Original Article

Are you my baby? Testing whether paternity affects behavior of cobreeder male acorn woodpeckers

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Natural selection is expected to favor males that invest more in offspring they sire. We investigated the relationship between paternity and male behavior in the acorn woodpecker (*Melanerpes formicivorus*), a cooperative breeder that lives in family groups including offspring that remain on their natal territory, sometimes for years, and cobreeders of both sexes. Regardless of group composition, only one communal nest is attended at a time. Whereas cobreeding females share maternity equally, one male usually sires the majority of young in the group's communal nest. Copulations are rarely observed, and thus it has not been possible to link paternity to sexual behavior. There were no differences among cobreeder males that did or did not sire young in their propensity to roost in the nest cavity at night. However, cobreeder males that attended females continuously prior to egg-laying were more likely to successfully sire young than males that did not, and the relative share of feeding visits and time spent at the subsequent nest were positively related to a male's realized paternity. These differences in male behavior were partly due to differences among males and partly to plasticity in male behavior covarying with paternity share. Feedings by males successfully siring young also involved a larger proportion of nutritionally valuable insect prey. Males are aware of their paternity success, apparently because of their relative access to females prior to egg laying, and provide more paternal care at nests in which they are more likely to have sired young.

Key words: acorn woodpecker, confidence of paternity, mate-guarding behavior, paternal care, paternity assurance, sperm competition.

INTRODUCTION

It has long been recognized in species with internal fertilization that paternity is less certain than maternity (Birkhead and Møller 1995). This fundamental difference has resulted in considerable interest in how sperm competition and paternity uncertainty affect the care males provide, referred to here as "paternal care" irrespective of whether or not the male has sired young in the nest (Westneat and Sherman 1993; Sheldon 2002). Although there is evidence for male paternal care covarying with paternity (Møller and Birkhead 1993; Dixon et al. 1994; Whittingham and Dunn 2001), numerous examples exist where no relationship has been detected (Whittingham

et al. 1993; Yezerinac et al. 1996; Dickinson 2003; Bouwman et al. 2005). The latter situation presumably arises because males at best have only a general sense of their paternity and withholding paternal care jeopardizes the survivorship of any young they may have sired, regardless of whether they have been cuckolded or not (Dunn and Cockburn 1996; Whittingham and Dunn 2001). Moreover, withholding care may come at a cost to future fitness if males benefit from saving resources for future reproduction or by weakening social ties among group members and thus reducing the probability of siring young in the future (Kubitza et al. 2015; Cockburn et al. 2017).

The relationship between paternity and parental care is even more complex in cooperative breeders in which parental care and feeding behavior is dependent on the behavior of multiple

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individuals (Hatchwell 1999; Heinsohn 2004). In superb fairy-wrens (*Malurus cyaneus*), a socially monogamous cooperative breeder with extraordinarily high rates of extrapair paternity, dominant males provide paternal care even when the majority of young in their nest are sired by extra-group males. Males feed less when they have less paternity, but only when there are helpers available to compensate for their reduced paternal care (Dunn and Cockburn 1996). In cooperatively polygynandrous dunnocks (*Prunella modularis*) and alpine accentors (*P. collaris*), cobreeder males sharing a female adjust their paternal care relative to their mating access to the female during her fertile period (Burke et al. 1989; Davies 1992; Hartley et al. 1995). In both these latter species, copulations are frequently observed and appear to provide a clear behavioral cue that males use to assess paternity (Davies et al. 1995).

Here, we address the relationship between paternity and paternal care in cooperatively breeding acorn woodpeckers (*Melanerpes formicivorus*), a species that exhibits both helping-at-the-nest by offspring from prior years (nonbreeding helpers) and cooperative polygynandry in which multiple cobreeder males—generally brothers or a father and sons—share access to one female, or, in approximately 23% of groups, two or more joint-nesting females that are themselves typically sisters or a mother and daughter (Barve et al. 2019; Koenig et al. 2020). Extra-group parentage does not occur, and all young are sired by birds within the group (Dickinson et al. 1995). Copulations are rarely observed and presumably hidden from other males (Brownson 2015). Regardless of group composition, only one communal nest is attended at a time at which all group members typically help. Incest is rare, as reproductive vacancies are filled by unrelated birds from outside the social group (Haydock et al. 2001). When more than one female breeds within a group, maternity within a nest is shared equally. In contrast, reproductive skew among cobreeder males is high and generally one of the cobreedere males sires the majority of young in a nest (Barve et al. 2019). Importantly, the identity of the successful cobreeder male often switches from one brood to the next (Haydock and Koenig 2002, 2003), and there are no obvious behavioral differences among cobreeder males that indicates which males have successfully sired young and which have not.

Experiments in acorn woodpeckers in which a cobreeder male was denied access to the breeder female found that males removed temporarily during the egg-laying period sometimes destroyed the eggs and forced renesting when they were returned to the group after the clutch was complete. This indicates that male care is dependent on certainty of paternity, which was experimentally reduced in these cases. However, when returned males did not destroy the nest, they subsequently provisioned offspring. Since males could not have sired young in these cases but are still related to young in the nest, this suggests that paternal care by cobreeder males is also influenced by indirect fitness (Koenig 1990).

Our goal here was to examine the behavior of cobreeder males both prior to and during nesting to determine if their behavior was influenced by their realized paternity. Thus, we tested the hypothesis that cobreeder males base the amount of paternal care they provide on their realized paternity. In some cases, we had data for the same males across multiple nesting attempts, allowing us to partition variation in behavioral differences among cobreeder males (between-male effects) from plasticity in the response of individual males (within-male effects) to varying levels of paternity (van de Pol and Wright 2009; Westneat et al. 2011).

METHODS

Study population

Acorn woodpeckers are common in oak woodlands (*Quercus* spp.) throughout much of far western North America and live in year-round territorial groups of up to 15 individuals of all ages and both sexes (Koenig et al. 2020). Group composition is highly variable, ranging from a breeding pair to a polygynandrous core of breeders along with their nonreproductive offspring from prior years. In all cases, however, groups are family-based and composed of close relatives, except that breeder males are unrelated to breeder female(s) (Dickinson et al. 1995; Haydock et al. 2001). The population studied was located at Hastings Reservation in central coastal California (36°23′ N, 121°33′ W); birds were color-banded for individual identification.

We considered only groups with cobreeder males in the analyses; such groups characterized 45.9% of breeding groups studied between 1986 and 2016 ($N = 1017$ group-years). The number of cobreeder males varied from two to seven, although most groups (91.9%) had two to four cobreeder males (Table 1). Determination of breeder or helper status of birds within a group was based on their relationship to the breeders of the opposite sex in the group. Thus, birds immigrating into a group, whether singly or as a coalition, were considered putative breeders, whereas young born into a group were considered nonbreeding helpers until such time, if any, that an unrelated, opposite-sex individual (or individuals) replaced the previous breeder(s) following death or emigration. Once unrelated, opposite-sex birds joined the social group, all helpers of the opposite sex inherited breeding status and became putative cobreeders along with any remaining same-sex breeders (Koenig et al. 1984, 1998). Nonbreeding helpers were not considered in the analyses, except where we were interested in the behavior of cobreeder males in groups with and without helpers.

Field data

We quantified attendance and following behavior of breeder females by cobreeder males in polyandrous groups prior to nesting, as these were the most obvious behaviors that were likely to correlate with paternity. We refer to this as "mate-guarding" behavior even though males were quite possibly trying to attend the female in hopes of increasing copulatory access rather than, or in addition to, thwarting copulations by other males (Mumme et al. 1983; Dickinson and Leonard 1996).

Mate-guarding watches were conducted during the 2009–2012 spring breeding seasons. All mate-guarding groups studied contained only a single breeder female, as trying to follow more

Table 1

Distribution of groups with different numbers of cobreeder males in the population, 1986–2016

Number of breeder males	Number of groups	Percent of groups
1	550	54.1
2	271	26.6
3	110	10.8
4	49	4.8
5	28	2.8
6	5	0.5
7	4	0.4
Total	1017	100.0

than one breeder female in a group simultaneously added a level of difficulty that was impractical. Polyandrous family groups were visited at least once per week beginning in March to determine when mate guarding was initiated. The dates of onset, duration, and conclusion of mate guarding were recorded for nesting attempts in 2010, 2011, and 2012. Once initiation of mate-guarding behavior was confirmed, the group was subjected to 3-h watches (range 3–9; mean = 4) centered on the granary (a group's storage facility for acorns) and nest trees within each group's territory. The length of time males spent mate guarding ranged from 7 to 32 days; thus, the total number of watches at each group varied depending on how long mate-guarding behavior persisted. Watches were conducted on nonconsecutive days and distributed more or less evenly throughout the mate-guarding period.

Mate guarding was quantified by means of two metrics, following behavior and attendance behavior, both of which followed the protocol of Mumme et al. (1983). For the first of these, successful follows were defined as the number of times the breeding female flew more than 15 m away from a breeding male and the male followed her within 30 s of her departure; an unsuccessful follow was when the male failed to follow the female. Following behavior was then defined as a proportion of successful follows made by a male during each 3-hr mate-guarding watch. For attendance, a male was considered to be attending a female as long as the female was within 15 m of him and within his view. Attendance behavior was then expressed as a proportion of the total time the subject male attended the female and both were within the observer's view during the watch. We also determined the timing of each watch relative to the first egg date (day 0); days before the first egg date were negative and those after were positive. Observations continued until mate-guarding behavior ceased, which generally coincided with the onset of incubation around day +2 or +3.

Next, we quantified the care-giving (paternal) behavior of cobreeder males at nests. Data were based on nest watches during which observers sat in blinds and, using spotting scopes, recorded all feeding visits during 3-h watches conducted during the 32–34-day nestling period (Weathers et al. 1990; Koenig and Walters 2016). The number of watches per nest varied from 1 to 17 (mean ± standard deviation = 3.0 ± 1.7). For each feeding visit, we recorded bird identity, size of bolus being fed (1 = no obvious food seen; 2 =medium-size bolus—food seen but causing the bill to expand only 1–2 mm; 3 = large bolus—food expanding the bill >2 mm) and whether the food bolus consisted of insects or acorns. Also recorded was the time birds spent inside the nest cavity potentially brooding nestlings. Data were obtained from a total of 2820 nest watches (9708 h of observation) conducted between 1986 and 2016.

In order to focus analyses on the relative effort of cobreeder males within groups, we modified the total number of feeds and total time spent in the nest by dividing values for each cobreeder male by the total feeds or time in the nest contributed by all cobreeder males in the group across all watches at that nest. We refer to these modified variables as share of feeding visits and share of time in the nest, respectively.

Like other species of woodpeckers, males generally spend the night in the nest cavity incubating eggs or brooding the young (Kendeigh 1952; Short 1982). Given that there were multiple cobreeder males in the groups studied here, we tested whether males successful at mating and fertilizing eggs were more likely to roost nocturnally in the nest cavity than unsuccessful males.

Between 2009 and 2012, we recorded cobreeder males roosting at 25 different nests. Identity was determined by watching nests at dusk with a spotting scope and illuminating the color bands on birds as they came in to roost with a flashlight. As with behavior at the nest, we divided the number of times a cobreeder male roosted nocturnally by the total number of times all cobreeder males in that group roosted in the nest cavity to give the share of nocturnal roosting.

Parentage analyses

All birds were bled for genotyping when captured, which was generally either opportunistically at nests or in roosting cavities (Stanback and Koenig 1994) or when banded as nestlings. Blood was stored in Longmire's solution (Longmire et al. 1988) and stored at −20 °C on-site until DNA extraction and analysis.

For parentage, we used 8–18 microsatellite loci developed for acorn woodpeckers from protocols modified from Armour et al. (1994), Gibbs et al. (1997), and Jones et al. (2002). Amplicons for each locus were produced in up to six multiplexed polymerase chain reactions (QIAGEN Multiplex Plus) and sized on an Applied Biosystems 3730 DNA analyzer using Liz 500 as a molecular weight standard. We tested the loci used in our parentage assignments for deviations from Hardy-Weinberg Equilibrium (HWE) and linkage disequilibrium using GenePop 4.7.5 (Rousset 2008) with 1000 dememorizations, 100 batches, and 1000 iterations per batch. Acorn woodpeckers have mean life expectancy of 5.11 for males and 3.99 years for females (Koenig and Mumme 1987); therefore, we ran the analyses for every 5-year span (1990, 1995, 2000, 2005, 2010, 2015) using 52–78 candidate parents in each.

To reduce deviation caused by presence of relatives, we first selected one male and one female candidate parent from each social group (usually individuals with breeding status), and then eliminated individuals that were confirmed first-order relatives, usually because they were from the same natal group. Of the 18 loci we commonly used in determining parentage, 8 deviated from HWE in at least 1 year. Consequently, we examined assignments for all offspring paying particular attention to two loci that were difficult to score accurately. Genotypes were either corrected by examining Mendelian transmission across generations for an allele, or deleted if we suspected a null allele. We controlled for false discovery rate (Benjamini and Hochberg 1995) in the linkage disequilibrium tests due to the large number of pairwise loci comparisons. No locus was in disequilibrium in more than 1 year; thus, we included all 18 loci in parentage assignments.

Parentage was determined using CERVUS 3.0.7 (Marshall et al. 1998). We accepted assignments that produced at least 95% confidence for a single father–offspring dyad and excluded every possible male group member with putative breeding status within the previous 2 years. For all parental assignments, at most two mismatches were allowed in the assigned parental–offspring triad. Overall, paternity was assigned for 85.0% of 3460 offspring sampled during the study. For further details regarding parentage assignment, see Barve et al. (2019).

Statistical analyses

Analyses were conducted in R 4.0.2 (R Core Team 2020) using linear mixed-effects models (procedure lmer in package lme4 1.1–23 [Bates et al. 2015]), and generalized linear mixed-effects models (procedure glmer in package lme4 and procedure glmmTMB in package glmmTMB 1.0.2.1 [Brooks et al. 2017]). $P < 0.05$ was

considered statistically significant. We used three overlapping measures of a male's realized paternity in each nest. First was an all-or-none measure indicating whether the male sired all nestlings for which paternity was determined (sired all nestlings). Second was a dichotomous variable indicating whether the male sired at least one nestling (sired ≥ 1 nestling). Third was the proportion of nestlings sired by the male (share of nestlings sired). The mean (± standard deviation) number of young in nests for which parentage was determined was 2.9 ± 1.4 (range 1–8). The number of cobreeder males was less than or equal to the number of young in 64% of nests. The significance of number of cobreeder males in the models was unchanged using only the subset of nests for which this was the case, and thus the analyses described below used all nests.

We assumed a binomial error structure in analyses where the response variable was dichotomous (sired all nestlings and sired ≥ 1 nestling) or a noncontinuous proportion (following behavior and proportion of nestlings sired). For continuous proportions (attendance behavior and share of time in nest), we rescaled the data to remove 0s and 1s using the equation $x_i^* = (x_i(n - 1) + 0.5)/n$, where x_i^* was the rescaled version of the variable (x_i) and n was the total number of observations in the dataset. We then used procedure glmmTMB to perform a beta regression with logit link to test for differences vis-à-vis the number of putative cobreeder males (Douma and Weedon 2019). We did not include other potential variables in the analyses (e.g., age of the males), as our goal was to determine whether or not there was a relationship between cobreeder behavior and paternal care, not to investigate the differences between males that sired young in a nest and those that did not. This latter issue will be pursued elsewhere.

We first tested the relationship between mate guarding and realized paternity. Because mate guarding occurs prior to and during the period when paternity is presumably being determined, the response variables in these analyses were our measures of paternity. Plots of following behavior and attendance behavior indicated that a large proportion of cobreeder males guarded the female almost continuously (Figure 1a,b). Thus, for analysis, we divided these indices into two categories based on whether males followed or attended the female ≥95% of the time or not. The two dichotomous mate-guarding indices were considered fixed effects, but were analyzed in separate models because they were highly correlated (Pearson $r = 0.66$, df = 276, $P < 0.001$). Also included as fixed effects were the number of cobreeder males and days prior to end of incubation. Analyses included records for each mate-guarding watch, and thus male ID nested within group ID were included as random effects. To visualize the effect of attendance behavior on subsequent paternity, we used the predict function to plot the predicted share of offspring sired by cobreeder males depending on whether they attended the female continuously (≥95% of the time) or not.

Next, we investigated the relationship between realized paternity and paternal behavior of males at the nest. Because paternal behavior takes place after paternity has been determined, the response variables in these analyses were the measures of paternal behavior (share of feeding visits, share of time in nest, and share of nocturnal roosting). Fixed effects included the number of putative cobreeder males (number of cobreeder males) and one of the three measures of paternity success. For share of feeding visits and share of time in the nest, we also included the presence of helpers and the interaction between number of cobreeder males and presence of helpers as fixed effects, and nest ID nested within group ID as random effects. Models investigating nocturnal roosting included only nest ID as a random effect. Two additional variables
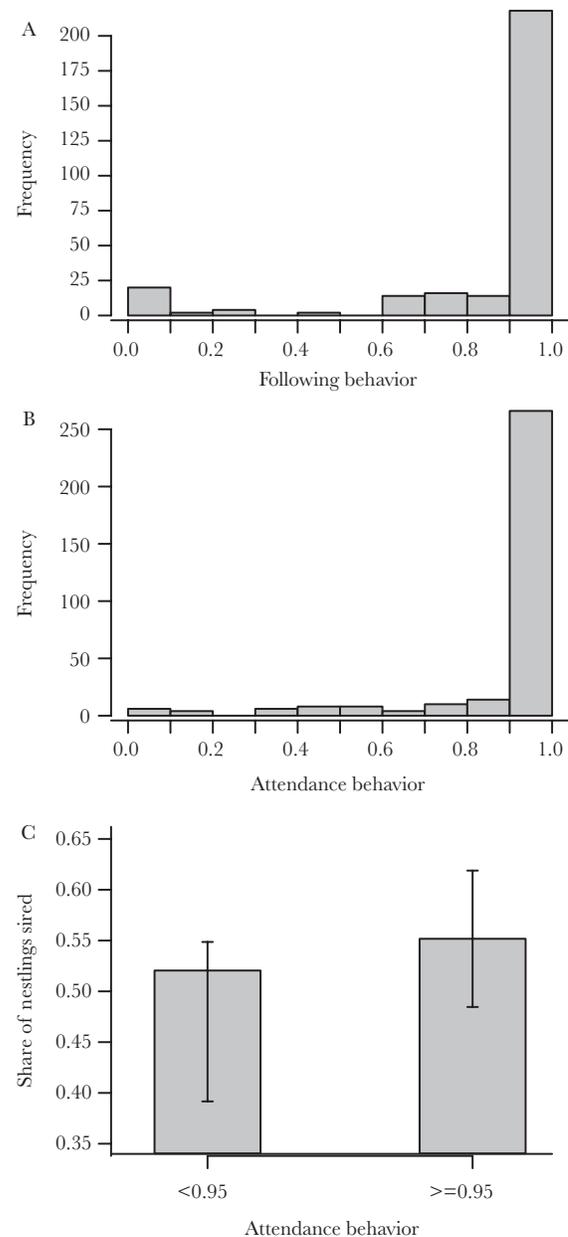
Figure 1
(a) The frequency with which cobreeder males followed the breeder female ($N = 290$ male-watches). Males followed the female ≥ 95% of the time during 71.0% of watches. (b) The frequency with which cobreeder males attended the breeder female ($N = 326$ male-watches). Males attended the female ≥ 95% of the time during 71.8% of watches. (c) The predicted mean ± standard error share of nestlings sired by cobreeder males attending the female < 95% and ≥ 95% of the time. For statistical results, see Table 2.

tested were mean bolus size and the proportion of feeds that consisted of insects—a food item of high nutritional quality—rather than acorns—a food item of relatively low nutritional quality and more easily acquired, as stored acorns are usually available from a group's granary (Koenig 1991). For bolus size, we calculated the mean size for all feeding visits for which estimates were obtained, weighting visits by the size of each bolus such that mean size = ([N bolus size = 1 visits × 1]+ [N bolus size = 2 visits × 2] + [N bolus size = 3 visits × 3])/(total N visits).

In the models for which share of feeding visits was a fixed effect, the interaction term between number of cobreeder males and presence of helpers was statistically significant. To visualize the effect of helpers on the share of paternal effort by cobreeder males, we used the predict function to plot the predicted share of feeding visits by cobreeder males with and without helpers, dividing cobreeders into those that sired all offspring and those that did not. The trends attributable to helpers for the other two indices of paternal care were qualitatively identical and not plotted. In all three models for which share of time in the nest was a fixed effect, the interaction term was not statistically significant and was omitted from the analyses presented.

Finally, we tested whether observed effects were due to differences among males (between-male effects) or plasticity in the paternal behavior of males relative to their paternity in the nest (within-male effects). For each male, we calculated mean paternity share at all nests at which he was a putative cobreeder and, for each nest, the difference between a male's observed paternity share and his mean paternity across all nests at which he was a cobreeder (centered paternity share). Including these two variables in a generalized linear mixed model as fixed effects separated within-male effects (centered paternity share) from between-male effects (mean paternity share). Including each cobreeder male's paternity share (the within-male effect) and the difference between the within- and between-male effects in a mixed model provided tests (based on the statistical significance of the difference variable) of whether the within- and between-male effects were statistically different (van de Pol and Wright 2009).

RESULTS

Mate-guarding behavior was quantified for 23 nests. In general, breeder males were highly vigilant in their surveillance of breeder females prior to egg laying. Overall, 71% of males followed and attended the female at least 95% of the time (Figure 1a,b). Partitioning these indices of mate-guarding behavior into two categories, we found no relationship between following behavior and paternity, but attendance behavior of the female was positively related to whether a male sired at least one offspring and the proportion of nestlings sired (Table 2; Figure 1c). In all models, the probability that any individual cobreeder male sired offspring

declined with the number of cobreeder males, and in one model, attendance behavior increased significantly as the watch was done closer to the start of incubation.

Overall, a large majority (790 of 839; 94.2%) of putative cobreeders were observed feeding at their respective nests. Nonetheless, there was a significant difference in feeding behavior among males related to paternity. Males successfully gaining paternity fed more frequently and spent more time in the nest cavity than less successful males (Figure 2; Table 3). More successful males were not, however, more likely to roost nocturnally in the nest cavity. In addition, there were again significant effects of the number of putative cobreeders, with the probability of paternity declining as the number of cobreeder males increased.

The models for feeding and time in the nest included the effects of helpers on the relationship between breeder paternity and paternal care (Table 3). For share of feeding visits, the interactions between presence of helpers and the measures of cobreeder reproductive success were statistically significant. The predicted share of feeding visits for putative cobreeder males with and without helpers depending on whether males did or did not sire all nestlings indicated that having helpers increased the share of feeding visits for males that sired all nestlings but decreased it for unsuccessful males (Figure 3). Thus, the presence of helpers magnified, rather than reduced, the difference in the share of feeding visits made by cobreeder males that successfully sired young.

Not only did cobreeder males successful at siring offspring feed more and spend more time at the nest, they also fed nestlings a higher proportion of insects than low-nutritional-quality acorns (Table 4). We detected no effect of paternity on the bolus size of food fed by cobreeder males.

Both between- and within-male effects contributed to observed differences in feeding visits. That is, cobreeder males differed in the extent to which they matched their paternal behavior to their realized paternity (between-male effect), and individual cobreeder males exhibited plasticity by adjusting their paternal behavior depending on their realized paternity at a particular nest (within-male effect). For time in the nest cavity, however, only the between-male effect was statistically significant (Table 5, top). There was no significant statistical difference between the between-male and within-male effects for either feeding or time in the nest (Table 5, bottom).

Table 2

Effect sizes ± standard error (*P*-value) of variables related to mate guarding by breeder males from generalized mixed models in which the dependent variables were (a) whether the male sired all nestlings or not; (b) whether the male sired at least one nestling or not; and (c) the proportion of nestlings sired by the male

Fixed effects	Response variable		
	(a) Sired all nestlings	(b) Sired ≥ 1 nestling	(c) Proportion of nestlings sired
(1) Following behavior (*N* = 170)			
Intercept	59.95 ± 19.98 (0.003)	10.66 ± 5.62 (0.06)	8.39 ± 2.39 (<0.001)
Number of cobreeder males	−24.89 ± 7.43 (<0.001)	−2.51 ± 0.89 (0.005)	−3.58 ± 0.75 (<0.001)
Days prior to end of incubation	0.32 ± 0.25 (0.20)	0.13 ± 0.09 (0.16)	0.03 ± 0.04 (0.39)
Following behavior	3.71 ± 3.90 (0.34)	−0.82 ± 1.08 (0.45)	0.29 ± 0.45 (0.53)
(2) Attendance behavior (*N* = 180)			
Intercept	26.71 ± 14.22 (0.06)	12.62 ± 5.65 (0.03)	6.63 ± 1.81 (<0.001)
Number of cobreeder males	−20.90 ± 7.13 (0.003)	−2.83 ± 0.88 (0.001)	−2.84 ± 0.54 (<0.001)
Days prior to end of incubation	0.46 ± 0.28 (0.10)	0.23 ± 0.09 (0.007)	0.06 ± 0.03 (0.06)
Attendance behavior	4.80 ± 4.79 (0.32)	2.03 ± 0.97 (0.04)	0.82 ± 0.35 (0.02)

Both following behavior and attendance behavior were divided into two categories (<0.95% and ≥ 95%). Sample sizes are number of watches.

A

B
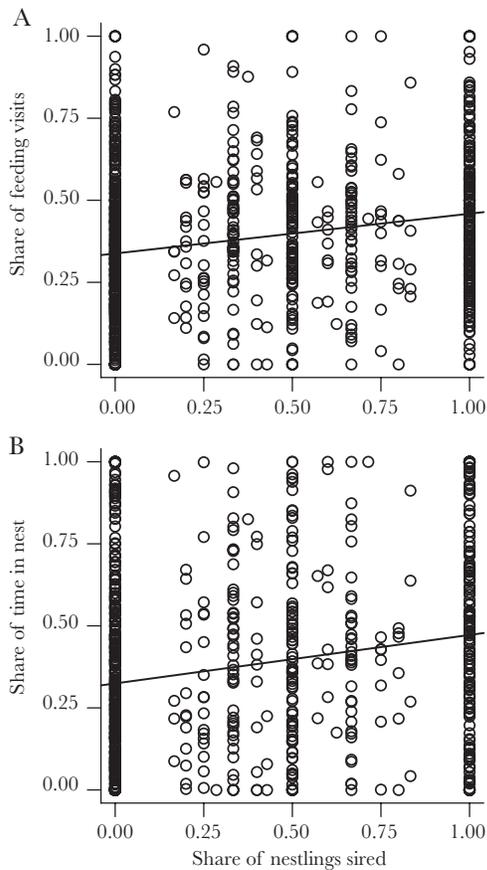
Figure 2

(a) The share of feeding visits made by cobreeder males plotted against the proportion of young sired in the nest. (b) The share of time in the nest plotted against the proportion of young sired in the nest. Lines represent linear regressions. For statistical results, see Table 3.

DISCUSSION

We investigated the relationship between paternal investment and realized paternity in the cooperatively polygynandrous acorn woodpecker, in which two to four (rarely up to seven) males share breeding status within the same social unit. One clear result was that the more cobreeder males that were in a group, the lower the probability that any one individual male sired young in the nest, consistent with high reproductive skew (Haydock and Koenig 2002, 2003; Barve et al. 2019). In terms of male behavior, mate-guarding by cobreeder males was generally intense and nearly all cobreeder males fed nestlings whether they successfully sired young or not. Nevertheless, cobreeder males that attended the female continuously during the prelaying period were more likely to sire offspring than those that did not, and males successfully siring young fed relatively more often, spent relatively more time at the nest, and were more likely to feed nutritionally high-quality prey (insects) than less successful males. This extends previous experimental work demonstrating that some cobreeder males will destroy a nest and force renesting when removed temporarily, denying them the opportunity to attend or copulate with the breeder female during the prelaying period (Koenig 1990).

Thus, acorn woodpeckers can be added to other cooperatively polyandrous or polygynandrous species, including dunnocks and

alpine accentors (Burke et al. 1989; Davies et al. 1995), Smith's longspurs (*Calcarius pictus*) (Briskie et al. 1998), and white-browed scrubwrens (*Sericornis frontalis*) (Whittingham and Dunn 1998) in which both a paternity cue—usually copulatory access during the female's fertile period—and a positive relationship between paternity and paternal care have been reported (Whittingham and Dunn 2001). Two apparent exceptions are the New Zealand pukeko (*Porphyrio porphyrio*) and Galápagos hawk (*Buteo galapagoensis*), both of which breed in polyandrous groups in which all males copulate with the breeder female, but no correlation between paternity and paternal care has been found (Jamieson et al. 1994; Faaborg et al. 1995; DeLay et al. 1996), although both systems warrant further study.

The systems discussed thus far include only species in which multiple males are unrelated to the breeder female and thus potential breeders, whereas the majority of work on kin discrimination in cooperative breeders has focused on nonbreeding helpers that are constrained from breeding due to incest avoidance (Koenig and Haydock 2004; Koenig et al. 2016). Studies of such nonbreeding helpers has revealed strong evidence for kin discrimination whereby helpers provide more care to young to which they are more closely related (Griffin and West 2003; Green et al. 2016). Differences in genetic relatedness in these cases typically depends on whether the genetic parent of the sex opposite that of the helper has been replaced by a new, unrelated individual or not, and thus whether helpers are full- or half-siblings to the young they are (or are not) helping to raise. In at least some cases, however, helpers have been found to use vocal recognition cues to assess kinship (Sharp et al. 2005; McDonald and Wright 2011). Given the impressive cognitive abilities of acorn woodpeckers to recognize and discriminate associations (Pardo et al. 2018, 2020), similar kin discrimination by nonbreeding helper acorn woodpeckers is possible. Here, however, we restricted our attention to the extent to which cobreeder males, all of which are attempting to mate and father young, can assess their success at siring offspring in the nest and adjust their paternal behavior accordingly. In contrast to the case of nonbreeding helpers, their genetic relatedness to young in the nest is dependent on their confidence of paternity as well as their ability, not yet tested in acorn woodpeckers, to discriminate young in the nest that they have or have not sired.

Beyond this distinction between kin discrimination by nonbreeding helpers and by potential cobreeders, there are several key differences between the acorn woodpecker breeding system and other cooperatively polyandrous and polygynandrous species. First, copulations in acorn woodpeckers are rarely observed. Instead, females engage in cryptic sexual behavior, possibly copulating inside roosting cavities (Brownson 2015). Cryptic sexual behavior may reduce conflict among males and obscure paternity (Møller and Birkhead 1993), thereby minimizing the possibility that some males will reduce provisioning at the nest (Westneat et al. 1990; Ben Mocha 2020). Since we do not observe copulations, we cannot test the hypothesis that male paternal care is dependent on copulating with the breeder female.

Another intriguing aspect of cryptic sexual behavior is that it is diametrically opposite the pattern found in several polyandrous species in which females mate openly and frequently, apparently with a similar result of obscuring paternity. Examples include tree swallows *Tachycineta bicolor* (Crowe et al. 2009), northern fulmars *Fulmarus glacialis* (Hunter et al. 1992), and African lions *Panthera leo* (Hrdy 1979; Packer and Pusey 1983; Davies and Boersma 1984). The idea that these very different behaviors—cryptic versus open and frequent sexual behavior—have potentially evolved in part

Table 3

Effect sizes ± standard error (*P*-value) of variables related to behavior at the nest by cobreeder males from generalized mixed models

	Response variable		
Fixed effects	(a) Share of feeding visits	(b) Share of time in nest	(c) Share of nocturnal roosting
(1) Sired all nestlings ($n = 480; 427; 123$)			
Intercept	0.808 ± 0.050 (<0.001)	0.422 ± 0.227 (0.06)	1.111 ± 0.469 (0.018)
N cobreeder males	-0.473 ± 0.013 (<0.001)	-0.317 ± 0.062 (<0.001)	-0.530 ± 0.160 (<0.001)
Sired all nestlings	0.149 ± 0.039 (<0.001)	0.350 ± 0.127 (0.006)	-0.360 ± 0.383 (0.35)
Presence of helpers	-0.065 ± 0.033 (0.04)	-0.043 ± 0.125 (0.73)	—
Sired all nestlings × presence of helpers	0.139 ± 0.051 (0.007)	—	—
(2) Sired > 1 nestling ($n = 835; 738; 123$)			
Intercept	0.865 ± 0.042 (<0.001)	0.526 ± 0.185 (0.004)	0.701 ± 0.539 (0.19)
N cobreeder males	-0.488 ± 0.010 (<0.001)	-0.359 ± 0.048 (<0.001)	-0.460 ± 0.162 (0.005)
Sired ≥ 1 nestling	0.091 ± 0.030 (0.003)	0.235 ± 0.092 (0.01)	0.248 ± 0.319 (0.44)
Presence of helpers	-0.133 ± 0.029 (<0.001)	-0.058 ± 0.094 (0.54)	—
Sired ≥ 1 nestling × presence of helpers	0.147 ± 0.038 (<0.001)	—	—
(3) Share of nestlings sired ($n = 835; 738; 123$)			
Intercept	0.866 ± 0.041 (<0.001)	0.491 ± 0.184 (0.008)	0.887 ± 0.527 (0.09)
N cobreeder males	-0.484 ± 0.010 (<0.001)	-0.351 ± 0.049 (<0.001)	-0.485 ± 0.163 (0.003)
Share of nestlings sired	0.093 ± 0.037 (0.012)	0.348 ± 0.114 (0.002)	0.083 ± 0.397 (0.83)
Presence of helpers	-0.124 ± 0.026 (<0.001)	-0.047 ± 0.094 (0.62)	—
Share of nestlings sired × presence of helpers	0.219 ± 0.047 (<0.001)	—	—

Results are summarized for nine models. Models in which the three measures of male reproductive success were fixed effects are in sections (1)–(3). Columns (a)–(c) summarize models in which the three different indices of paternal care were used as response variables. Presence of helpers and the interaction between the measure of male reproductive success and presence of helpers was included in the (a) and (b) models; however, the interaction term was not statistically significant for any of the (b) models and was omitted from the results presented here. Sample sizes in parentheses are for analyses (a), (b), and (c), respectively.

with the same adaptive result has not, as far as we know, been previously recognized.

A second way in which the acorn woodpecker system differs from many other cooperative polyandrous species is that there is no extra-group paternity (Dickinson et al. 1995; Haydock et al. 2001), as is fairly common in white-browed scrubwrens (Whittingham et al. 1997) and rampant in superb fairy-wrens (Dunn and Cockburn 1996). Instead, young not sired by a particular male acorn woodpecker are invariably sired by one of his cobreeders, and there is no variation in paternity share among singleton males, who sire all young in the nests of their group (Dickinson et al. 1995). A high proportion of groups, however, contain nonbreeding helpers, irrespective of the number of breeder males. Helpers provide compensatory care, allowing breeders to reduce their parental effort (Koenig and Walters 2012), but, as shown here, do not reduce the positive correlation between paternity and paternal care among cobreeder male acorn woodpeckers.

A key difference between acorn woodpeckers and many other cooperatively polyandrous species is that cobreeder acorn woodpeckers are close relatives. This, combined with the absence of extra-group parentage, means that offspring are closely related to all breeders regardless of the offspring's genetic parents. Koenig and Mumme (1987) estimated the mean relatedness between cobreeder males and offspring in a group to be between 0.293 and 0.362, depending on the number of cobreeder males. Consequently, there are significant inclusive fitness benefits to be gained by cobreeder males even if they fail to sire *any* young in a nest, in contrast to species in which cobreeders are nonrelatives and thus the coefficient of relatedness between a male and offspring sired by his cobreeders is 0.

In species in which cobreeders (or extrapair males) are nonrelatives, there should be strong selection for kin discrimination (Kramer and Russell 2014). Given the close genetic relatedness of cobreeders to all offspring in acorn woodpecker nests, however, we would expect much weaker selection for kin discrimination. It is consequently impressive and somewhat surprising that cobreeder male acorn woodpeckers adjust their paternal care based on their paternity. It remains to be tested whether males recognize individual offspring that they have or have not sired, although this is probably unlikely (Kempenaers and Sheldon 1997).

Differences in feeding behavior and time spent at the nest were due to both differences among males (between-male effects) and, in the case of share of feeding visits, plasticity in the propensity for males to feed relatively more at nests where they had greater paternity share (within-male effects). The significant between-male effects in feeding behavior and time in the nest cavity made by cobreeder males suggests that differences among males related to personality, age, or some other phenotypic character are likely to be important for these aspects of paternal care. Plasticity in male behavior (within-male effect) was also important, particularly in the case of feeding behavior. In general, parenting behaviors are highly responsive to environmental changes (Royle et al. 2012, 2014), and careful study of the house sparrow (*Passer domesticus*) had suggested that personality and plasticity are interrelated (Westneat et al. 2011). More detailed analyses of these phenomena could reveal a great deal about the selective factors driving the unusual polygynandrous mating system of acorn woodpeckers (Dingemanse and Wolf 2013; Alonzo 2015).

For males to adjust their paternal behavior based on their realized paternity, as found here, the benefit of reducing care must exceed the cost (Dunn and Cockburn 1996), and provising at the nest must entail a cost in general. Potential benefits of reduced care include gaining additional mating opportunities and increased male
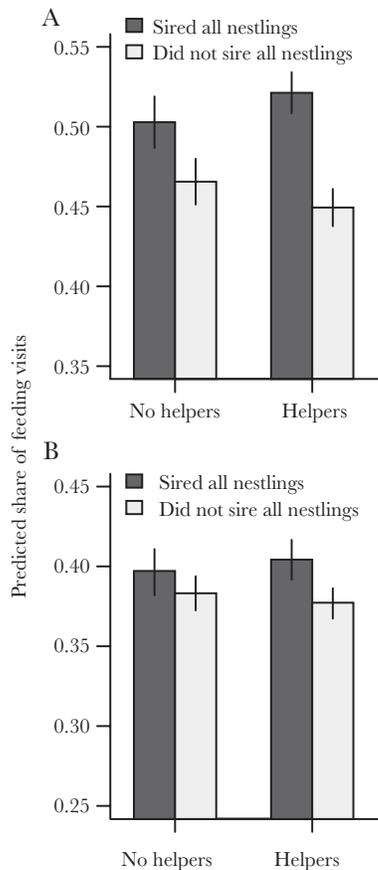
Figure 3

Predicted values for the share of feeding visits by cobreeder males for groups with (a) two cobreeder males and (b) three cobreeder males, with and without helpers, partitioned between males that sired all nestlings and those that did not. For statistical results, see Table 3.

survival, whereas a potential benefit of increasing care is greater paternity share in subsequent broods (Whittingham and Dunn 2001). There is no extra-group paternity in this population, so males feeding less do not gain the opportunity for additional matings elsewhere. Whether males feeding at a nest experience higher survivorship remains to be tested, although it would seem unlikely given that the difference in provisioning rates is small. More likely is the possibility that males providing more care may benefit by a greater paternity share in future breeding attempts, but this remains to be tested as well.

We propose two factors that render provisioning offspring costly in general. First, second nests of acorn woodpeckers are often initiated before nestlings have fledged from the first nest (Koenig et al. 2020). Thus, cobreeders that continue to provide paternal care at a nest are foregoing the opportunity to mate guard a female that may be about to lay eggs in a second nest. Second, recent work has found that cobreeders spend an unexpectedly large amount of time foraying off their territory (Barve et al. 2020). Thus, males caring for offspring are giving up the opportunity to engage in such extra-territorial forays. Although the reasons for such forays are as yet unclear, foregoing such forays to provision young is another cost of paternal care and provides a rationale for the differences in behavior between males with and without paternity at nests.

Table 4

Effect size ± standard error (*P*-value) of mean bolus size and the proportion of insects fed by cobreeder males for models in which the dependent variables were (a) whether the male sired all nestlings or not; (b) whether the male sired at least one nestling or not; and (c) the share of nestlings sired by the male

	Response variable	
Fixed effects	(a) Mean bolus size	(b) Proportion of insects fed
(1) Sired all nestlings (*N* = 446; 480)		
Intercept	1.973 ± 0.098 (<0.001)	0.763 ± 0.042 (<0.001)
Number of cobreeder males	−0.069 ± 0.035 (0.05)	−0.470 ± 0.013 (<0.001)
Sired all nestlings	−0.027 ± 0.032 (0.39)	0.230 ± 0.026 (<0.001)
(2) Sired ≥1 nestling (*N* = 779; 835)		
Intercept	2.038 ± 0.076 (<0.001)	0.757 ± 0.036 (<0.001)
Number of cobreeder males	−0.085 ± 0.026 (0.001)	−0.477 ± 0.011 (<0.001)
Sired ≥ 1 nestling	−0.028 ± 0.025 (0.26)	0.179 ± 0.019 (<0.001)
(3) Share of nestlings sired (*N* = 779; 835)		
Intercept	2.024 ± 0.075 (<0.001)	0.758 ± 0.034 (<0.001)
Number of cobreeder males	−0.084 ± 0.026 (0.001)	−0.474 ± 0.010 (<0.001)
Share of nestlings sired	0.006 ± 0.009 (0.55)	0.075 ± 0.007 (<0.001)

Results are summarized for six models. Rows list the independent variables (where (1)–(3) are the measure of male reproductive success used as a fixed effect in the models) while columns (a) and (b) list the response variables. Samples sizes in parentheses are for models in columns (a), and (b), respectively.

Table 5

Effect size ± standard error (*P*-value) of variables related to behavior at the nest by cobreeder males from models separating within-male and between-male effects

	Response variable	
Fixed effects	(a) Share of feeding visits (*N* = 835)	(b) Share of time in nest (*N* = 738)
(1) Test of within- and between-male effects		
Intercept	0.755 ± 037 (<0.001)	0.405 ± 0.169 (0.02)
N cobreeder males	−0.475 ± 0.010 (<0.001)	−0.340 ± 0.047 (<0.001)
Within-male effects (centered paternity share)	0.193 ± 0.035 (<0.001)	0.254 ± 0.165 (0.12)
Between-male effects (mean paternity share)	0.251 ± 0.032 (<0.001)	0.421 ± 0.152 (0.006)
(2) Test of relative size of within- vs. between-male effects		
Intercept	0.755 ± 037 (<0.001)	0.405 ± 0.169 (0.02)
N cobreeder males	−0.475 ± 0.010 (<0.001)	−0.340 ± 0.047 (<0.001)
Within-male effects (paternity share)	0.193 ± 0.035 (<0.001)	0.254 ± 0.165 (0.12)
Between-male − within-male effects	0.059 ± 0.048 (0.22)	0.167 ± 0.223 (0.45)

Results are summarized for four models. Rows list the fixed effects while columns (a) and (b) list the response variables.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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