

Habitat Saturation Results in Joint-Nesting Female Coalitions in a Social Bird

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ABSTRACT: Joint nesting by females and cooperative polyandry—cooperatively breeding groups with a male-biased breeder sex ratio—are little-understood, rare breeding systems. We tested alternative hypotheses of factors potentially driving these phenomena in a population of joint-nesting acorn woodpeckers (*Melanerpes formicivorus*). During periods of high population density and thus low independent breeding opportunities, acorn woodpecker females formed joint-nesting coalitions with close kin. Coalitions were typically associated with groups with a male bias. We found strong evidence for both inter- and intrasexual conflict, as joint nesting conferred a fitness benefit to some males, a significant fitness cost to females, and no gain in per capita reproductive output for either sex. Such conflict, particularly the cost to females, may be an important reason why joint nesting is rare among cooperatively breeding taxa.

Keywords: acorn woodpecker, cooperative breeding, cooperative polyandry, cobreeding, population density, reproductive skew.

Introduction

Cooperative breeding systems among vertebrates exist in a variety of forms, including monogamous pairs with non-breeding helpers, joint-nesting monogamous pairs, and cobreeding polygamous individuals with or without non-breeding helpers (Cockburn 1998). The number of breeders of each sex in a cooperatively breeding social group is driven by a combination of the physical environment, including food (Koenig 1981a); the social environment, including the sex ratio of the population (Clutton-Brock and Harvey 1978); evolutionary history (Ligon and Burt 2004; Ekman and Ericson 2006); and the sexual conflicts that arise as each sex tries to maximize its fitness (Davies 1989).

Cooperative polyandry is a mating system where the number of breeding males exceeds the number of breeding females, with multiple males provisioning the offspring (Faa-

borg and Patterson 1981; Hatchwell 2009). Three forms of cooperative polyandry, found in both mammals and birds, include (1) a coalition of two males breeding with one female (Terborgh and Goldizen 1985); (2) a coalition of two or more males breeding cooperatively with more than one female, where each female has a separate nest and males provision the offspring at more than one nest (Heinsohn et al. 2007); and (3) a coalition of males breeding cooperatively with two or more joint-nesting females, raising offspring together in one nest where all group members provision or care for the offspring (Vehrencamp and Quinn 2004; Gilchrist 2006).

In birds, cooperative polyandry involving joint-nesting females is rare, occurring in only about 2.5% of cooperatively breeding taxa (Vehrencamp 2000; Riehl 2013) or ~0.2% of all avian species, assuming a prevalence of cooperative breeding of 9% (Cockburn 2006). Thus, a comprehensive analysis of the costs and trade-offs of joint nesting is required to understand the factors that might drive the rarity of this behavior given the otherwise widespread spatial and phylogenetic distribution of cooperative breeding among avian taxa.

Joint nesting may reduce individual fitness in some taxa because of the physiological challenges associated with raising a combined brood, equal to the individual potential clutch size, summed over all joint-nesting females. Yet in the scarcity of independent breeding opportunities, joint nesting is likely to be more beneficial than forgoing reproduction (Gowaty 1981). In some taxa, joint nesting leads to greater nesting success than independent breeding due to cooperative nest defense (Riehl and Strong 2018). Joint nesting is also associated with species where males engage in a significant proportion of incubation (McRae 1996a; Vehrencamp and Quinn 2004).

Intraspecific brood parasitism is considered a potentially important behavioral precursor and evolutionary pathway to joint nesting among females (McRae 1996b). If the breeding female is not able to evict the parasitizing female, the latter may be permitted to provision the combined offspring (Bebbington et al. 2017). If the parasitizing female

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is related to the breeding female, however, inclusive fitness benefits may offset any direct fitness losses (Yom-Tov 1980; McRae 1996b; Zink and Lyon 2016).

Investigators of joint-nesting or cobreeding female systems have proposed three ecological hypotheses to explain its evolution: (1) resource availability—resources for reproduction are sufficient for multiple females to breed together (Eggert and Müller 1992); (2) resource defense—multiple females can defend a resource (i.e., territory) better against challengers than a single female (Hannon et al. 1985); and (3) habitat saturation (supersaturation)—habitat saturation constrains independent breeding, leading to the formation of joint-nesting coalitions (Vehrencamp 2000; Dickinson and Hatchwell 2004).

The resource availability hypothesis predicts that female coalitions should be larger in high-quality territories or in times of resource abundance, while the resource defense hypothesis posits that coalitions that win reproductive contests for a breeding vacancy in high-quality territories should be larger than those in low-quality territories. The resource availability and resource defense hypotheses are not mutually exclusive because it is difficult to tease apart the confound of whether high-quality territories host large coalitions because of the abundance of resources or because high-quality territories are prized and lead to competition among larger coalitions.

The habitat saturation hypothesis predicts that habitat saturation should lead to a higher mean number of breeder females per group due to a decrease in independent breeding opportunities. The prediction is independent of territory quality and suggests that females may cobreed when independent breeding opportunities are rare and any direct fitness greater than zero should be favored over remaining as a nonbreeding helper.

Regardless of the ecological drivers of joint nesting, female coalition size affects the individual fitness of female and male breeders in opposite ways. For example, females are predicted to derive greater fitness benefits in polyandrous groups where male breeders outnumber female breeders (Chao 1997). The increased number of breeder males presumably can provision a larger number of nestlings, increasing each individual female's reproductive output. Thus, although females maximize fitness when they are the sole breeder with multiple cobreeding males, joint-nesting female coalitions likely increase per capita fitness by associating with groups where the sex ratio is male biased. In contrast, sole breeder males gain highest fitness benefits in polygynous groups with multiple joint-nesting females (Vehrencamp 2000). Thus, at the individual level, a male-biased sex ratio increases per capita fitness for females, but a female-biased sex ratio increases per capita fitness for males.

Per capita fitness of cobreeding males in groups with joint-nesting females may be influenced in two ways: (1) as-

suming that a single male cannot monopolize matings with multiple females, reproductive skew among males is likely to decrease, and (2) because of the larger number of young produced by joint-nesting females relative to a singleton female, per capita reproduction by males is likely to increase. If, however, the group does not produce proportionally more offspring per breeder male, then while some males benefit from increased equity in parentage, the per capita fitness benefits for all breeder males would be determined by the overall output of the group. These differences in how direct benefits to males and females are influenced by the number of breeders of the same and opposite sex highlight the inter- and intrasexual conflicts related to fitness in polygynandrous taxa.

Acorn woodpeckers (*Melanerpes formicivorus*) live in polygynandrous social groups at the Hastings Natural History Reservation that frequently include cobreeding males (~52% of groups), joint-nesting females (~21% of groups), and nonbreeding helpers of both sexes (~65% of groups; Haydock and Koenig 2003; Koenig et al. 2016). Cobreeding males and joint-nesting females are closely related within sex: mean relatedness among cobreeding males is 0.46 while between joint-nesting females is 0.41 (Koenig and Mumme 1987; J. Haydock, W. D. Koenig, and E. L. Walters, unpublished data). Groups with a single breeding female have, on average, a polyandrous sex ratio of breeders (mean number of breeder males per female = 1.76, $n = 611$). Mating outside of the group or between breeders and helpers is rare (Dickinson et al. 1995). Moreover, no traits suggesting dominance within cobreeding males or females are known (Haydock and Koenig 2002, 2003; Koenig et al. 2011a).

Adults may disperse to become breeders in nonnatal groups, but acorn woodpeckers do not disperse to become helpers in such groups as is sometimes found in other cooperatively breeding species (Groenewoud et al. 2018). Over the course of the 50-year study, the population has increased approximately threefold, attributed almost entirely to the addition of new groups within the study area (N. D. G. Hagemeyer, M. B. Pesendorfer, W. D. Koenig, and E. L. Walters, unpublished manuscript).

Although largely insectivorous, acorn woodpeckers are dependent on oak acorns (*Quercus* spp.) as food (Koenig et al. 1995), which they hoard in defended storage facilities known as granaries (Koenig et al. 2011b). Autumn acorn crops, which vary considerably from year to year, are an important predictor of both adult woodpecker survivorship and woodpecker productivity the following spring (Koenig and Walters 2015). Owing to the critical importance of this food resource, acorn crops have been quantified at Hastings Natural History Reservation since 1980 (Koenig et al. 1994).

The quality of each territory was assigned to each social group in each year of the study based on the size of the group's granaries (1: <1,000 storage holes; 2: 1,000–2,500;

3: >2,500). High-quality territories are occupied almost continuously, while low-quality territories are often abandoned during years of low acorn availability (Hannon et al. 1987).

The dependence of this species on acorns, the ability to measure territory quality, the determination of molecular parentage, and the collection of detailed demographic data, combined with the increase in population size observed over the course of the long-term study, provide a unique opportunity to test hypotheses driving the size of female coalitions in a cooperatively polygynandrous taxon.

Hypotheses and predictions. We quantified individual fitness costs and benefits of joint nesting for both males and females and tested predictions related to the drivers of formation, size, and maintenance of joint-nesting female coalitions in acorn woodpeckers (table 1). There were three predictions of the resource-based hypotheses: (1) the number of joint-nesting females in social groups should be greater in higher-quality territories and in years following abundant acorn crops, (2) per capita female reproduction should increase with female coalition size, and (3) singleton females should be more likely to be replaced by a coalition of two or more females in high-quality territories. The population density-based hypothesis predicted that the number of joint-nesting females in a social group should increase with population density.

We quantified costs and benefits to individual fitness by examining whether reproductive skew in breeder males decreased with an increasing number of breeder females in the group and whether groups with female coalitions fledged

more offspring per breeder male. We tested for trade-offs in joint-nesting females by examining whether female coalition size varied positively with the number of breeder males in the group and whether reproductive skew among females changed with increasing female coalition size.

Methods

Field Methods and Ecology of Acorn Woodpeckers

We assembled a 34-year (867 group years) demographic data set spanning 1982–2016 throughout which acorn woodpecker groups ($n = 72$) were censused continuously. Group size varied from two to 15 (mean \pm SD = 4.98 ± 2.16), and coalition size of female breeders ranged from one to three (mean \pm SD = 1.33 ± 0.56) while that of males ranged from one to seven (mean \pm SD = 1.89 ± 1.13). We used only groups that had been monitored continuously for the entire period by keeping the study area perimeter consistent, allowing population size to be used as a proxy for density. The number of active groups and population size varied with year (groups: range = 29–72, median = 42; population size: range = 92–313, median = 152).

Individuals that remained on their natal territory with their putative parents were categorized as helpers (Koenig et al. 2016). Group members not living on their natal territories or living with birds of the opposite sex that were non-relatives were considered putative breeders (Koenig et al. 1998). Parentage determination has generally supported

Table 1: Hypotheses and their predictions for the formation and size of joint-nesting female coalitions

Hypothesis and prediction	Response variable	Predictor variable(s)
Resource-based hypotheses:		
Female coalitions will be larger in higher-quality territories	Coalition size	Territory quality
Female coalitions will be larger in high acorn crop years	Coalition size	Acorn crop
Female coalitions have higher per capita reproduction per female than singleton females	Young fledged	Coalition size
Singleton females on high-quality territories will be evicted by larger coalitions	Turnover rate	Territory quality
Population-based hypothesis:		
Mean female coalition size increases with population size	Number of breeder females	Population size
Effect on female fitness:		
Reproductive skew in females is not affected by coalition size	Reproductive skew index in females	Number of breeder females
Female coalition size is positively related to the number of breeder males in the group	Number of breeder females	Number of breeder males
Effect on male fitness:		
Reproductive skew in males decreases with an increase in female coalition size	Reproductive skew index in breeder males	Number of breeder females
Young fledged per breeder male increases with female coalition size	Per capita young fledged per breeder male	Number of breeder females

Note: Included are the response variables and fixed effects used to test each prediction in linear mixed models.

these demographic assumptions, including the finding that not all putative breeder males sire young at any particular nest but that with longer tenure in a group, most putative breeders eventually sire offspring (Haydock and Koenig 2002).

Turnover in breeders of a particular sex is driven by several factors, including but not limited to individual mortality, number of breeders of that sex, and, in some circumstances, number of helpers of the same sex in the group (Koenig et al. 1994, 2016). We define a turnover as the replacement of all breeders of a particular sex due to dispersal or death. We recorded group size, number of breeders of each sex, number of helpers of each sex, and number of young fledged for each social group for each breeding attempt ($n = 867$).

Breeder Female Turnover Index

Individuals in the study population become breeders by either dispersing to a new territory or inheriting their natal territory when the opposite-sex parent dies (Haydock et al. 2001; Koenig et al. 2016). To see whether female coalitions more frequently fill the breeding vacancy created by the disappearance of singleton females, we used only instances where all breeder females were replaced during a “power struggle”—an event in which competing coalitions fight for a breeding vacancy (Koenig 1981b; Hannon et al. 1985). Joint dispersal is common, and thus for groups that experienced a turnover in breeder females, we calculated the direction of change in the number of breeder females—that is, whether the group had the same, more, or fewer breeder females following the turnover.

Given a maximum of three females in a breeding coalition, the degree of change in the number of breeder females could range from a minimum of -2 (three females replaced by one female) to a maximum of $+2$ (one female replaced by three females). We calculated mean female turnover for each of the three territory quality categories and repeated the analysis by combining groups in low- and medium-quality territories and compared them against groups in high-quality territories to test whether larger female coalitions were more likely to win breeding vacancies in high-quality territories.

Methods of Parentage Assignment

Adult acorn woodpeckers were caught opportunistically at nests or in roosting cavities (Stanback and Koenig 1994), banded with a unique color combination to facilitate later identification, and sampled to collect 75 μL of blood for genotyping. Likewise, nestlings (usually ~ 21 days of age) were banded and had a similar volume of blood drawn. Blood was stored in Longmire’s solution (Longmire et al. 1988) and temporarily stored at -20°C on-site until it was

shipped to Gonzaga University and stored at -80°C for subsequent DNA extraction and analysis.

Because of the complex social structure of acorn woodpecker groups, particularly the close relatedness of cobreeding males and joint-nesting females (which are often full siblings but unrelated to opposite-sex breeders), parentage assignment is challenging despite the absence of extragroup parentage (Dickinson et al. 1995). We typically used eight microsatellite loci for these analyses, but up to 16 were used when needed, developed for acorn woodpeckers using protocols modified from Armour et al. (1994), Gibbs et al. (1997), and Jones et al. (2002). Amplicons for each locus were produced in three multiplexed polymerase chain reactions (QIAGEN Multiplex Plus) and sized on an Applied Biosystems 3730 DNA analyzer using Liz 500 as a molecular weight standard. Genotypes were assigned using GeneMapper version 5 (Applied Biosystems), and all allele calls were checked manually for accuracy.

We determined parentage using CERVUS (Marshall et al. 1998) and accepted assignments that produced at least 95% confidence for a single mother-father-offspring triad (based on logarithm of the odds scores), which thus excluded every other possible triad of group members, including all individuals that had been observed in the group within 2 years prior to an offspring being produced. We dropped all cases where offspring could be assigned to more than one triad with 95% confidence. We used a 2-year time period in the analysis to include birds we may have mistakenly considered absent from the group at the time an offspring was produced.

Parentage Analyses and Parentage Skew Index

To investigate whether male or female breeders received fitness benefits by the addition of joint-nesting females in the group, we calculated the B index of reproductive skew for cobreeding males and joint-nesting females for each group and each nest as follows:

$$B = \sum_{i=1}^N \left(p_i - \frac{n_i}{N_t} \right)^2 - \left(1 - \frac{1}{N} \right) / K,$$

where i was each breeding attempt, p_i was the proportion of parentage assigned to a breeder for each breeding attempt, n_i was the tenure of the individual in the group (which we set to 1 since we calculated skew for each breeding attempt), N_t was the total tenure, N was the number of breeders of the sex in question (therefore N_t was equal to N), and K was the total number of young genotyped in the nest. The B index (henceforth “skew index”) varies from -1 to $+1$, where $+1$ equals complete reproductive monopoly, 0 equals reproductive equitability, and -1 indicates greater than expected equitability (Nonacs 2000).

Apart from how equally reproduction is shared, the skew index is influenced by the number of individuals that can

potentially parent offspring, the number of offspring produced, and the tenure of each individual in the group. We tested whether the number of breeder females in the group affected the skew among males in groups with one, two, or three breeder females and whether skew in breeder females differed among coalitions of two or three breeder females.

Statistical Analyses

Linear mixed models were used for all analyses (table 1), where group size (a metric that covaries with number of breeder females, number of breeder males, and number of helpers) and territory identity were treated as random effects. Likewise, in models testing differences in reproductive skew, number of breeder males and territory identity were also treated as random effects. Analyses were conducted in R 3.3.1 (R Development Core Team 2018). The package lmerTest was used for linear mixed models (Kuznetsova et al. 2015), and the package data.table (Dowle et al. 2017) was used for data set manipulation.

Results

Resource-Based Hypotheses

Female coalition size was not predicted by either territory quality ($B = 0.001$, $df = 300$, $P = .97$; fig. 1a) or the prior autumn's acorn crop ($B = -0.03$, $df = 748$, $P = .29$), although groups in high-quality territories had on average

more than one breeder female (mean \pm SD = 1.35 ± 0.63). There was no significant difference in the frequency with which singleton females replaced a larger coalition than vice versa, irrespective of whether territory quality was divided into three ($B = 0.08$, $df = 123$, $P = .66$; fig. 1b) or two ($B = -0.13$, $df = 123$, $P = .88$) levels. The number of nestlings fledged in each breeding attempt was positively associated with the number of breeder females in a group ($B = 0.50$, $df = 820$, $P < .001$), but groups with two and three joint-nesting females did not fledge proportionally more offspring than groups with singleton females (fig. 1c).

Population-Based Hypothesis

Mean female coalition size of all groups in the population was positively associated with population size ($B = 0.12$, $df = 760$, $P = .001$; fig. 2).

Effect of Joint-Nesting Females on Fitness

Parentage assignments were based on genotyping of 673 male and 587 female potential parents. Sample sizes for specific analyses are provided below.

Influence of Joint-Nesting Females on Breeder Male Fitness. Reproductive skew for males was calculated based on paternity assignments of 3,313 nestlings in 716 nests. Reproductive skew among males decreased in groups with more than

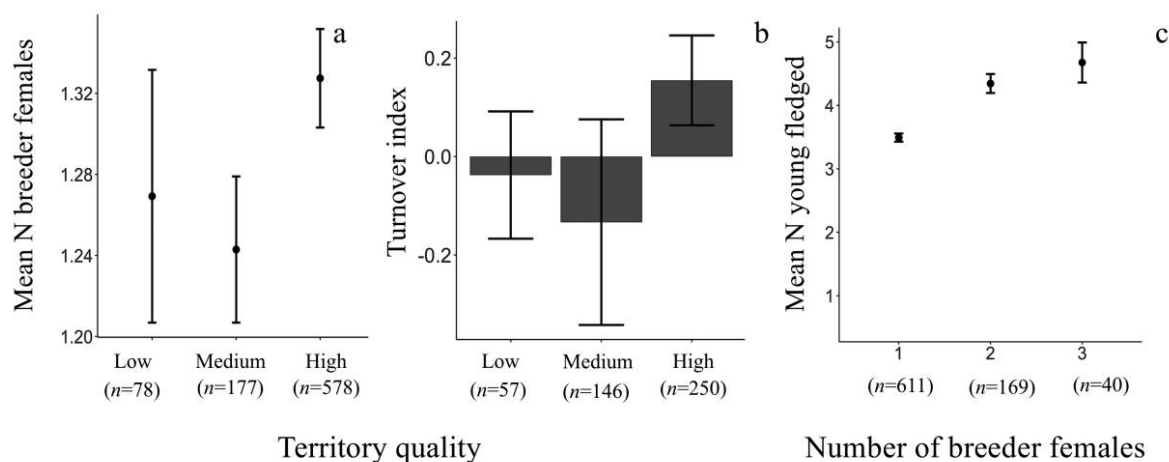


Figure 1: a, Number of breeder females as a function of territory quality. Differences are not statistically significant. b, Mean turnover index bar plot (positive values = replaced by a larger number of females, 0 = replaced by the same number of females, negative values = replaced by a smaller number of females) as a function of territory quality. Mean turnover indexes are not statistically significant across territory quality. c, Mean number of young fledged per breeding attempt as a function of the number of breeder females in the social group. Error bars denote standard errors.

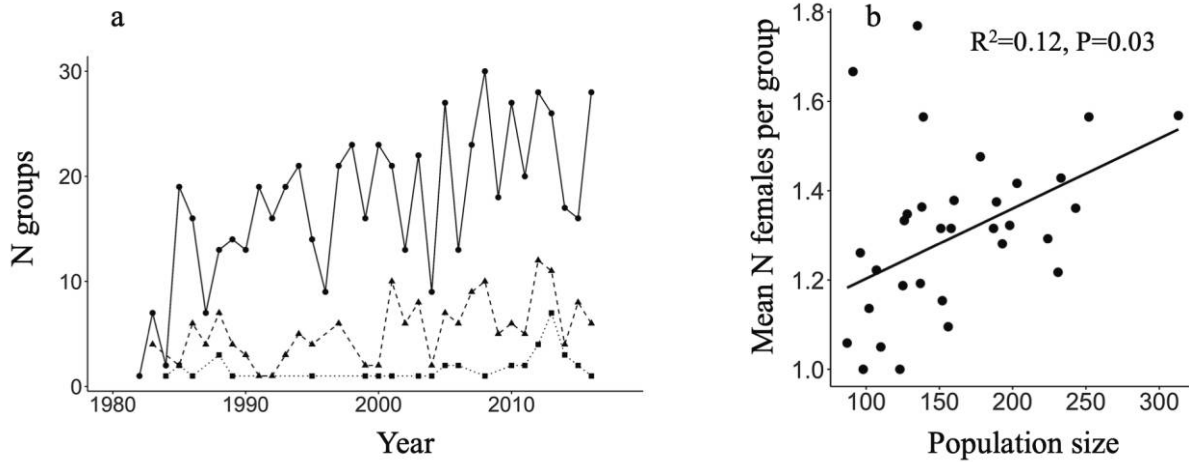


Figure 2: *a*, Number of groups with three-female coalitions increases with the number of groups in the population. A solid line and circles indicate counts of one-female groups, a dashed line and triangles indicate counts of two-female groups, and a dotted line and squares indicate counts of three-female groups. *b*, Mean number of breeder females in a group increases with population size; circles represent the mean number of breeder females in a group at each annual population size over the course of the study ($n = 34$ years). The diagonal line represents a prediction based on a linear regression model.

one female; thus, a larger proportion of the breeder males benefited from female joint nesting ($B = -0.13, df = 193, P < .001$; only groups with more than one breeder male were included) but was not significantly different between groups with two and three breeder females (Kruskal-Wallis test, $\chi^2 = 0.01, df = 1, P = .98$; fig. 3*a*). Within a nest, young fledged per breeder male did not change with the number of breeder females ($B = 0.09, df = 651, P = .35$).

Influence of Joint-Nesting Females on Breeder Female Fitness. Reproductive skew among two- and three-female coalitions was calculated using maternity assignments for 406 nestlings (two-female nests, $n = 104$; three-female nests, $n = 11$). The number of breeder males was a significant predictor of female coalition size ($B = 0.08, df = 742, P < .001$; fig. 3*b*). Skew was significantly higher in three- versus two-female coalitions (Wilcoxon ranked sum test, $W = 41, P < .001$; fig. 3*c*).

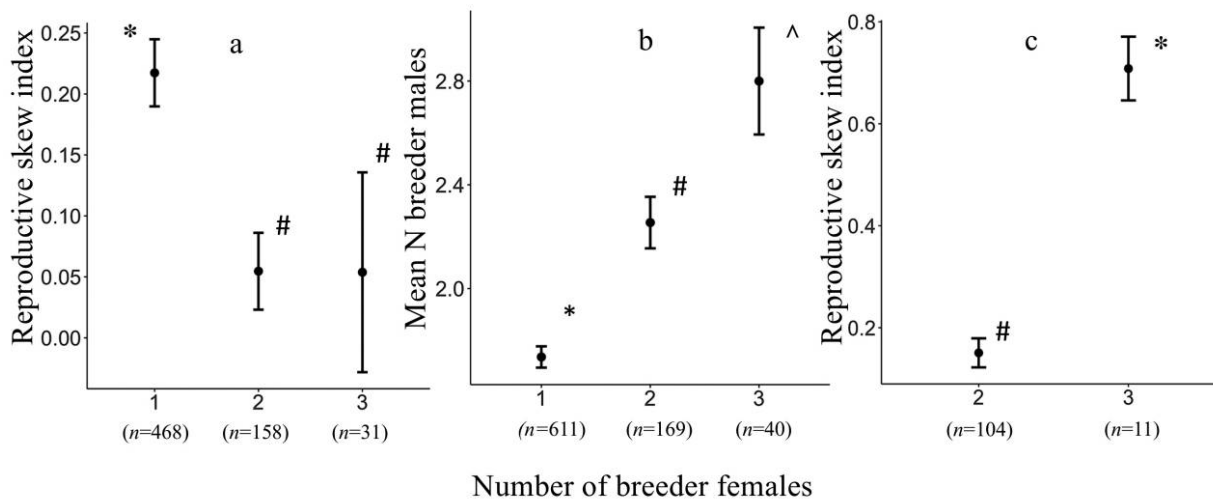


Figure 3: *a*, Male reproductive skew per nest as a function of the number of breeder females. *b*, Number of breeder males as a function of the number of breeder females. Each mean in *b* is significantly different from the other two. *c*, Female reproductive skew per nest as a function of the number of breeder females. The n values in parentheses represent the number of nests used in the analyses. Symbols show significant differences. Error bars denote standard errors.

Discussion

Our results support the hypothesis that joint-nesting coalitions in female acorn woodpeckers formed when population density was high and independent breeding opportunities were low and thus were driven by habitat saturation and not by territory quality, acorn abundance, or the ability of larger coalitions to win power struggles in high-quality territories. In terms of the fitness consequences of female joint nesting on males, we found that reproductive skew among males in groups with two and three females was significantly lower than in groups with a singleton breeder female and that the number of young fledged per male was not affected by the number of joint-nesting females. Thus, a more equitable division of paternity may provide direct fitness for some males, but on average, in groups with more than one male, male reproductive output does not change with variation in breeder female number. Females increase individual fitness by forming coalitions in groups where the number of breeder males is greater than the number of breeder females, thus maintaining a beneficial, polyandrous sex ratio, but coalitions of females nonetheless suffer fitness costs by a reduction in per capita reproductive output compared to singleton females.

Habitat saturation has been considered a potentially important mechanism driving the frequency of polygynandrous breeding systems for at least 35 years (Koenig and Pitelka 1981; Emlen 1982). More recently, the “supersaturation” hypothesis of Dickinson and Hatchwell (2004) proposes that cooperative polygamy evolves in populations living at high density due to decreased independent breeding opportunities. This hypothesis predicts that as competition for breeding opportunities intensifies with increased population density, individuals will form same-sex coalitions to win breeding vacancies and eventually achieve breeding opportunities as cobreeders. Thus, habitat saturation potentially facilitates the formation of joint-nesting female coalitions, a relatively rare behavior even among cooperative breeders and one that is exhibited by only ~21% of the social groups in the population studied here (Haydock and Koenig 2003).

Other factors almost certainly play important roles for the evolution of joint nesting. For example, female cobreeders in acorn woodpeckers as well as other joint-nesting taxa, including house mice (*Mus musculus*) and dormice (*Glis glis*), are close kin. This suggests that inclusive fitness benefits of nesting with close relatives may be an important factor offsetting the reproductive costs of joint nesting (Manning et al. 1995; McRae 1996a; Pilastro et al. 1996). Another important common trait between acorn woodpeckers and other taxa with joint-nesting females is males substantially contributing to the incubation of eggs. Male incubation is hypothesized to be an important precursor for joint nesting, as incubating males might allow multiple females to lay

within the nest or prevent females from destroying eggs laid by other females (Vehrencamp 2000). How or if male incubation directly drives joint nesting in acorn woodpeckers remains to be determined.

Female coalitions may also form through female helpers inheriting breeding status and becoming cobreeders following breeder male turnover. However, this is rare among acorn woodpeckers. In our long-term data set, only 69 out of 2,966 females followed have inherited breeding status following breeder male turnover compared to 298 out of 3,214 males that have inherited following a breeder female turnover. The number of breeder male turnovers explained very little variation in population size ($R^2 = 0.09$, $df = 27$, $P = .06$), suggesting that the observed increase in the number of breeder females per group with population density was driven by a combination of larger coalitions winning competitions for female turnovers and female helpers inheriting territories.

Acorn woodpeckers are one of only five altricial avian taxa known to exhibit joint nesting (Vehrencamp 2000; Riehl 2013). Because of the importance of parental provisioning in these species, resource-based hypotheses predict that female coalitions should form and persist in high-quality territories and that such coalitions should otherwise evict singleton females from such territories. Our results did not support either prediction. Our index of territory quality measured a group’s capacity to store acorns based on the size of the group’s granary (Hannon et al. 1985). Because these storage facilities can take decades to construct, territories with large granaries are relatively rare and are highly prized (Koenig et al. 1995). There are other features, however, associated with high-quality territories that remain to be tested, such as the number and quality of nesting and roosting sites within these territories, factors that could potentially affect overall territory quality in this species (Koenig and Walters 2014).

Female acorn woodpeckers were unable to produce proportionally more offspring relative to singleton breeder females. Two important factors may drive reproductive output in the population. The first is the habitat being spatiotemporally heterogeneous (Koenig et al. 2011b; Koenig and Walters 2015). Even though acorn woodpeckers are primarily insectivorous, the previous year’s acorn crop has a strong effect on reproductive output (Koenig et al. 2011b). This results in resource availability within a particular territory varying across years (Koenig et al. 2008). Thus, coalitions of two and three females producing two and three times the number of offspring as singletons, respectively, may not be ecologically feasible due to poor acorn crop irrespective of territory quality (Hannon et al. 1987).

The second factor that may drive reproductive output is the number of nestlings fledged possibly being constrained by the number of eggs that can be incubated successfully. For example, ratites have a large body mass-to-egg mass

ratio that facilitates the incubation of large clutches (Rahn et al. 1975; Meiri et al. 2015). The ability to incubate a large clutch is considered an important step in the evolution of joint nesting in this taxonomic group (Vehrencamp and Quinn 2004). Unlike ratites, acorn woodpeckers have large eggs relative to body size (Koenig et al. 2009), limiting the number of eggs that can be incubated efficiently as is seen in other joint-nesting passerines (Baglione et al. 2006). For example, in nests with eight or more eggs (about twice the average clutch size laid by a single acorn woodpecker female), mean hatching success was 0.71 ($n = 38$) compared with 0.83 ($n = 875$) across nests with less than eight eggs. As cavity nesters, acorn woodpeckers are also restricted by the size of the nest cavity, a constraint that potentially affects clutch size (Slagsvold 1989; Wiebe et al. 2006). Thus, environmental and ecological factors, combined with physiological limitations, may constrain the number of nestlings produced by females with significant costs for females breeding in a coalition (Bebbington et al. 2017).

Our findings do not support the hypothesis that female coalitions in acorn woodpeckers form because they are able to better compete for high-quality territories. Territory defense by all group members is well documented in acorn woodpeckers (Koenig et al. 2016), as it is in other cooperatively breeding taxa, such as pukekos (*Porphyrio melanotus*; Lambert et al. 1994) and both Asiatic and African lions (*Panthera leo*; Mosser and Packer 2009; Chakrabarti and Jhala 2017). Nonetheless, once established, even singleton breeder female acorn woodpeckers are rarely challenged by larger coalitions; rather, turnovers generally occur only when there is a breeding vacancy (Mumme et al. 1988). Group territorial defense also makes calculation of the tenure of female coalitions irrelevant since male breeders and helpers defend territories and thus females are not ousted simply because they lose coalition members. Tenure length of an individual is thus likely associated with a combination of both territory quality and group size. Moreover, the coalition size of closely related females involved in power struggles to fill a breeding vacancy may be larger than the number of females that eventually settle on the territory (Hannon et al. 1985). Hence, coalition size may be most critical during the power struggle itself rather than postturnover when routine territory defense has been established.

We found a strong effect of female joint nesting on individual fitness in both males and females. In males, female joint nesting increased equity in parentage within a clutch. Extragroup parentage is rare in this species (Haydock and Koenig 2003), and since joint-nesting females lay eggs synchronously with males showing intense mate guarding (Mumme et al. 1988), one male is unlikely to monopolize matings with multiple females in social groups where other breeder males are present. Thus, compared to groups with a single breeder female, reproductive skew was dramatically

reduced among breeder males in groups with joint-nesting females (fig. 3a). However, the mean number of young fledged per breeder male did not increase with an increase in the number of joint-nesting females. Thus, more males gained parentage, but overall, individual males did not receive increased direct fitness benefits as the number of joint-nesting females increased.

We found that reproductive skew for females was low in joint-nesting female pairs but significantly increased in three-female coalitions (fig. 3c). Female acorn woodpeckers in coalitions maintain equity in reproduction by removing and destroying eggs until all joint-nesting females lay synchronously in the same nest in both two- and three-female coalitions (Mumme et al. 1988). Our findings, however, suggest that three-female coalitions may not be able to synchronize laying as effectively. The significant increase in skew when coalition size increased from two to three (fig. 3c) resulted in a significant loss in direct fitness for at least one of the females. Dominance hierarchies within female coalitions are difficult to discern, and thus we were unable to tease apart loss in fitness based on social dominance. There is an additional fitness cost to females, however, as three-female coalitions fledged only ~1.5 times the number of nestlings as singleton females (fig. 1c), half the number needed to maintain per capita fitness.

Despite the potential loss in fitness by being part of a coalition, females may increase reproductive output by joint nesting in groups with a male-biased sex ratio of breeders (Chao 1997). Females in such groups benefit from multiple males provisioning offspring, a pattern observed in Galápagos hawks (*Buteo galapagoensis*; Faaborg and Patterson 1981) and dunnocks (*Prunella modularis*; Davies 1989). Despite their presence, nonbreeding helpers in acorn woodpecker groups do not provision as much as breeders (Koenig and Walters 2012). Thus, joint-nesting female acorn woodpeckers are predicted to increase direct fitness by living in a group with a male-biased cobreeder sex ratio (Chao 1997).

Other factors influencing fitness consequences of joint nesting remain to be tested. For example, individuals living on high-quality territories have higher annual survival probability (Koenig et al. 2016), but whether longer life offsets the fitness costs of joint nesting is unknown. Similarly, because we are unable to differentiate between death and dispersal of individuals (Koenig et al. 1996), it is possible that joint nesting is a temporary arrangement for young females, dispersing again whenever an independent breeding opportunity arises. Finally, individual reproductive success in any given year is driven by a wide range of factors, including the previous year's acorn crop, home group size and composition (number of helpers and breeders), and territory quality, to name a few (Koenig et al. 2016), and is also driven by the bird's age and body condition. These confounding variables make it difficult to tease apart the costs of joint nesting

on the fitness of individuals when they are in a cobreeding coalition or breeding independently.

Our results highlight the influence of both ecological and demographic factors and the sexual conflicts inherent in driving the evolution and maintenance of mating systems. To the extent that habitat saturation motivates joint nesting in females, it remains to be determined why this phenomenon is not more common among other cooperatively breeding taxa. Males in cooperatively breeding species often benefit by forming coalitions to acquire and defend high-quality territories (Mumme et al. 1988) or through cooperative courtship displays, such as in turkeys (*Meleagris gallopavo*; Krakauer 2005) and lance-tailed manakins (*Chiroxiphia lanceolata*; DuVal 2013). Moreover, a cobreeding male that joins a breeding pair can provision nestlings, potentially increasing reproductive output (Chao 1997).

Female coalitions can produce more offspring than singleton females, but this is offset by limited food resources, physiological constraints on brooding and incubation due to relative egg size, and added provisioning requirements for the augmented number of young (Bebbington et al. 2017) that results in decreasing per capita reproductive output for each additional breeder female (Vehrencamp 2000). Females thus incur a significant loss in direct fitness when joint nesting compared to independent breeding. The meager direct fitness benefits are nevertheless greater than remaining as a helper with no direct fitness. Coalitions of females are thus likely maintained through an “uneasy truce” where the loss of direct fitness is a trade-off for the low probability of successful dispersal as a singleton (Mumme et al. 1988; Chao 1997). These physical, physiological, social, behavioral, and environmental factors likely limit the number of species that can maintain a cooperatively polyandrous mating system with joint-nesting females even though populations of most cooperatively breeding taxa experience habitat saturation to some extent (Emlen 1982).

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Two female woodpeckers attending a joint nest. Photo © Bruce Lyon.