

Fitness consequences of within-brood dominance in the cooperatively breeding acorn woodpecker

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Abstract Social dominance confers potential advantages in terms of access to superior resources, habitats, and breeding opportunities. In the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*), within-brood dominance among juveniles is correlated with relative body size as nestlings. Capitalizing on this relationship, we investigated the fitness consequences of dominance by means of paired comparisons of broodmates. We found that (1) larger fledglings retained at least some of their size advantage as adults; (2) overwinter survival of larger, dominant fledglings was significantly greater than subordinates, but was not relatively greater when resources were poor than when they were good; (3) among birds surviving their first winter, there were no differences vis-à-vis dominance in terms of the proportion of birds acting as helpers or inheriting their natal territory. However, larger, dominant males were present in the study area longer than subordinates, suggesting that they either survived better or were more successful at gaining reproductive opportunities; (4) if only one male broodmate became a helper instead of dispersing, he was significantly more likely to be the smaller subordinate,

consistent with the view that helping is a best-of-a-bad-job strategy; and (5) there were no significant differences in reproductive success among pairs of male broodmates that cycled together as adults, consistent with prior work failing to detect a phenotypic correlation of reproductive skew. Our results indicate that within-brood dominance relationships established as juveniles have significant effects on first-year survivorship and at least some aspects of adult fitness.

Keywords Acorn woodpecker · Cooperative breeding · Dominance · Helping-at-the-nest · *Melanerpes formicivorus* · Reproductive skew

Introduction

Dominance relationships allowing individuals priority of access to resources are widely recognized as having important fitness consequences, influencing not only survival but dispersal and reproductive success (Ekman 1990; Duckworth and Badyaev 2007; Foerster et al. 2007; Ratcliffe et al. 2007; Silk 2007). Among nestlings and juveniles, the aggression involved in establishing dominance hierarchies is often particularly crucial since infanticide and death is a frequent result of poor performance (Mock and Parker 1997; Drummond 2006). Less is known, however, about how dominance established early in life affects the life history and fitness of adults, in part because adult dominance hierarchies are typically confounded by factors such as age, sex, and social context, factors that often have their own independent effects on fitness. Two potential solutions to this problem are (1) to control for confounding factors statistically or (2) to compare broodmates whose backgrounds are in most ways identical. The latter approach is particularly powerful, especially if

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relative size translates into social dominance within broods, in which case simple measurements of nestlings allow for comparisons of apparent survivorship and success of individuals of the same age that share the same residency, experience, parental quality, territory quality, and food supply (Stanback 1994).

Comparing broodmates to determine the consequences of dominance has been particularly successful in socially complex species in which a goal has been to understand why some individuals delay dispersal and remain in their natal territory, often as non-breeding helpers, while others disperse and attempt to breed independently. In red-cockaded woodpeckers (*Picoides borealis*), for example, smaller, subordinate siblings are more dispersive than dominants and only subordinates with missing dominant brothers stay to become helpers, indicating that there is considerable competition over philopatry and that delayed dispersal confers significant fitness benefits (Pasinelli and Walters 2002; Hewett Ragheb and Walters 2011). Similar results indicating that delayed dispersal was the preferred option by dominant siblings were found for the Siberian jay (*Perisoreus infaustus*), a species with delayed dispersal but no helping (Ekman et al. 2002), largely due to nepotistic benefits offspring gain by remaining with their parents (Griesser and Ekman 2004, 2005). These results suggest that the fitness benefits of philopatry in some group-living species may be considerably greater than previously suspected despite prior studies indicating that delayed dispersal is generally a best-of-a-bad job strategy (Emlen 1982; Koenig et al. 1992; Dickinson and Hatchwell 2004).

In the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*), broodmates typically remain together on the natal territory at least through their first winter and often much longer, during which time they are potentially in competition with each other for food, access to roost holes, and other communal resources. Furthermore, competition and cooperation among siblings often persist long after their first year since acorn woodpeckers are polygynandrous, with approximately 50% of groups contain coalitions of cobreeding males that compete for matings within the group and 20% contain coalitions of joint-nesting females that lay their eggs communally within the (single) nest cavity. Both male and female coalitions are typically made up partly or entirely of siblings (Koenig and Mumme 1987), often from the same brood. Such sibling coalitions may either disperse as a unit and compete for reproductive vacancies elsewhere in the population (Koenig 1981; Hannon et al. 1985) or inherit and become cobreeders in their natal territory following the death and replacement of breeders of the opposite sex (Koenig et al. 1998). In either case, within-brood dominance relations have consequences that potentially last throughout their reproductive lives.

Dominance interactions are often difficult to observe and require considerable investment by investigators in time and effort to determine. Fortunately, prior work in our population has demonstrated a close link between relative nestling size and subsequent within-brood dominance among fledglings, most strongly with relative wing length but also with relative body weight. Specifically, in dyadic interactions, dominants had, on average, a wing length 7.2 mm longer and weighed 4.2 g more than subordinates when they were banded, both highly significant differences (Stanback 1994). Similarly, nestlings that were heavier or had longer wings than the brood average were significantly more likely to be dominant than birds lighter or with shorter wings than the brood average (Stanback 1994). It is therefore possible to infer the effects of relative dominance on fitness in this species by means of measurements taken while broodmates are still in the nest.

Our work was conducted on a population of acorn woodpeckers studied since 1972 in central coastal California. Specifically, we investigated the relationship of dominance established on the basis of size as nestlings to post-fledging mortality, adult size, and subsequent fate as adults, including their (1) probability of delaying dispersal and remaining as a helper on their natal territory, (2) probability of inheriting and becoming a breeder on their natal territory, (3) probability of becoming a breeder elsewhere in the study area (4) overall survival and/or time remaining in the study area, and (5) relative success as cobreeders. We also tested for the influence of the acorn crop, a key food resource, on the fitness consequences of dominance by comparing results in good vs. poor acorn crop years.

We predicted that larger, dominant nestlings would experience greater overwinter survivorship than smaller subordinates (Table 1), a relationship found previously by Stanback (1994), although his results were not statistically significant. Assuming that dominance-related aggression is more common and has greater fitness consequences when resources are limited (Ewald 1985), we predicted that survival of dominants would be significantly enhanced in poor, but not necessarily good, acorn years. Of particular interest to the evolution of cooperative breeding is the relationship between dominance and dispersal. In many species, including at least one cooperative breeder, subordinates are more likely to disperse than dominants (Christian 1970; Gauthreaux 1978; Pasinelli and Walters 2002), a finding known as the social dominance hypothesis. Prior work in acorn woodpeckers, however, has indicated that birds compete vigorously for outside breeding opportunities (Koenig 1981; Hannon et al. 1985) and in general are “making the best of a bad job” when they delay dispersal and help (Koenig et al. 2011). Thus, counter to the social dominance hypothesis, we predicted that dominant

Table 1 Predictions and summary of results of differences in behavior and fitness between dominants and subordinates

| Variable | Prediction | Results |
|-------------------------------------------------|---------------------------------------------------------|----------------------------------------------------------------------------------------|
| Overwinter survival | Greater among dominants | Greater among dominants |
| Influence of the acorn crop | Survival of dominants enhanced more in poor acorn years | Dominant survival advantage 8.0% in good acorn years but only 3.6% in poor acorn years |
| Delayed dispersal and helping | More likely by subordinates | Among males, if only one helped, it was more likely to be the subordinate |
| Inheriting the natal territory | More likely by subordinates | No significant differences |
| Achieving breeding status within the population | More likely by dominants | No significant differences |
| Length of time present in the study area | No clear prediction | Larger males present longer |
| Relative success as a cobreeder | Possibly greater among dominants | No significant differences |

individuals would be more likely to disperse while subordinates would be more likely to delay dispersal and help in their natal group. In parallel with this prediction, we expected that subordinates, remaining longer on their natal territory, would be more likely to inherit breeding status, but that dominants would be more likely to achieve breeding status within the population as a whole. Given the different strategies we expected dominants and subordinates to pursue, we had no strong expectation as to whether dominants or subordinates would remain in the study area longer.

The relative success of cobreeders is of particular interest from the perspective of reproductive skew theory (Johnstone 2000; Magrath et al. 2004; Koenig et al. 2009), which posits that a dominant individual controls the partitioning of reproduction in cooperative societies. Although prior analyses have thus far failed to confirm the existence of such dominance control in cobreeding coalitions of acorn woodpeckers (Haydock and Koenig 2002, 2003), we have not previously examined our data for the possibility that dominance, established as nestlings, might affect reproductive skew as an adult. If differences were found, we expected dominants to be more successful than subordinates.

Material and methods

We studied a population of individually marked acorn woodpeckers at Hastings Natural History Reservation in central coastal California, USA, between 1972 and 2010. The mean number of territories followed was 37 (range 7 to 56) while the mean number of adults in the population was 164 (range 27 to 263). Birds in this population live in family groups ranging in size from two to 15 individuals including one to seven cobreeder males, one to three joint-nesting females, and zero to 10 non-breeding helpers of either sex (MacRoberts and MacRoberts 1976; Koenig and

Mumme 1987). Regardless of composition, groups maintain only one nest at a time at which all or the majority of group members brood and provision nestlings (Mumme et al. 1990). We attempted to find all nests in the population and generally banded and measured nestlings when they were 21 days old; nestlings fledge when they are 30–34 days old (Weathers et al. 1990). Following fledging, young remain in their natal group at least until February following fledging. Thus, post-fledging survivorship was measured by whether birds survived to their first February or not. A small proportion of young (approximately 2.6% of those surviving to their second year) was not observed following fledging (and thus initially thought to have died prior to their first February) but subsequently was observed alive in the population; these individuals were included in those surviving to February. Subsequently, young may disperse and breed elsewhere in the population (often in same-sex sibling coalitions), inherit and breed in their natal territory following the death and replacement of the breeders of the opposite sex by unrelated birds, or remain as non-breeding helpers aiding their parents raise younger siblings (Koenig et al. 1998).

Brood size is variable, with the number of nestlings present at banding ranging between one and eight (mean \pm SD = 3.19 \pm 1.24, $N=1,124$). Although fledglings are sexually monomorphic, birds acquire dimorphic adult plumage during a post-juvinal molt around 4 months of age. Thus, surviving fledglings were sexed visually following their post-juvinal molt. In addition, we sexed 258 fledglings produced between 1986 and 1993 that did not survive past their post-juvinal molt (Koenig et al. 2001) using molecular techniques (Griffiths et al. 1996, 1998; Ellegren 1996).

Measurements taken at banding included body weight measured to the nearest 0.1 g using a 100-g Pesola balance, wing chord measured to the nearest millimeter with a wing ruler, and bill length (total exposed culmen) measured to the nearest 0.1 mm using calipers. Stanback (1994) found that wing length at banding was in general a better predictor of

dominance than body weight at banding. Both, however, were highly significant, and thus we used both metrics as proxies for relative dominance within broods. We note, however, that neither measure of size predicted the outcome of dominance interactions in more than 79% of cases, and thus our analyses are likely to underestimate the true benefits of dominance status in this population.

In contrast to several other species, including song sparrows *Melospiza melodia* (Arcese and Smith 1985), Arabian babblers *Turdoides squamiceps* (Carlisle and Zahavi 1986), and red-cockaded woodpeckers (Hewett Ragheb and Walters 2011), male acorn woodpecker fledglings are not more aggressive than, nor systematically dominant to, females (Stanback 1994). Thus, although we analyzed sexes separately among broodmates surviving to February of their second year, we did not attempt to analyze sex-specific survivorship prior to this time.

To test for the fitness consequences of dominance, we used matched pairs of broodmates. When more than two broodmates were available, we used the largest and the smallest as measured by the two metrics of body weight and wing length at banding. For analyses involving birds surviving to their second year, only same-sex broodmates surviving their first winter were used. Comparisons made between pairs of broodmates included (1) whether they survived their first winter (February of their second year); (2) body size as adults; (3) whether they were a non-breeding helper in their natal group as a second-year bird; (4) whether they eventually inherited and bred on their natal territory, regardless of age; (5) whether they eventually became a breeder anywhere in the study area; (6) the total number of years they survived or were present in the study area; and (7) the number of offspring parented in cases where broodmates became cobreeders with each other.

All tests except for survival through the first winter and body size as adults were restricted to same-sex broodmates that had died or were no longer present in the study at the time of the analyses. Since some birds dispersed off the study area, our test of whether birds became a breeder in the study area was a measure of recruitment within the study population but not of survivorship, particularly for females, which are more likely to disperse than males (Koenig et al. 1996, 2000).

Adult size was determined from recaptures made anytime subsequent to fledging. Because there is no seasonal variation in body size in this species (Koenig et al. 2005), we did not control for time of year of capture. When birds were recaptured multiple times, we used the mean across recaptures. Variables tested were adult body weight and wing chord. In addition, for each individual we calculated an index of condition based on the residuals of a sex-specific regression of weight on wing chord using recaptures of all adults during the study ($N=932$ males and

831 females). We then tested whether broodmates that were larger at banding were larger when recaptured as adults using binomial tests.

To determine parentage, we used microsatellites developed using genomic libraries enriched for various repeat motifs as described by Armour et al. (1994) and by Genetic Identification Systems (GIS), from which we optimized 15 polymorphic loci. The average expected heterozygosity was 0.79; observed heterozygosities ranged from 0.45 to 0.89. For paternity analysis, the combined exclusionary power with one known parent was >0.999 and for the first parent was >0.997 . PCR products were sized on an Applied Biosystems 3730 DNA analyzer following manufacturers' protocols, and genotypes were assigned using GeneMapper version 3.5 (Applied Biosystems). Parentage was assigned within social groups using CERVUS v. 3.0.3 (Kalinowski et al. 2007). More detailed methods will be published elsewhere.

Acorn woodpeckers are critically dependent on a highly variable acorn crop, which has important effects on reproductive success, survivorship, and group stability (Hannon et al. 1987; Koenig and Mumme 1987; Koenig and Stahl 2007). We tested for differential effects of dominance vis-à-vis the acorn crop using data collected between 1980 and 2010, during which time we assessed mean crop size the prior autumn each year by counting a sample of acorns on 250 marked trees distributed among all five major oak species (*Quercus* spp.) present in the study area. The acorn crop was estimated by the mean of the \ln -transformed number of acorns counted in 30 s ($xLN30 = \ln[N \text{ acorns counted} + 1]$) across all trees surveyed (Koenig et al. 1994a, b). Across all 31 years of the survey, $xLN30$ ranged from 0.42 to 3.06 (mean \pm SD = 1.69 ± 0.73). In order to contrast dominance effects when resources were potentially limited vs. abundant, we compared years when $xLN30$ was below the long-term mean crop size ($N=17$ years) with those when it was above the mean ($N=14$ years).

For each pair of broodmates, we compared their subsequent apparent survivorship and fate using Fisher exact tests (for binary response variables) and Wilcoxon matched-pairs signed-ranks tests (for continuous variables). In some cases, we maximized the potential conflict between pairs of broodmates by restricting analyses to those among which only one of the two broodmates achieved the desired goal (i.e., survived or inherited their natal territory) and tested the results using binomial tests. In order to test for an interaction between the effects of dominance and resources (that is, whether survival of dominants was enhanced in poor acorn years), we examined the survivorship of all fledglings relative to one another within a brood using standardized values for wing length and body weight for each bird within its brood. Thus, the relative weight of bird

i in brood b was calculated as $(\text{weight}_i - \text{mean weight}_b) / \text{standard deviation of weight}_b$. We then performed general linear models of overwinter survivorship on relative size, the acorn crop, and the interaction between these two variables, using a binomial error distribution. Analyses were performed in R 2.11.1 (R Development Core Team 2010).

Results

Overwinter survival

Overwinter survival (from fledging to the following February) among the matched pairs of broodmates was significantly greater for dominant fledglings compared to subordinates using all pairs based on both wing length and body weight at banding and among pairs in good acorn years based on wing length (Fig. 1). In general, overwinter survivorship was significantly greater when the acorn crop was good. We found no evidence, however, for an interaction between the effects of dominance and resources (Table 2). That is, survivorship was not relatively greater for

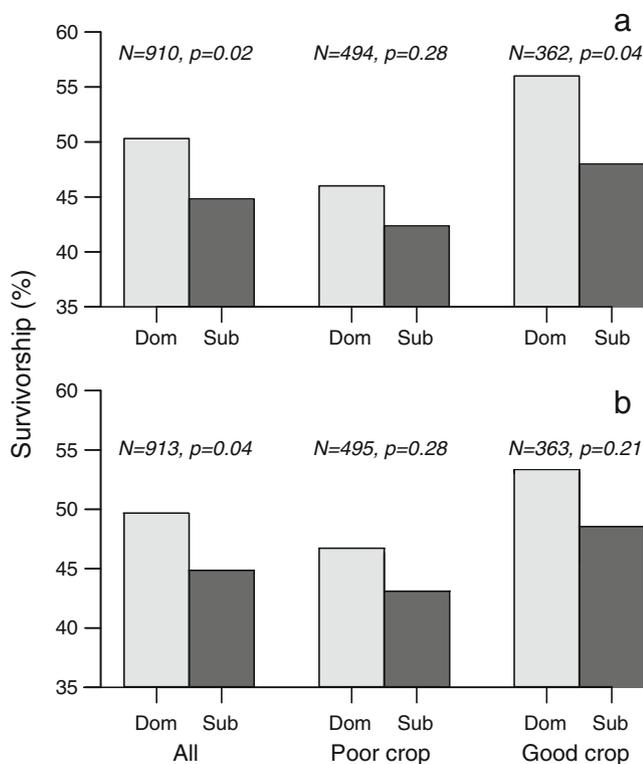


Fig. 1 Mean overwinter survivorship of broodmates depending on **a** relative wing length and **b** relative body weight at banding for all data, poor acorn crop years, and good acorn crop years. Sample sizes and p values for tests comparing dominants and subordinates are listed. Survivorship of dominants was 4.8–5.5% greater than subordinates using all pairs, 3.7% greater in poor acorn years, and 4.9–8.1% greater in good acorn years

dominants compared to subordinates when resources were poor than when they were good.

Parallel analyses were performed using matched pairs of broodmates among which only one of the two individuals survived their first winter. Results (not shown) were the same as those using all pairs of broodmates; that is, dominants were in all cases more likely to survive the winter than subordinates, with the differences being statistically significant for all pairs of broodmates based on either wing length or body weight and in good acorn years when based on wing length. The proportion of broodmate pairs among which the larger, dominant individual survived the winter whereas the smaller, subordinate individual did not ranged from 55.1% to 59.5% ($N=147$ –150 pairs, depending on the test).

Adult body size

We were able to compare the relative size of broodmates as nestlings with size as adults for 47 pairs of males and 24 pairs of females. Results revealed significant relationships between nestling body weight and adult body weight for both males and females (Table 3). In addition, nestling body weight correlated significantly with the index of adult condition in females but not for males.

Success of second-year birds

Using all pairs of broodmates surviving their first winter, we found no significant differences among either males or females in terms of the proportion of dominants vs. subordinates that helped as second-year birds, eventually inherited and became breeders on their natal territory, or eventually bred in the study area (Fig. 2a; data for females not shown). We also found no significant differences among female broodmates even when restricting analyses to cases in which only one of the two achieved the target position (i.e., helped as a second-year bird, inherited, or bred). When restricting analyses in this way for males, however, we found that significantly more subordinates than dominants (determined by relative wing length) helped as second-year birds: of such pairs, 19 of 27 (70.4%) birds that helped in their second-year were smaller, subordinate individuals (binomial test, $p=0.05$). We found no significant difference in the probability that dominants and subordinates inherited their natal territory or became breeders (Fig. 2b).

We found no significant differences among female broodmates that survived through their first winter in terms of the number of years they survived or were present in the study area. Among male broodmates, we found no significant difference when individuals were matched based on wing length, but larger, dominant males (based on body weight) were present significantly longer in the study area than smaller, subordinate males (Fig. 3).

Table 2 General linear models of overwinter survivorship on relative body size (wing length; body weight), the acorn crop (xLN30), and the interaction between the two variables

| Variable | Mean ± SE effect size | z value | p value | N |
|-------------------------------|-----------------------|---------|---------|-------|
| Relative wing length | 0.116±0.089 | 1.30 | 0.20 | 2,844 |
| Mean acorn crop | 0.337±0.051 | 6.58 | <0.001 | |
| Wing length × mean acorn crop | 0.001±0.052 | 0.01 | 0.99 | |
| Relative body weight | 0.080±0.064 | 1.26 | 0.21 | 2,861 |
| Mean acorn crop | 0.327±0.051 | 6.42 | <0.001 | |
| Body weight × mean acorn crop | -0.025±0.032 | -0.77 | 0.44 | |

Relative success as cobreeders

We determined the number of young parented by 18 pairs of cobreeder males and seven pairs of joint-nesting females that were broodmates and that differed in size when they had been banded as nestlings. Although dominant birds tended to parent slightly more offspring than subordinate individuals [mean ± SE for male dominants vs. subordinates (based on wing length)=4.67±1.12 vs. 4.06±1.40, $N=18$; for females=5.14±1.61 vs. 4.00±2.23, $N=7$; for male dominants vs. subordinates (based on body weight)=5.58±1.48 vs. 5.58±1.97, $N=12$; for females=11.00±2.52 vs. 9.67±4.67, $N=3$], in no case was the difference significant (Fig. 4; only data based on wing length at banding shown).

Discussion

Although social dominance correlates with a variety of variables either known or likely to influence fitness in both non-cooperative (Ekman 1990; Duckworth and Badyaev 2007; Foerster et al. 2007; Ratcliffe et al. 2007; Silk 2007) and cooperative breeders (Pasinelli and Walters 2002; Hewett Ragheb and Walters 2011), few studies have investigated how

dominance hierarchies established as nestlings or juveniles translates into fitness or behavioral differences as adults. In this study, we used size differences among nestlings, known to correlate with dominance as juveniles, to investigate how within-brood dominance affects the probability of delayed dispersal and helping, inheritance of the natal territory, and ultimately achieving a breeding position within the study area in the cooperative breeding acorn woodpecker (Table 1).

On average, nearly half of nestlings banded when they were 21 days old (about 10 days prior to fledging) survived to their first spring, when dispersal first takes place. Our results demonstrate that within-brood dominance, as determined by relative size of nestlings, significantly influences their future prospects, with larger, dominant broodmates having significantly greater overwinter survivorship than their smaller broodmates. This finding adds to the already considerable hatch-order advantage of chicks emerging from earlier-laid eggs (Stanback 1991) and helps explain egg destruction by joint-nesting females, a behavior in which females destroy eggs laid by cobreeders in a way that minimizes asynchronous hatching and the costs a bird might otherwise suffer by laying later-hatching eggs that are likely to produce less competitive fledglings, if they survive at all (Mumme et al. 1983; Koenig et al. 1995).

Table 3 Relationship of nestling size to adult size using paired same-sex broodmates; statistics from binomial tests

| Nestling character | Adult character | Dominant larger as adult | Subordinate larger as adult | p value |
|--------------------|-----------------|--------------------------|-----------------------------|---------|
| Males | | | | |
| Wing length | Wing length | 26 | 16 | 0.16 |
| Wing length | Body weight | 29 | 18 | 0.14 |
| Wing length | Condition | 27 | 19 | 0.30 |
| Body weight | Wing length | 22 | 11 | 0.08 |
| Body weight | Body weight | 25 | 12 | 0.047 |
| Body weight | Condition | 24 | 13 | 0.10 |
| Females | | | | |
| Wing length | Wing length | 14 | 10 | 0.54 |
| Wing length | Body weight | 16 | 8 | 0.15 |
| Wing length | Condition | 16 | 8 | 0.15 |
| Body weight | Wing length | 11 | 8 | 0.65 |
| Body weight | Body weight | 17 | 3 | 0.003 |
| Body weight | Condition | 17 | 3 | 0.003 |

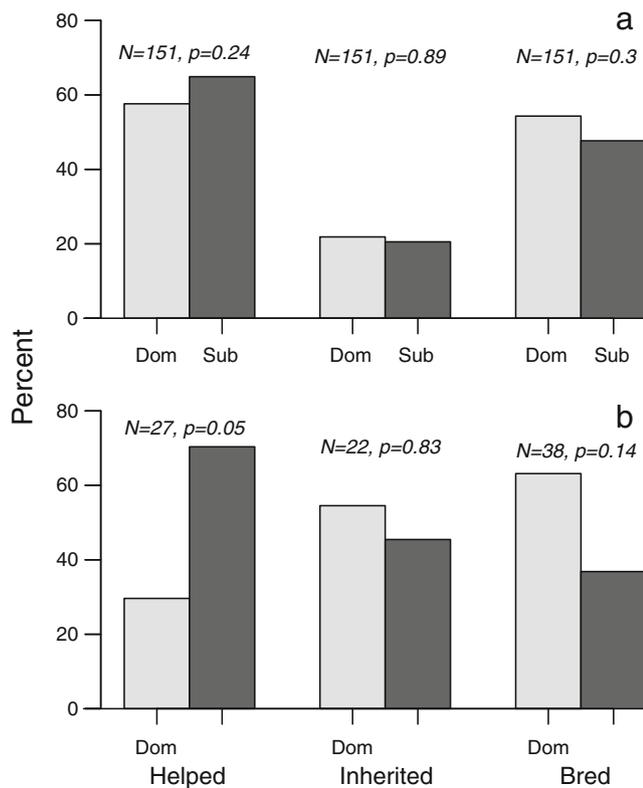


Fig. 2 The mean percent of male fledglings surviving their first winter that helped in their natal group as second-year birds, inherited and became a breeder in their natal group, and became a breeder somewhere in the study area, divided into dominants and subordinates as determined by relative wing length at banding. **a** Pairwise comparisons of male broodmates using all data; statistics from Fisher exact tests. **b** Using pairs of male broodmates where only one engaged in the target activity (helped, inherited, or bred); statistics from binomial tests

A similar relationship between dominance and juvenile survivorship was found by Stanback (1994), although sample sizes were small and the differences were not statistically significant. In general, we found a greater difference between broodmates when ranked according to

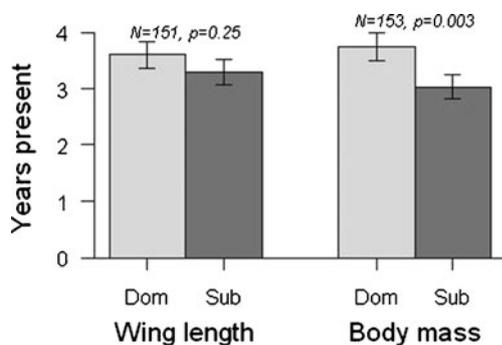


Fig. 3 Mean (\pm SE) number of years paired sets of male broodmates lived or were present in the study area divided between dominants and subordinates as determined by relative wing length and relative body weight at banding. Comparisons by Wilcoxon matched-pairs signed-ranks tests

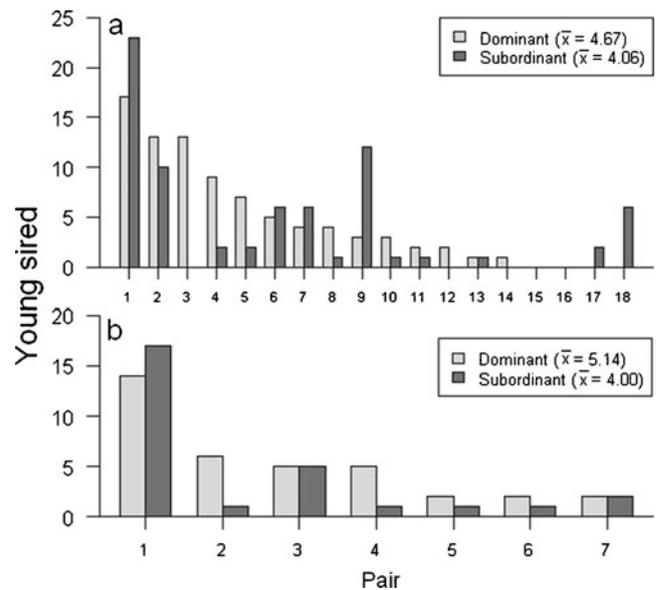


Fig. 4 Young parented by pairs of cobreeding broodmates, one of which was dominant and one of which was subordinate based on relative wing length at banding, determined by parentage analysis. **a** males ($N=18$, Wilcoxon matched-pairs signed-ranks test, $p=0.58$); **b** females ($N=7$, $p=0.28$). In a few cases, the birds being compared were not the only cobreeders and neither sired any offspring (as in **a**), pairs 15 and 16). Results based on body weight (not shown): males ($N=12$, $p=0.59$); females ($N=3$, $p=0.75$)

their wing length than according to body weight, in accord with Stanback’s (1994) conclusion that relative wing length was a better predictor of subsequent dominance than body weight, most likely because wing length is a more reliable indicator of overall size than body weight.

Although the acorn crop significantly influenced over-winter juvenile survivorship as expected—survivorship was greater when the acorn crop was good—its effect on the relative benefits of dominance were opposite expectations. In poor acorn years, subordinate survival (as determined by relative wing length) was 3.6% less than dominants, a difference that was not significant, while in good acorn years subordinates survived 8.0% less than dominants, a significant difference ($p=0.04$). Comparing birds of the same status (dominant or subordinate) in good vs. poor acorn years, dominants survived 5.7% better in good acorn years while subordinates survived only 3.2% better. Thus, although differences in resource availability enhanced juvenile survivorship for all birds, increased dominance conferred more of a survivorship advantage when resources were abundant than when they were limiting, contrary to our prediction. The behavioral mechanisms causing this unexpected result would clearly be of interest to investigate in more detail.

The fitness benefits of dominance and larger size did not end once birds survived their first winter (Table 1). Three significant differences were detected. First, we found that

for both sexes, heavier nestlings were heavier as adults, a phenotypic advantage that is likely to have beneficial fitness consequences in terms of survivorship. Second, when only one of two male broodmates became a helper as a second-year bird, it was significantly more likely to be the smaller, subordinate bird than the larger dominant individual, as predicted. Differences in the probability of inheriting the natal territory and achieving breeding status in the population were not significant between dominants and subordinates, contrary to our expectations.

Thus, in accord with the greater propensity for dispersal found among more aggressive male western bluebirds *Sialia mexicana* (Duckworth and Badyaev 2007), but counter to the cooperatively breeding red-cockaded woodpecker (Pasinelli and Walters 2002; Hewett Ragheb and Walters 2011), the non-cooperative Siberian jay (Ekman et al. 2002), and the social dominance hypothesis (Christian 1970; Gauthreaux 1978), it is subordinates, not dominants, that are more likely to remain in their natal territory as helpers when only one of them does so. This result indicates that, at least some cases, the competitive advantage of dominance allows birds to disperse more than subordinates and that helping is an option pursued by relatively inferior, subordinate birds unsuccessful at obtaining reproductive opportunities elsewhere in the population, a result supporting the observation that helpers compete vigorously for outside breeding opportunities (Koenig 1981; Hannon et al. 1985) and gain relatively small fitness benefits and are thus “making the best of a bad job” by helping rather than attempting to breed on their own (Koenig et al. 2011).

The finding that subordinates are more likely to remain as helpers than dominants is plausibly related to the third significant difference we detected, which was that dominants surviving to their first spring—determined by body weight in this case—remained in the study area significantly longer than subordinates. Because we are not able to distinguish between death and long-range dispersal (Koenig et al. 1996), we cannot be sure about the cause of this difference, but it is at least consistent with the hypothesis that subordinates, although less likely to disperse overall, may disperse farther when they do leave.

Acorn woodpeckers are particularly unusual in that it is relatively common for same-sex broodmates to ultimately cobreed together as adults. For example, 57 of 151 pairs (37.7%) of male broodmates that survived to their first spring were known to eventually cobreed together for at least one season, while 25 of 128 (19.5%) of female broodmates did so. We tested to see if partitioning of parentage between such individuals was related to size at banding and thus dominance as fledglings. Our sample sizes are currently relatively small, especially for females, but in no case did differences between putative dominants

and subordinates in the number of offspring parented in cobreeding attempts for either males or females approach significance.

The failure of dominants to monopolize parentage within cobreeding units is not surprising in the case of joint-nesting females that, because of egg destruction (Mumme et al. 1983; Koenig et al. 1995), are egalitarian and divide maternity of joint broods equally (Haydock and Koenig 2003). The situation among cobreeder males, however, is more ambiguous. Although considerable skew in paternity is typically found within broods, analyses of skew vis-à-vis age, adult body weight, or adult condition failed to detect any phenotypic correlate with success (Haydock and Koenig 2002). Indeed, switching of paternity, whereby one male cobreeder sires all or a majority of a brood in one nest while one of his cobreeders does so in a subsequent nest, is relatively common and suggests that reproductive partitioning may be equitable at the level of multiple, rather than individual, nests. Although more work remains to be done, our results here add dominance as indicated by relative nestling size as another phenotypic character that fails to correlate with subsequent reproductive skew among cobreeders in this population. This result counters expectations of concessions models predicated on the assumption that a dominant individual controls reproductive partitioning among cobreeding coalitions (Johnstone 2000; Magrath et al. 2004), and thus adds to the empirical difficulties of applying current reproductive skew models to this system (Koenig et al. 2009).

In summary, dominance relationships established as a consequence of relative body size as nestlings have significant consequences to overwinter survival and subsequent behavior of acorn woodpeckers, with larger, dominant broodmates experiencing greater survival and being less likely to remain as a helper in cases where only one of the two broodmates did so. There were no differences between dominants and subordinates, however, in the relative number of offspring parented among those that eventually cobred together in the population. Thus, size–dominance relationships established in the nest have significant fitness consequences in this species that last into some, but not all, aspects of their adult lives. Given that dominance is only imperfectly related to the indices of body size used here (Stanback 1994), it is likely that the advantage of dominance documented here is an underestimate of the real fitness benefits gained by dominant individuals in this population.

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