breeding position by dispersing from their natal territory in their lifetime (Koenig et al. 2000). This indicates that males face greater constraints on dispersal than do females.

Reproductive Skew in Cobreeding Males versus Joint-Nesting Females

Reproductive skew among cobreeding males was significantly greater than simulated skew with random assignment of parentage (hereafter, SR) when skew was calculated both on a nest-by-nest basis and for each set of cobreeders by combining all offspring produced while together (table 4; randomization tests, both $P < .001$). In contrast, reproductive skew among cobreeding females was less than SR on a nest-by-nest basis and significantly less than SR when considering all offspring produced while they were joint nesting (table 4; randomization test, $P < .05$). Reproductive skew was significantly greater among cobreeding males than among joint-nesting females both on a nest-by-nest basis and when considering sets of cobreeders (randomization tests, both $P < .001$).

The fact that reproductive skew was higher for nest-by-nest comparisons than for sets of nests produced by the same cobreeders indicates that the most successful bird in one nest was not necessarily the most successful in subsequent nests. Indeed, it was uncommon to have a single cobreeding male or joint-nesting female that was consistently the most successful across all nests produced by the same set of breeders. A single male in each group was able
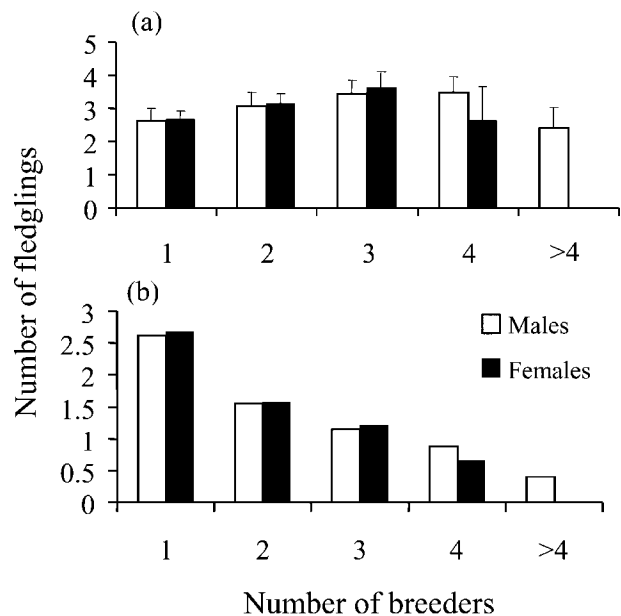
Figure 1: Mean reproductive success in relation to the number of male versus female breeders measured by (*a*) the number fledged per year per group and (*b*) the number fledged per year per breeder. Means are adjusted for the number of opposite-sex breeders, the number of helpers, whether or not there was a breeder turnover since the previous breeding season, and the presence or absence of acorn stores during the breeding season.

Table 2: Factors influencing survival of breeders in acorn woodpeckers

Explanatory variable and sex	Standardized estimate	χ^2	P
Acorn stores in breeding season:			
Male	.18	23.1	<.001
Female	.15	11.1	<.001
Age:			
Male	−.03	.4	.52
Female	−.06	1.4	.24
Number of breeding females:			
Male	−.02	.2	.64
Female	−.16	11.4	<.001
Number of breeding males:			
Male	.02	.1	.81
Female	.04	.7	.41
Number of helpers:			
Male	.02	.1	.72
Female	.06	1.3	.25

Note: Yearly survival is measured from September 1 to August 31. Standardized estimates indicate the magnitude and direction of each explanatory variable (logistic regression; N [male] = 1097 individual years, N [female] = 730 individual years; data from 1974 to 1999).

to maintain a dominant share of reproduction in only six of 24 cases (25%) with at least two nests, and cobreeder males never tied in overall success across all nests produced. Among cobreeder females, each female produced the same number of offspring in three cases, while in the remaining eight sets, the same female did not produce the most offspring across all nests.

Reproductive Skew among Cobreeding Males versus Variation in Ecological Constraints

The effect of ecological constraints on observed skew among cobreeder males was examined by comparing skew from nests produced when breeding vacancies were common versus uncommon during the 3-mo period before the date that the last egg was laid. In both groups, observed

Table 3: Yearly percent survival of breeding males and females in relation to acorn stores and the number of breeders of the same sex

Sex and acorn stores in breeding season	Probability of survival		
	One breeder	Two breeders	Three breeders
Male:			
Yes	.80	.80	.80
No	.63	.63	.64
Female:			
Yes	.79	.73	.66
No	.64	.56	.48

skew was significantly greater than SR (table 5), but the simulation factors that were required to obtain the observed values were significantly higher among cobreeders when vacancies were uncommon during the 3 mo before nesting (randomization test, $P < .05$).

The above analysis considers only two levels of ecological constraints by asking whether dispersal opportunities were common or uncommon. However, both ecological constraints and reproductive skew vary continuously. Consequently, we plotted mean reproductive skew versus mean number of vacancies for each breeding season for which we had at least five nests with parentage data. There was a significant relationship between mean reproductive skew and the mean number of vacancies that had been available 3 mo before nesting (fig. 2a; $F = 6.6$, df = 1, 5, $R^2 = 0.56$, $P = .05$), but the relationship was no longer significant for vacancies available within 1 yr before nesting ($F = 6.6$, df = 1, 5, $R^2 = 0.47$, NS). An alternative and perhaps more accurate method is to consider relative availability by dividing the number of vacancies by the number of potential competitors. There was no significant relationship using this index of ecological constraints (3 mo before nesting: fig. 2b; $F = 0.5$, df = 1, 5, $R^2 = 0.1$, NS; 1 yr before nesting: $F = 0.4$, df = 1, 5, $R^2 = 0.08$, NS). There was also not a significant correlation between the relative number of vacancies and the mean number of offspring produced during each breeding season ($P > .5$), indicating that the potential relationship between reproductive skew and ecological constraints was not masked by differences in reproductive output.

Finally, we examined reproductive skew versus the number of cobreeders in a group, predicting that as the number of cobreeding males increases, ecological constraints decrease. This is expected because, other things being equal, a coalition of two or more breeders, such as could leave from groups of at least three cobreeders, would be more competitive in contests over breeding vacancies than a single breeder leaving from a pair of cobreeders (Hannon et al. 1985).

We found no significant differences between any comparisons among different group sizes whether reproductive skew was calculated for each nest or for sets of cobreeders (table 6). The observed levels of reproductive skew increased with the number of breeders, but this was mostly due to differences in reproductive output, as indicated by the lack of a clear pattern in the simulation factor (s_f) values (table 6).

Reproductive Skew among Cobreeding Males versus Relatedness and Relationship

Cobreeding status can be achieved simultaneously for all same-sex breeders in the group, as when sibling coalitions

Table 4: Reproductive skew in cobreeding males compared with joint-nesting females

| | | | Observed | Simulations | |
| | | | reproductive | Random | s_f for obtaining |
Sex and skew calculated for each	N	Mean N offspring ± SE	skew	assignment	observed skew[a]
Males:					
Nest	99	3.0 ± .1	.76	.42***	6.7
Set of cobreeders	40	7.4 ± .7	.49	.23***	3.4
Females:					
Nest	44	4.3 ± .3	.25	.28	.87
Set of joint nesters	22	8.6 ± 1.1	.09	.17*	.41

Note: Actual skew values are calculated according to Reeve and Keller (1995). Significant differences refer to the actual skew compared with the simulated skew when all offspring are assigned randomly with no reproductive advantage between cobreeders.

[a] Simulation factors (s_f) greater than 1 created a relative advantage (s_f to 1) between successively ranked cobreeders in the average probability (with normal distribution) of being a parent. Values less than 1 cause a portion of the offspring to be assigned randomly with no parenting advantage between breeders (s_f) and the remaining portion ($1 - s_f$) to be assigned deterministically by dividing young produced as evenly as possible among the breeders.

* $P < .05$.

*** $P < .001$.

disperse to fill a breeding vacancy. Sibling coalitions may or may not all be full siblings, depending on whether parentage was shared in their natal group. Alternatively, cobreeding status can be obtained at differing times, as when sons and/or nephews ascend in their natal group to breeding status alongside their (previously breeding) father and/or uncle. Thus, we can divide data on parentage by the process of how breeding status was obtained rather than by relatedness per se. We divided our data set by this method because dominance relationships and hence the ability of dominants to control subordinate reproduction may differ depending on the process of obtaining breeding status.

On a nest-by-nest basis, there was no significant difference in reproductive skew between cobreeders that obtained breeding status simultaneously versus cobreeders that obtained breeding status at differing times (table 7). However, after combining sets of nests produced by the same cobreeders, we found that reproductive skew was significantly lower among siblings than among other combinations of relatives (table 7; randomization test, $P < .05$).

Although most cobreeders are either full siblings or a father and son ($r = 0.5$), some are less closely related. We compared relatedness among cobreeders that were closely related ($r = 0.5$) versus cobreeders that were more distantly related ($r < 0.5$) based on demographic records, the assumption of no outside mating (Dickinson et al. 1995), and parentage results for groups with cobreeders (Haydock et al. 2001). Only the relatedness of the three oldest cobreeders was included in the classification for groups that had four or more cobreeders in order to avoid having relatedness confounded by the number of cobreeders and because the youngest individuals with breeder status in very large coalitions were never observed to successfully sire offspring regardless of relatedness. There was no significant difference in reproductive skew between the two levels of relatedness for nests, but skew was significantly

**Table 5:** Reproductive skew compared with the frequency of dispersal opportunities for cobreeding males

| | | | Mean | Simulations | |
| | | | observed | Random | s_f for obtaining |
Dispersal opportunities	N	Mean N offspring ± SE	skew	assignment	observed skew[a]
Common	20	2.7 ± .3	.63	.47*	3.2
Uncommon	79	3.1 ± .1	.79	.41***	8.7

Note: The number of breeding vacancies was counted for all groups in our study population at 3 mo before the date that the last egg was laid for each nest. If the number of vacancies was less than or equal to the average number of vacancies for all nests, opportunities were considered uncommon. Vacancies were common if they were more frequent than the average number of vacancies.

[a] See table 4 for explanation of the simulation factor (s_f).

* $P < .05$.

*** $P < .001$.
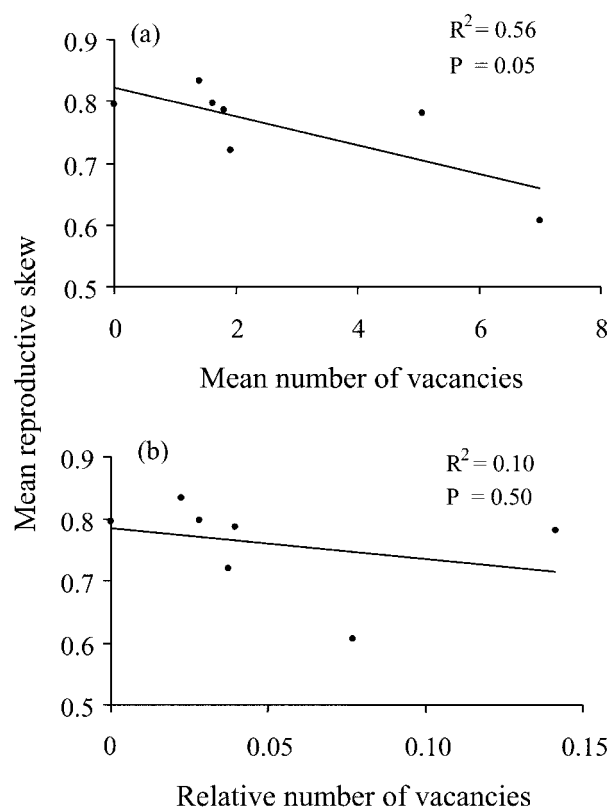
Figure 2: Annual mean reproductive skew versus (*a*) mean number and (*b*) relative number of breeding vacancies in the population 3 mo before the egg laying. Mean number of vacancies is determined by averaging the number of vacancies that became available within 3 mo before the penultimate egg date for each nest. Relative number of vacancies was calculated by dividing the number of vacancies by the number of potential competitors for each nest and taking the average value across all nests.

lower among more closely related sets of cobreeders when combining all nests (table 7; randomization tests, $P < .05$).

Discussion

Both concessions and restraint versions of reproductive skew theory are based on transactional interactions among potential breeders, whereby direct reproduction is exchanged for other fitness benefits including increased reproductive productivity of the group, increased indirect fitness, and increased survival (Vehrencamp 1979; Emlen 1982; Stacey 1982; Vehrencamp 1983*b*; Reeve and Ratnieks 1993). For both types of models, group membership is controlled by the dominant individual. However, in the concessions model, reproduction is completely controlled by the dominant (Reeve and Ratnieks 1993), whereas in

the restraint model, reproduction is controlled by the subordinate (Cant 1998). Consequently, dominants are considered to have complete control in models based on concessions and incomplete control for models based on restraint.

Both models employ Hamilton's (1964) rule to predict expected levels of reproductive skew according to demographic parameters including ecological constraints, the benefits of cooperation, and the relatedness among group members (Reeve and Keller 2001). For example, the concessions model predicts that the subordinate's share of reproduction decreases as relatedness to the dominant increases because offspring produced by a closely related dominant breeder will increase indirect fitness benefits to the subordinate. In contrast, the restraint model makes the opposite prediction because the level of subordinate reproduction that the dominant will tolerate before evicting the subordinate increases with increasing relatedness due to the greater indirect fitness benefits obtained by the dominant.

Most current models of reproductive skew have only considered two potential breeders. A complication in models involving more than two breeders of the same sex is that the predicted patterns of skew are influenced by whether the relationship between group productivity and group size is a decreasing or increasing function relative to group size. Current models, however, make similar predictions to concessions-based models that consider two potential breeders, provided that additional breeders offer decreasing benefits to group productivity (Johnstone et al. 1999; Reeve and Emlen 2000), as is the case in acorn woodpeckers (fig. 1). Thus, generalized tests of the two models using a combination of group size, as performed here, would appear to be appropriate.

A summary of our results is provided in table 8. In support of the concessions model, reproductive skew is significantly higher among cobreeding males than jointnesting females, as predicted by the greater advantages of group living and greater constraints to dispersal on males compared with females. Additional support for the concessions model is provided by the significantly greater skew observed among male coalitions in years when ecological constraints to dispersal were greater, as indexed by the absolute number of vacancies during the 3 mo before breeding (table 5; fig. 2*a*).

However, further tests fail to yield additional support for concessions theory. Expanding the number of vacancies to include those available during the entire year, we found no significant relationship across years between vacancies and skew. More damagingly, no relationship was found when the number of vacancies was divided by the number of potential breeders (fig. 2*b*), yielding what should be a more accurate index of the relative constraints on inde-

Table 6: Reproductive skew according to the number of cobreeding males

| | | | Mean | Simulations | |
| | | | observed | Random | s_f for obtaining |
N cobreeder males	N	Mean N offspring ± SE	skew	assignment	observed skew[a]
Skew calculated for each nest:					
Two	71	2.9 ± .1	.75	.41***	7.4
Three	18	3.4 ± .3	.73	.40***	5.3
Four or more	10	3.0 ± .3	.88	.53*	8.8
Skew calculated for each set of cobreeders:					
Two	25	8.2 ± .9	.42	.19***	3.3
Three	9	6.8 ± .1	.57	.22**	4.0
Four or more	6	5.0 ± .1	.63	.35	3.1

[a] See table 4 for explanation of the simulation factor (s_f).
* $P < .05$.
** $P < .01$.
*** $P < .001$.

pendent breeding experienced by birds in a particular year. Both these results fail to support either the concessions or restraint models of skew.

Two other tests also failed to support the predictions of concessions theory. Larger male cobreeder coalitions should be able to obtain other breeding positions more easily and thus should be subject to reduced ecological constraints. However, larger coalitions exhibited more, not less, skew using the Reeve and Keller index, while there was no apparent relationship between coalition size and skew using our simulation factors. Finally, skew was either lower (using sets of cobreeders) or higher but not significantly different (using individual nests) between more closely related cobreeder male coalitions. The results of these tests are thus consistent with neither model of reproductive skew.

In sum, of the four tests conducted, two provide support for the concessions model. Even for these, however, am-

biguities remain. For example, the support for concessions provided by the contrast between males and females is predicated on the assumption that observed skew in both sexes is under dominant control. However, egg destruction among joint-nesting females would appear to render such control unlikely (Mumme et al. 1983b; Koenig et al. 1995). To the extent that this is true, the lack of skew observed among such females is most likely a consequence of chance combined with the relatively equal competitive abilities of joint-nesting females rather than concessions on the part of the dominant (Haydock and Koenig 2002). If females do not meet this assumption of constraints theory, then no comparison with skew among joint-nesting females is valid, and the comparison with cobreeder males cannot provide strong evidence in support of concessions theory, even though the sex difference is in the direction predicted based on differences in ecological constraints and benefits of group living.

Table 7: Reproductive skew according to the relatedness and relationship of cobreeding males

| | | | Mean | Simulations | |
| | | | observed | Random | s_f for obtaining |
Relationship or relatedness	N	Mean N offspring ± SE	skew	assignment	observed skew[a]
Skew calculated for each nest:					
Father/uncle and sons	30	3.1 ± .3	.78	.43***	7.22
Siblings	67	3.0 ± .1	.75	.41***	6.67
$r = .5$	83	2.9 ± .1	.78	.43***	7.53
$r < .5$	16	3.2 ± .2	.68	.37***	5.07
Skew calculated for each set of cobreeders:					
Father/uncle and sons	14	6.6 ± 1.0	.57	.23***	4.23
Siblings	25	7.9 ± 1.0	.42	.23***	2.81
$r = .5$	31	7.9 ± .9	.44	.22***	2.98
$r < .5$	9	5.7 ± 1.1	.67	.28***	5.65

[a] See table 4 for explanation of the simulation factor (s_f).
*** $P < .001$.

Table 8: Summary of tests made of reproductive skew and the model (concessions, restraint, or neither) supported by the results

Comparison	Basis of prediction	Observed skew	Source	Supported model
Males versus females	Benefits of group living and constraints on independent breeding greater for males	Greater in males	Table 4	Concessions (but see text)
Annual variation in ecological constraints (males only)	Absolute number of vacancies 3 mo before breeding	Greater when vacancies uncommon and constraints greater	Table 5	Concessions
Annual variation in ecological constraints (males only)	Relative number of vacancies 3 mo before breeding	No significant relationship	Table 5	Neither
Number of cobreeders (males only)	Constraints greater for smaller coalitions	Greater among larger coalitions (using observed skew); no relationship (using simulation factor)	Table 6	Restraint or neither
Relatedness of cobreeders (males only)	Indirect fitness benefits to dominants or subordinates increases with relatedness	Significantly lower among close relatives using sets of cobreeders; nonsignificantly higher among close relatives using nests	Table 7	Restraint or neither

This difficulty may also apply to males, where a lack of consistency in which one male fathers the majority of offspring from one nest to the next, along with the failure of either age, size, or condition to predict success, raises the possibility that even among male cobreeders there may be no individual in consistent, complete control of reproduction (Haydock and Koenig 2002). Further, it is possible that the assumption used here and in all prior treatments of reproductive skew theory that paternity of offspring within broods is determined independently is inappropriate in this population, where 68% of broods are parented by a single male breeder rather than having broods with shared paternity (Haydock and Koenig 2002). To the extent that skew should be calculated on a brood-by-brood basis, skew among cobreeder males is greatly reduced compared with what is expected to occur by chance, further reducing the strength of the comparison between the sexes, if not the other tests conducted here.

The second result providing support for concessions theory, that skew is greater among cobreeder males in years when the number of vacancies 3 mo before the breeding season is uncommon and thus constraints on independent dispersal presumably greater, suffers from fewer difficulties than the male versus female comparison. Unfortunately, this result does not hold up when the number of vacancies is divided by the number of potential competitors, which should be at least as good, if not a better, index of ecological constraints. Thus, although suggestive, this result cannot be considered to provide strong support for the concessions model.

Given the contradictory results summarized in table 8 combined with the considerations discussed above, we conclude that it is unlikely that either the concessions or restraint models can be used alone to provide a framework for understanding sociality and reproductive partitioning in acorn woodpeckers. This does not mean that skew theory in some form may offer no insight into patterns of skew. In particular, mixed models that incorporate skew theory based on reproductive transactions and reproductive contests among potential breeders (Reeve et al. 1998; Cant and Johnstone 2000; Reeve and Keller 2001) may be more successful at explaining reproductive partitioning in acorn woodpeckers. The complexity of these models and the difficulty of accurately estimating the necessary parameters are beyond the scope of our current analysis. In any case, we expect that it will be necessary to include mate choice and sperm competition in order to explain skew in acorn woodpeckers, particularly among male cobreeders (Haydock and Koenig 2002).

Tests of reproductive skew theory have been applied to a taxonomically diverse set of animal societies. In eusocial insects, concessions models have been successful in explaining patterns of reproductive partitioning in some cases (Reeve et al. 2000; Reeve and Keller 2001), but other studies have found little support for transactional models of reproductive skew (Field et al. 1998; Seppä et al. 2002; Sumner et al. 2002). Similarly, empirical tests on vertebrate societies have yielded mixed or, at best, indirect support for transactional models based on concessions (Clutton-Brock 1998; Crespi and Ragsdale 2000; Clutton-Brock et al. 2001). For example, Jamieson (1997) found that two populations of pukeko (*Porphyrio porphyrio*) differing in relatedness also differed in skew as predicted by reproductive concessions. Meanwhile, several studies have

found indirect support for concessions in the form of greater skew among more closely related breeders, including lions (*Panthera leo*; Packer et al. 1991), banded mongooses (*Mungus mungo*; De Luca and Ginsberg 2001), white-winged choughs (*Corcorax melanorhamphos*; Heinsohn et al. 1999), and Arabian babblers (*Turdoides squamiceps*; Lundy et al. 1998), with a study on laughing kookaburras (*Dacelo novaeguineae*; Legge and Cockburn 2000) finding the opposite relationship. Except for the ambiguous evidence presented here, no study on vertebrates has yet to demonstrate that variation in ecological constraints within a population predicts reproductive skew.

At present, we can only speculate as to the causes of this apparent difference between social insects, where concessions theory appears to work well in some species, and vertebrate societies, where success has been more limited. One difference that is likely to be important is the unisexual nature of many social insect societies, which are functionally composed of females. This eliminates the potential complications of intersexual interactions, including mate choice, from playing a role in reproductive partitioning. Thus, skew is exclusively under the purvey of females in many social insects but likely influenced by the opposite sex in nearly all vertebrate societies.

A second important difference appears to be the degree to which the assumption of complete control is met. Such control appears to be common among at least smaller insect societies, where it can be maintained through well-developed social and pheromonal dominance. In contrast, such control appears to be far more difficult to maintain consistently within vertebrate groups. In Galápagos hawks (*Buteo galapagoensis*), for example, reproductive success appears to be randomly distributed among breeding males, suggesting a lack of control (Faaborg et al. 1995). In banded mongooses, males do not have complete control over females they guard, and females appear to have no control over whether subordinate females breed (Cant 2000; De Luca and Ginsberg 2001). In meerkats (*Suricata suricatta*), no evidence was found that dominant females granted concessions to subordinate females in order to prevent them from leaving the group and helping in future reproductive efforts (Clutton-Brock et al. 2001).

Together, our results along with those from prior studies indicate that successful models of reproductive skew in vertebrates will have to include within-group variables such as competitive interactions among potential breeders of the same sex (Cant and Johnstone 2000) and mate choice (Cant and Reeve 2002). Only with such added complexities is it likely that reproductive skew theory will be able to fulfill the promise of providing a general framework for investigating the factors shaping animal societies (Keller and Reeve 1994).

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