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Lifetime inclusive fitness effects of cooperative polygamy in the acorn woodpecker

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Although over 50 y have passed since W. D. Hamilton articulated kin selection and inclusive fitness as evolutionary explanations for altruistic behavior, quantifying inclusive fitness continues to be challenging. Here, using 30 y of data and two alternative methods, we outline an approach to measure lifetime inclusive fitness effects of cooperative polygamy (mate-sharing or cobreeding) in the cooperatively breeding acorn woodpecker *Melanerpes formicivorus*. For both sexes, the number of offspring (observed direct fitness) declined while the number of young parented by related cobreeders (observed indirect fitness effect) increased with cobreeding coalition size. Combining these two factors, the observed inclusive fitness effect of cobreeding was greater than breeding singly for males, while the pattern for females depended on whether fitness was age-weighted, as females breeding singly accrued greater fitness at younger ages than cobreeding females. Accounting for the fitness birds would have obtained by breeding singly, however, lifetime inclusive fitness effects declined with coalition size for males, but were greater for females breeding as duos compared to breeding singly, due largely to indirect fitness effects of kin. Our analyses provide a road map for, and demonstrate the importance of, quantifying indirect fitness as a powerful evolutionary force contributing to the costs and benefits of social behaviors.

acorn woodpecker | cooperative breeding | cooperative polygamy | inclusive fitness | *Melanerpes formicivorus*

Cooperative breeding is a relatively uncommon but widespread reproductive strategy in vertebrates including birds, mammals, and fishes (1–3). It consists of two main phenomena. The more common is helping at the nest in which individuals ("helpers"), beyond a core pair of breeders, assist in raising nondescendant young. The primary evolutionary drivers of helping behavior are either ecological constraints, rendering helping the "best of a bad job" for individuals unable to find a territory or mate and breed independently, or benefits derived from social cooperation among group members in temporally variable environments (4, 5). In either case, helpers rarely parent young in their natal group, primarily because of incest avoidance (6). Instead, indirect fitness (i.e., kin selection) is an important factor selecting for helping behavior, since most helpers are young that delay dispersal and assist their genetic parents (7, 8). In Tibetan ground tits *Pseudopodoces humilis*, for example, the indirect fitness helpers gain by increasing the lifetime reproductive success of related breeders compensates for loss in personal reproductive success (direct fitness), resulting in an apparent behavioral polymorphism in which about 25% of adult males act as helpers each year (9).

The second phenomenon encompassed by cooperative breeding is cooperative polygamy, in which more than two breeding adults form stable social groups with or without helpers (8). Several forms are known, depending on whether females nest by themselves with cobreeding males, nest jointly with one or more females, and whether cobreeding males and joint-nesting females share mates. Overall, however, cooperative polygamy is rare, occurring in only about 2.5% of cooperatively breeding taxa (8, 10). As a result, the ecological influences and evolutionary consequences of this phenomenon are poorly understood.

Acorn woodpeckers *Melanerpes formicivorus* exhibit both forms of cooperative breeding (11–13). A large proportion of birds act as nonbreeding helpers in their natal group for one or more years, due primarily to ecological constraints that restrict dispersal and independent breeding (4, 14). Similarly, cooperative polygamy (cobreeding by males; cobreeding, or joint-nesting, by females) has been proposed to be driven by ecological constraints (7, 10, 15), but alternatively, cobreeding may confer benefits that result in greater lifetime fitness compared to independent breeding (11). For example, cobreeders may be better able to defend their territory from potential usurpers (13) or their nests from predators (16). Cobreeding may also generate indirect fitness benefits that exceed direct fitness losses (17). Yet another possibility is that the strategies of cobreeding and singular breeding may

Significance

Sharing mates (cooperative polygamy or cobreeding) is a rare, poorly understood behavior. We determined the lifetime inclusive fitness effects of cobreeding in the cooperatively breeding acorn woodpecker *Melanerpes formicivorus*, including direct fitness (personal reproduction) and indirect fitness (reproduction by cobreeding kin). The results indicated no inclusive fitness advantage to cobreeding for males compared to breeding singly, whereas females breeding as duos experienced higher inclusive fitness than singletons, due largely to indirect fitness effects. Results demonstrate the role of indirect selection as a powerful evolutionary force and highlight key differences among factors selecting for mate-sharing between the sexes in this highly social species.

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Table 1. Estimation of inclusive fitness effect of cooperative polygamy

Fitness component	Description	Values multiplied by	Details
Observed direct fitness	Lifetime reproductive success	r_{po}	*N* offspring parented by *i*
Observed indirect fitness	*N* offspring of *j's*	$r_{po} \times r_{cob}$	*N* young produced by the same-sex cobreeders that were *not* parented by *i*
Observed inclusive fitness	Observed direct fitness + observed indirect fitness		
Alternative direct fitness effect	*N* offspring parented by *i* in the absence of all *j's*	Dominant breeder: r_{po} Subordinate breeder: $r_{po} \times p_{disp}$	Dominant breeder: assumes *i* breeds singly. Subordinate breeder: assumes *i* leaves group and attempts to breed by itself
Alternative indirect fitness effect	*N* offspring of *j's* in the absence of *i*	Dominant breeder: $r_{po} \times r_{cob} \times p_{disp}$ Subordinate breeder: $r_{po} \times r_{cob}$	Dominant breeder: assumes *j's* are expelled and attempt to breed elsewhere. Subordinate breeder: assumes *j's* breed without *i*
Net direct fitness effect	Observed direct fitness – alternative direct fitness effect		Net fitness derived through direct reproduction
Net indirect fitness effect	Observed indirect fitness – alternative indirect fitness effect		Net fitness derived through indirect (kin) selection
Inclusive fitness effect	Net direct fitness effect + net indirect fitness effect		Total fitness effect

i = focal individual; *j's* = same-sex cobreeders.
Coefficient of relatedness between parents and their genetic offspring = r_{po}; between cobreeders = r_{cob}. Probability of dispersing and obtaining a territory and mate = p_{disp}, which varied depending on the size of the coalition (*Materials and Methods*).

be a behavioral polymorphism that confers equivalent lifetime fitness benefits (18).

Here, we quantify the lifetime inclusive fitness effects of cooperative polygamy relative to singular breeding by acorn woodpeckers using two methods. Quantifying the consequences of cobreeding in this system is challenging because, during an individual's breeding lifetime, it may breed singly in some years and as part of a coalition in others. We address this problem by determining the fitness effects of cobreeding in each year over the lifetime of individuals and comparing the fitness of individuals in the population based on their cobreeding histories. This approach avoids many of the difficulties associated with estimating lifetime inclusive fitness effects (19–21) and can be applied to other long-lived species whenever individual behavior varies temporally and the fitness of relevant behavioral alternatives can be estimated.

A second difficulty in quantifying inclusive fitness is the lack of clear terminology and confusion over its definition (21–24). As defined by Hamilton (25, 26), inclusive fitness is the effect of behaviors performed by a focal individual on his or her own fitness and any related individuals affected by the focal individual's behaviors. Inclusive fitness is therefore the property of an individual (22) and interpretable in comparison to individuals not engaging in the relevant behaviors (21). Fitness effects are often cast in the form of "Hamilton's rule" $rb - c > 0$, where c is the cost to the focal individual performing the behavior, b is the benefit to the recipients conferred by the behavior of the focal individual, and r is the coefficients of relatedness between the focal individual and recipients. Here, we estimate the lifetime inclusive fitness effects of a specific behavior—cooperative polygamy—rather than the broad-sense inclusive fitness of an individual as originally conceived by Hamilton. Further, we sidestep the nuanced, but important, distinctions among inclusive fitness, Hamilton's rule, and kin selection (22) to focus on a method for empirically estimating inclusive fitness effects, thereby encouraging studies that will illuminate the role of inclusive fitness and kin selection in the evolution of social adaptation.

A series of values are required to estimate the lifetime inclusive fitness effect of a behavior (27–29). Building on prior studies (30), the terminology we use for these quantities is summarized in Table 1. We refer to the number of offspring of the focal individual as observed direct fitness and the number of offspring the focal individual would have produced had it not performed the behavior as alternative direct fitness effect. Net direct fitness effect is then observed direct fitness minus alternative direct fitness effect. Net indirect fitness effect is the effect of the behavior of the focal individual on recipients (observed indirect fitness) minus the indirect fitness recipients would have achieved had the behavior not been performed (alternative indirect fitness effect). Observed inclusive fitness is observed direct fitness plus observed indirect fitness, while the inclusive fitness effect of the behavior is net direct fitness effect plus net indirect fitness effect. In all cases, components are weighted by the genetic relatedness between the focal individual and recipients; thus, 0.5 unit = 1 offspring equivalent (31). We add "effect" to all terms except the observed fitness values to emphasize that they pertain to the behavior of interest. For brevity, however, we do not always include "effect" when referring to these components below.

Fitness values were determined in two ways. First, we used the lifetime number of offspring produced. This assumed a stable population over time, as each offspring was counted the same irrespective of when during the life of an individual it was produced (32). We contrast fitness based on the number of offspring produced with fitness estimated using projection matrices, a commonly used approach that accounts for the timing of reproduction by weighting early reproduction more heavily (33, 34). These two methods yield identical results for populations at equilibrium (35). However, our population grew steadily over the study period (12), and thus projection matrix-based fitness measures are potentially appropriate.

We examined the relationship between fitness components and an index of cooperative polygamy (the mean cobreeder coalition size in which a bird belonged over its breeding lifetime) using a regression approach. Models included mean coalition size (both linear and, when statistically warranted, second-order polynomials), thus incorporating other life-history differences potentially related to mean coalition size. For example, if birds that bred in larger cobreeder coalitions lived longer or on higher-quality territories, such differences would be incorporated into the effects of mean breeding coalition size (11, 15). We visualized the fitness effects of cooperative polygamy by estimating the components of inclusive fitness for values of mean coalition size varying from 1 to 4.25 for males and 1 to 3.25 for females. To understand the differences between the results from the two analyses, we calculated mean age of first reproduction for males and females.

Results

Life histories were compiled for 566 birds (320 males and 246 females) that bred within the population from 1987 to 2006 inclusive, over which period paternity was determined for 85% and maternity for 87% of offspring using genetic tools (N = 2,186). The mean (±SE) number of years birds bred in the population was 4.00 ± 0.19 (range 1 to 17) for males and 3.40 ± 0.17 (range 1 to 14) for females. For both males and females, modal breeding coalition size was one (breeding singly) (*SI Appendix*, Fig. S1). The maximum breeder coalition size observed was eight for males and four for females, but 93.7% of male coalitions (N = 821) were three or fewer and 97.4% of female coalitions (N = 808) were one or two birds. Among birds present as breeders for ≥ 2 y, 40% of males (N = 91 of 228) and 37% of females (N = 61 of 166) bred both singly and with at least one other bird during their lifetimes.

Mean coalition size significantly affected nearly all components of fitness in both sexes (*SI Appendix*, Tables S1 and S2). In males, observed direct fitness generally decreased while observed indirect fitness generally increased with coalition size (Fig. 1 *A* and *B*). After accounting for the fitness birds would have achieved had they bred singly (alternative direct and indirect fitness), net direct fitness was unrelated to mean coalition size estimated by offspring produced but curvilinearly related to coalition size based on projection matrices (Fig. 1 *C* and *D*). In contrast, net indirect fitness decreased significantly with coalition size based on offspring produced but was unrelated to coalition size using projection matrices. Observed inclusive fitness peaked at intermediate-sized coalitions (duos and trios), while inclusive fitness effect decreased linearly using both methods (Fig. 1 *E* and *F*).

Similarly, in females, observed direct fitness decreased, and observed indirect fitness generally increased, with mean coalition size (Fig. 2 *A* and *B*). Both methods found no statistical relationship between net direct fitness and mean coalition size, while net indirect fitness peaked at intermediate-sized coalitions (Fig. 2 *C* and *D*). The inclusive fitness effect of cobreeding was curvilinearly related to mean coalition size using both methods of estimating fitness (Fig. 2 *E* and *F*). In contrast, observed inclusive fitness declined linearly with increasing mean coalition size estimated by offspring produced but peaked at intermediate-sized coalitions when estimated by projection matrices.

We investigated the differences in observed inclusive fitness of both sexes estimated by the two methods by determining the

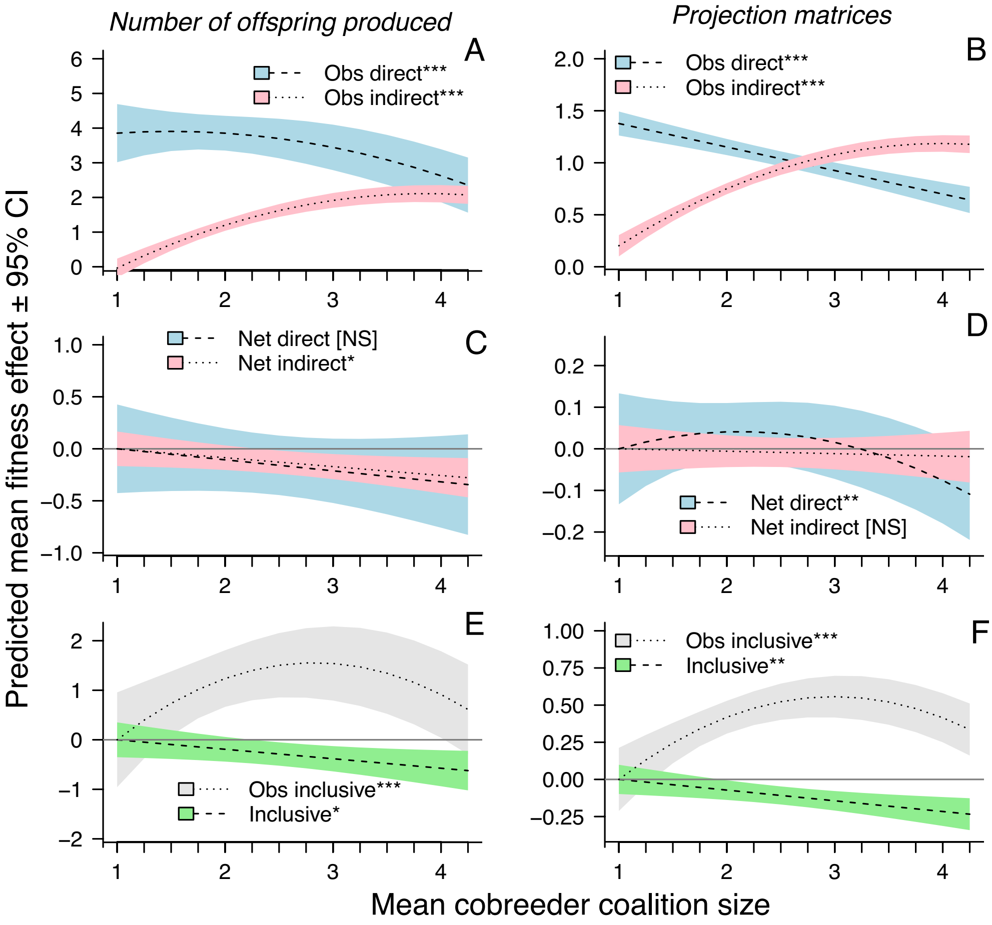

Fig. 1. Estimated lifetime fitness effect (mean ± 95% CI) of male fitness using number of offspring on left side (N = 320) and projection matrices on right side (N = 260) as a function of mean cobreeder coalition size. (*A* and *B*) Observed direct and observed indirect fitness effect; (*C* and *D*) net direct and net indirect fitness effect; (*E* and *F*) observed inclusive and inclusive fitness effect. Significance values from regression models including linear and (when significant) quadratic effects: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = $P > 0.05$. Statistical details in *SI Appendix*, Tables S1 and S2.

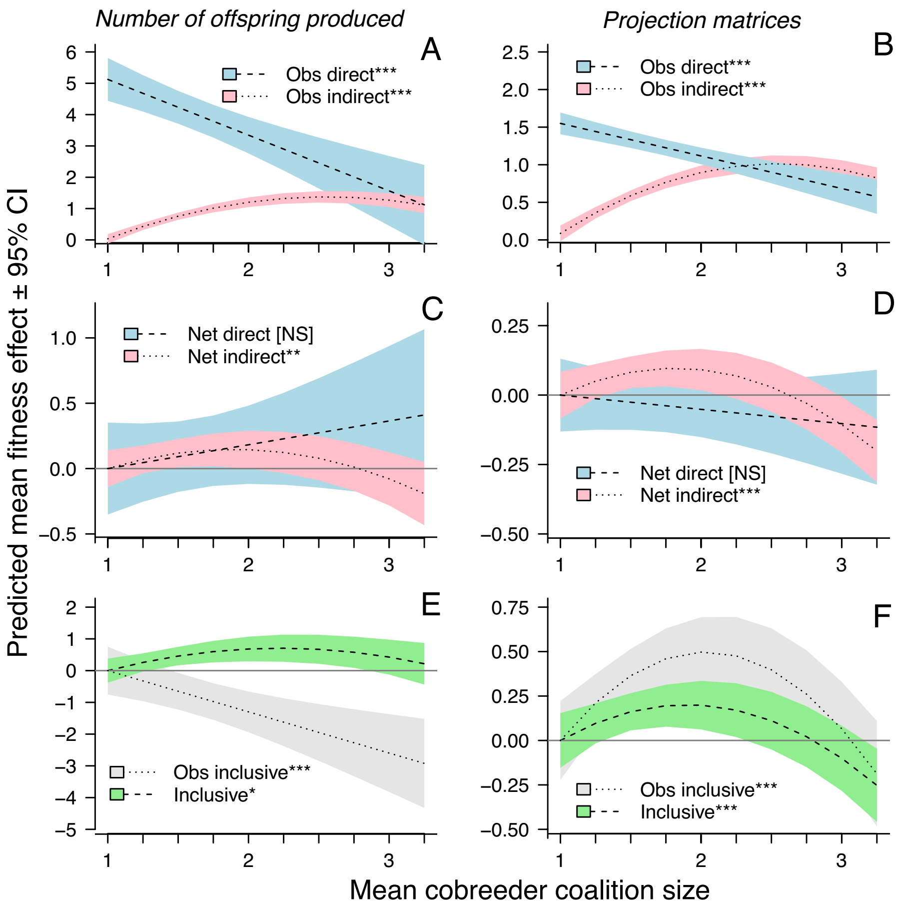

Fig. 2. Estimated lifetime fitness effect (mean ± 95% CI) of female fitness using lifetime number of offspring on left side ($N = 246$) and projection matrices on right side ($N = 144$) as a function of mean cobreeder coalition size. (*A* and *B*) Observed direct and observed indirect fitness effect; (*C* and *D*) net direct and net indirect fitness effect; (*E* and *F*) observed inclusive and inclusive fitness effect. Significance values as in Fig. 1. Statistical details in *SI Appendix*, Tables S1 and S2.

relationship between mean coalition size and age of first reproduction (*SI Appendix*, Table S3). For males, there was no significant relationship between age of first reproduction and mean coalition size (Fig. 3*A*), consistent with the similarity of the results for the two methods in terms of the relationship between observed inclusive fitness and mean coalition size (Fig. 1 *E vs. F*). In contrast, for females, age of first reproduction declined significantly with mean coalition size (Fig. 3*B*). Thus, females breeding in coalitions bred earlier than females breeding singly. This difference was sufficiently strong to alter the shape of the relationship between observed inclusive fitness and mean coalition size from declining linearly with increasing coalition size using the number of offspring produced (Fig. 2*E*) to maxing out at intermediate coalition size using projection matrices (Fig. 2*F*).

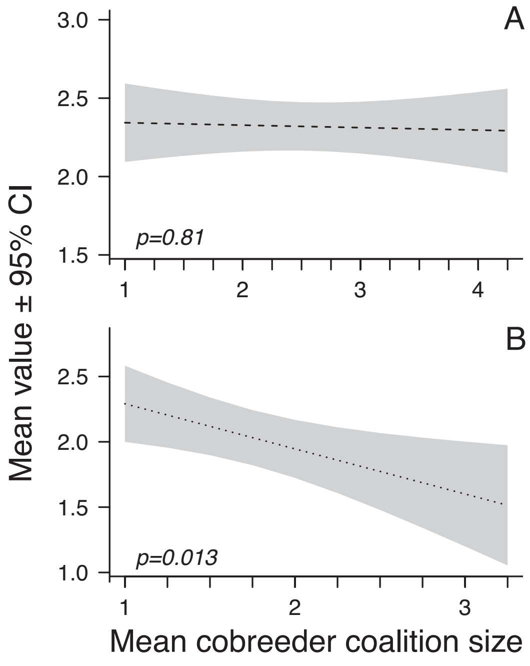

Fig. 3. Age of first reproduction (mean ± 95% CI) as a function of mean cobreeder coalition size. (*A*) Males ($N = 260$); (*B*) females ($N = 144$). *P* value of model listed; full statistical details in *SI Appendix*, Table S3.

Discussion

Understanding the direct and indirect fitness components of a behavior requires the partitioning of fitness. Consider indirect fitness, the relative importance of which can be quantified by the "index of kin selection" or "index of indirect selection" (27, 29), the proportion of observed fitness made up by indirect effects. For the cobreeding behavior considered here, this index is zero for birds that always breed singly since such birds have no cobreeders to provide indirect fitness but increases to near 0.5 for birds breeding in large coalitions (*SI Appendix*, Fig. S2), a value comparable to the relative importance of helping behavior in Florida scrub-jays *Aphelocoma coerulescens* (29). Indirect fitness is a major factor contributing to the observed fitness effects of cooperative polygamy in the woodpecker population.

Indirect fitness is even more important to the inclusive fitness effect of cobreeding. The net direct fitness effect did not differ with mean coalition size for either sex when estimated by the number of offspring produced (Figs. 1*C* and 2*C*). This suggests that for both sexes, the inclusive fitness effect of cobreeding estimated by the number of offspring was primarily determined by net indirect fitness effects—the net benefit (or cost) of breeding in a coalition compared to breeding singly in terms of young parented by cobreeders. This demonstrates the importance of stripping fitness values as proposed by Hamilton (the difference between "observed fitness" and "net fitness effect") when quantifying the relative importance of direct and indirect fitness to the inclusive fitness effect of a behavior.

We conclude that cooperative polygamy yields fitness benefits for females cobreeding as duos but that male fitness declines with increasing cobreeder coalition size, results that hold when estimated by both number of offspring produced, and age-sensitive projection matrices (Fig. 2*D*). These results contrast with previous analyses, which generally failed to find clear fitness advantages to joint-nesting for females (11, 13, 15, 18) while concluding that small coalitions (duos and trios) of males outperformed singletons (11, 13). These prior studies were mostly based on demographic models and relied solely on lifetime number of offspring parented. Here, we go beyond these prior analyses by using empirical data rather than population genetic models, by employing two alternative methodologies (one of which is sensitive to breeding age) for estimating fitness effects, and, most importantly, by calculating all components of Hamiltonian inclusive fitness of cooperative polygamy rather than only those that can be directly observed. The approach used here substantially advances prior quantitative attempts to estimate the inclusive fitness consequences of a complex social behavior in vertebrate populations.

Why do acorn woodpeckers breed in nonoptimal-sized coalitions or, in the case of males, in coalitions at all? The answer to the latter question, and the relatively rare cases of females joint-nesting in coalitions larger than two, is most likely ecological constraints, which also explain delayed dispersal and helping behavior in this population (14). For females, however, joint-nesting is relatively rare (36), despite the apparent fitness benefit of breeding as a duo. This disconnect is at least in part due to a lack of same-sex relatives (usually siblings) with which to cobreed, as well as the physiological cost of joint-nesting imposed by egg destruction (37, 38).

Our analyses illustrate a way forward for estimating inclusive fitness effects associated with complex social behaviors that change over an individual's lifetime or in cases where more than one alternative behavior is observed (39). This distinguishes our study from most previous analyses of inclusive fitness effects, including those of helping behavior (9, 34). Partitioning fitness into observed, alternative, and net components allows the selective factors acting on behaviors to be more accurately identified and studied. Detailed analyses of the direct and indirect fitness consequences of behaviors such as those conducted here ultimately promise to provide unambiguous evidence supporting the critical role of kin selection as the powerful evolutionary force envisioned by Hamilton over 50 y ago.

Materials and Methods

Field Sampling and Study Population. Acorn woodpeckers are a common resident of oak woodlands in western North America (40). We studied the population of these birds at Hastings Natural History Reservation in central coastal California, USA (36°23′ N, 121°33′ W) between 1972 and 2022 (13, 41). Acorn woodpeckers live in permanently territorial family groups consisting of between one and eight cobreeding males competing for matings with one to four joint-nesting females, which lay their eggs in the same nest cavity, along with up to 10 nonbreeding helpers of either sex that are offspring of the group from prior years. Groups within the same population vary in size and composition, ranging from a simple pair to groups with multiple cobreeding males and joint-nesting females.

Cobreeder males are close relatives, consisting of brothers (full or partial), a father (and/or uncle) and his sons (and/or nephews), or a combination of both; similarly, joint-nesting females consist of sisters (full or partial) or a mother (and/or aunt) and her daughter (and/or niece) (*SI Appendix*, Fig. S3). Extra-group parentage is rare, and offspring that remain as helpers do not reproduce except following the death and replacement of breeders of the opposite sex, at which point they may inherit breeding status and become cobreeders along with the other breeders of the same sex within the group (usually their father or uncle if a male; their mother or aunt if a female). Thus, all birds within a group are close relatives, except that male cobreeders are unrelated to female cobreeders and incest is rare (13, 36, 42). This close genetic relatedness among group members creates the potential for kin selection to be an important factor in the evolution of their unusual social behavior.

We captured, color-banded, and took blood samples for genetic analyses from all individuals either as nestlings or when caught as adults at nests or in roosting cavities (13, 43). Group composition was determined by censusing social groups at approximately bimonthly intervals. Nesting activity was monitored, and young were banded 10 to 12 d prior to fledging (44). Only birds born through 2006 were considered, minimizing the probability of birds living beyond 2016, the last year for which parentage data were available.

Territorial inheritance, which can occur following the replacement of the opposite-sex breeders by unrelated individuals (42), is common among males. Analyses indicated no significant differences in the relationships between components of fitness and mean cobreeding coalition size between birds inheriting their natal territory and those that dispersed and bred elsewhere in the population. Consequently, birds inheriting their natal territory were included in the analyses. A second dichotomy was whether breeders were born in the study area or immigrated from elsewhere. There were no significant differences in the relationships between components of fitness and mean cobreeding coalition size between birds born in the study area and immigrants. Thus, immigrants were included in the analyses of the number of offspring produced. Immigrants could not be included in the projection matrix analyses as their age was generally unknown.

Territory quality (14) and turnover in breeder composition were used in our models estimating reproductive success. As a proxy for territory quality, we used the size of a group's "granary", the tree or structure in which the birds cache acorns each autumn (40). We distinguished three categories of granaries, low-quality (<1,000 storage holes); medium-quality (1,000 to 2,500 holes); and high-quality (>2,500 holes). The second variable was whether the group had undergone a turnover in breeder composition from the prior year. Three categories were recognized: groups exhibiting a turnover by both sexes from the prior year; groups experiencing a turnover by one sex from the prior year; and those with no turnover in breeders from the prior year.

An equally important factor included in our models was the size of the prior autumn's acorn crop (45). This was estimated based on visual surveys performed annually on 250 individually tagged trees distributed among the five species of oaks (genus *Quercus*) common in the study area (46, 47).

Genetic Analyses. Young parented by individual breeders were determined by genetic parentage analyses using the blood samples taken when birds were banded. Parentage was determined using CERVUS 3.0.7 (48).

Estimation of Lifetime Fitness. Analyses were conducted using R 4.0.2 (49). For each year a bird was a breeder, we determined its observed direct fitness (number of young parented) and its observed indirect fitness (number of young parented by cobreeders). We then determined the bird's alternative direct fitness and alternative indirect fitness for that year under the assumption that the bird attempted to breed singly and its cobreeders (if any) bred without it. The number of young parented by, and relatedness between, cobreeders was made using genealogies based on parentage analyses.

We estimated the lifetime direct and indirect fitness consequences of cobreeding by summing annual number of offspring produced (32) and using population projection matrices for sexually reproducing, diploid organisms with age-structured life histories. This latter method weights early reproduction more heavily (33–35) and is justified here as the population grew steadily from 52 to 219 over the length of the study (12).

Estimation of alternative direct and alternative indirect fitness was dependent on both the probability of successful dispersal to a new territory and the dominance status of the focal individual within the coalition. We varied the probability of successfully obtaining a territory (p_{disp}) depending on coalition size, from $p_{\text{disp}} = 0.35$ for lone individuals to 0.55 for coalitions of three or more birds. Whether a bird was dominant within its breeding coalition or not affected the alternative fitness it would have achieved had it not bred in the coalition; dominants would presumably exclude cobreeding subordinates, while a subordinate would be expelled and be forced to find a breeding opportunity elsewhere (Table 1). Based on previous work (50, 51), we assumed that the oldest bird in a breeding coalition was dominant.

With rare exceptions, cobreeders are close relatives—either siblings or "parents" and their offspring, where the "parent" may or may not be the genetic parent, but is itself a close relative of the genetic parent (36, 42). As such, cobreeders vary in relatedness (r_{cob}) from 0.25 (half-siblings) to 0.5 (full siblings or parents and their genetic offspring). We estimated coefficients of relatedness between cobreeders using pedigrees going back two generations whenever possible. Averaged across all cobreeder-years and weighted according to the number of young parented, overall average r_{cob} values between cobreeder males were 0.40 (0.20 via fathers and 0.20 via mothers) and 0.43 between cobreeder females (0.23 via fathers and 0.20 via mothers). The distribution of known or inferred relatedness, and coefficients of relatedness, between pairs of cobreeders is illustrated in *SI Appendix*, Fig. S3.

Each year a bird (i) was present as a breeder or cobreeder, we generated estimates for the components of fitness as described in Table 1. Only fitness values during years a bird bred were included. Values for each year were summed (number of offspring produced) or used in projection matrices, from which the dominant eigenvalue estimated lifetime fitness. Because we were interested in estimating the effects of cobreeding relative to breeding singly, we adjusted final lifetime inclusive fitness values such that values for birds breeding singly their entire lives were set to zero.

Although parentage analyses were used to determine observed direct fitness and observed indirect fitness, alternative direct fitness and alternative indirect fitness were estimated from a model using data from the population at large, as described in *SI Appendix*.

Estimation of Fitness vis-à-vis Cobreeding. We used linear models to test for the relationships between mean cobreeder size (*xcob*; the mean size of the cobreeding coalition in which a bird bred during its breeding lifespan) and different fitness components. For males, *xcob* ranged from 1 to 7; for females, *xcob* ranged from 1 to 4. Because prior analyses have indicated that the relationship between mean cobreeder size and fitness is likely to be nonlinear in at least some cases, we included a quadratic term, which was removed when statistically nonsignificant ($P > 0.05$). For visualizing the effects of cobreeding on different components of fitness, we used the *predict* function in R to estimate the fitness of birds whose *xcob* ranged from 1 to 4.25 (for males) and 1 to 3.25 (for females) in intervals of 0.25.

Age of first reproduction was determined by averaging the age that birds first attained breeder status. Linear models tested for relationships between mean cobreeder size using both linear and quadratic terms, but for both sexes, the quadratic term was not significant and was dropped.

Data, Materials, and Software Availability. All study data are included in the article and/or *SI Appendix*.

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