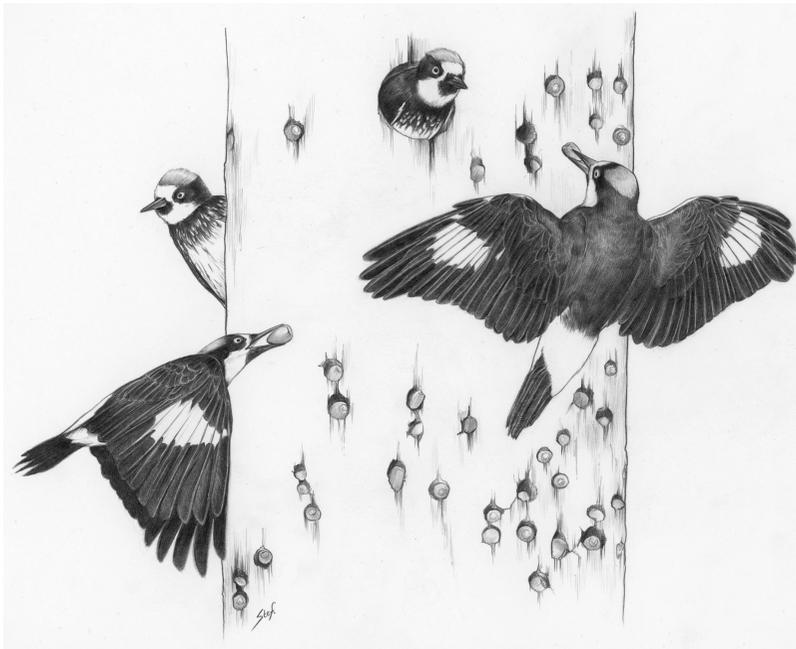


Acorn woodpeckers: Helping at the nest, polygynandry, and dependence on a variable acorn crop

Walter D. Koenig, Eric L. Walters, and Joseph Haydock



Introduction

The acorn woodpecker (*Melanerpes formicivorus*) plays an important role in the history of cooperative breeding. It was one of the earliest species for which cooperative breeding was noted with more than two individuals feeding at a single nest as well as apparent mate-sharing (Myers 1915; Leach 1925; Michael

1927). Subsequently, in his classic *Animal Dispersion in Relation to Social Behaviour*, V. C. Wynne-Edwards singled out the acorn-storing habits of this species as a means by which birds assessed the food supply and adjusted their breeding so as to avoid overexploitation of resources. Indeed, Wynne-Edwards suggested that acorn storing was “the perfect example of an epideictic rite, combining as it does a sampling of the

Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior, eds W. D. Koenig and J. L. Dickinson. Published by Cambridge University Press. © Cambridge University Press 2016.

food-supply, a territorial symbol (the tree), and social competition" (Wynne-Edwards 1962: 325). Four years later, cooperative breeding in this species was predicted to be based (this time accurately) on kinship in G. C. Williams's *Adaptation and Natural Selection*, written to counter the group-selectionist bent of Wynne-Edwards (Williams 1966).

It was but a few years after Williams' prediction, itself an outgrowth of W. D. Hamilton's (1964) papers introducing inclusive fitness theory, that Michael and Barbara MacRoberts began a study of acorn woodpeckers at Hastings Reservation in central coastal California, a field station run by the Museum of Vertebrate Zoology at the University of California, Berkeley. During the years of their work from 1968 to 1974 they banded 139 birds and described many aspects of their ecology and social behavior (MacRoberts and MacRoberts 1976). It is their study that the senior author took up in July 1974 and has worked on continuously ever since along with a series of students and collaborators, most recently the two coauthors of this manuscript. The work summarized here is thus a product of over 40 years of study during which time we have banded over 5,500 individuals and followed over 1,600 nests. We also refer when appropriate to earlier parallel studies conducted by Peter Stacey at Water Canyon, New Mexico and The Research Ranch in southeastern Arizona (Stacey and Bock 1978; Stacey 1979a, 1979b), updating results summarized in Koenig and Stacey (1990).

Acorn woodpeckers are a New World species found in oak woodlands along the Pacific Coast of North America between southern Washington State and Baja California, the American Southwest, and the mountains of western Mexico, Central America, and northern Colombia. On the Pacific Coast of California, where our study was conducted, adults (but not fledglings up until their prebasic [or postjuvenile] molt several months after fledging) are sexually dichromatic and slightly, but significantly, sexually dimorphic in size (mean \pm standard deviation [S.D.] mass of adult males is 80.1 ± 4.7 g [$N=345$] compared to 76.5 ± 4.7 g [$N=432$] for females). Acorn woodpeckers eat a diverse array of insects, which they primarily flycatch and glean from bark, as well as on sap and fruit, including most prominently

acorns harvested from oaks (mostly trees of the genus *Quercus*) and store in individually-drilled holes in storage trees, or granaries. Vertebrates, including small lizards, bats, and nestling swallows, are also eaten occasionally (Fajer et al. 1987). Exceptions to their extensive use of stored acorns include populations that have been observed in central Mexico (Koenig and Williams 1979) and Colombia (Kattan 1988), which do not necessarily store acorns, and a few populations in the southwestern United States that are known to be migratory (Stacey and Bock 1978).

No population of acorn woodpeckers has yet been described that does not facultatively breed cooperatively, although group size varies considerably, from a mean of 4.5 birds (range 2–15) during the spring breeding season at Hastings Reservation to a mean of 2.2 birds (range 2–3) in the largely migratory (and mostly noncooperatively breeding) population studied by Stacey at the Research Ranch in Arizona. Groups in a third population studied by Stacey in Water Canyon, New Mexico, were intermediate in size (Koenig and Stacey 1990). Of the small proportion of groups at the Research Ranch that contained more than a pair, most were trios that included a nonbreeding helper. Thus, cooperative polygamy was absent in the Research Ranch population, and even helpers were uncommon and only found among groups that managed to gather and store enough food to remain resident through the winter (Stacey and Bock 1978).

In contrast, at Hastings Reservation, 39% of groups consist of breeding pairs, 31% of groups consist of at least two cobreeder males (maximum = 8) and one breeder female; 9% consist of at least two joint-nesting females (maximum = 4) and one breeder male, and 14% are polygynandrous groups consisting of two or more cobreeder males and at least two joint-nesting females (data from 1,481 group-years studied during the breeding season between 1972 and 2012). The presence of nonbreeding helpers in a group is similarly variable: of the 1,481 group-years, 42% had no helpers and 58% had between one and 10 helpers (mean \pm S.D. = 1.55 ± 1.85), which are of both sexes but slightly male-biased (of 2253 helpers, 1294 [57.4%] were male). Thus, there is considerable variability in group composition both within and between populations.

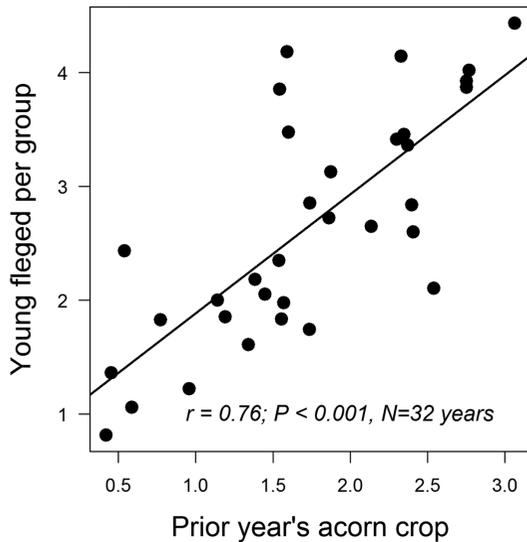


Figure 13.1. Mean young fledged per group versus the prior autumn's acorn crop.

Along the Pacific Coast of the United States, where acorn woodpeckers are resident and dependent on stored acorns, populations are largely restricted to areas with at least two species of oaks, most likely because the higher diversity reduces the probability of an acorn crop failure, and populations vary less in numbers from year to year in areas where the diversity of oak species is greater (Bock and Bock 1974; Koenig and Haydock 1999). The strong effect of the acorn crop on the demography of acorn woodpeckers within a population is vividly demonstrated by the catastrophic effects of acorn crop failures on group composition and population size (Hannon et al. 1987) and, conversely, a strong correlation between the size of the acorn crop and subsequent reproductive success of the population (Figure 13.1) including autumnal nesting – a relatively rare event among temperate-zone birds – in years of particularly prolific acorn crops (Koenig and Stahl 2007). The relationship between reproductive success and the prior autumn's acorn crop is considerably stronger than the relationship between reproductive success and other environmental factors, including rainfall or temperature during either the winter or the breeding season (Koenig et al. in press).

Oaks are in general mast-fruited species among which the acorn crop is a “pulsed” resource whose availability varies greatly not only seasonally but from year to year (Koenig et al. 1994). For the acorn woodpeckers, seasonal access to acorns is supplemented with alternative food resources and acorn storage, while variability in acorn availability from year to year is reduced as a result of oak species diversity. At Hastings Reservation, for example, birds have access to between three and five species of oaks, depending on the location of their territory. Nonetheless, populations are subject to considerable variability in conditions from year to year, which has effects not only on reproductive success but on survivorship, population size, group composition, and the behavior of individuals within groups (Koenig et al. in press).

Except for years of acorn crop failures and a few populations (such as that studied by Stacey in Arizona), groups are resident and territorial throughout the year, defending their territory intraspecifically against intruders from other groups and interspecifically from a wide range of other birds and mammals that try to steal acorns from their granaries (MacRoberts and MacRoberts 1976). Birds do, however, regularly foray outside their usual home ranges, foraging for acorns when the crop is poor (Koenig et al. 2008) and (as non-breeding helpers) searching for reproductive vacancies (Koenig et al. 1996). Breeder dispersal also occurs, and is surprisingly common, with 10%, or if we include birds that left the study area and returned, 25% of birds leaving the first territory on which they hold breeding status. Breeding dispersal occurs primarily to avoid incest or to move to a territory of higher quality (Haydock et al. unpubl. data).

Cooperation and competition

Social and genetic mating system

Acorn woodpecker groups are family-based and, as indicated above, consist of two categories of birds: breeders and helpers. Breeder males consist of a coalition of brothers or of fathers and their sons, all of which compete for matings with the breeder female(s).

Similarly, breeder females are a coalition of sisters or a mother and her daughter, all of which generally lay their eggs in a single nest cavity. Because of communal nesting, a group has only a single nest at a time regardless of its composition; only one exception to this rule has been found during the study thus far. Helpers are offspring from the communal nests that delay dispersal and remain in their natal group but do not participate in breeding. Helpers remain in their natal territory for a variable length of time during which they contribute to group activities including acorn storage, feeding of nestlings, and territorial defense, while engaging in forays off the territory in search of reproductive vacancies elsewhere (Koenig et al. 1996).

Birds within groups are consequently all genetically closely related to each other (siblings or parent/offspring), the exception being that the breeder males are generally unrelated to the breeder females. Nonetheless, birds within groups exhibit an impressive array of competitive, as well as cooperative, behaviors. Among breeder males, competition for matings is expressed by mate guarding, but strong mate-guarding behavior only occurs when there are two or more cobreeder males within a group and not when there is only a single breeder male and one or more helper males – the latter constrained from attempting to breed because of incest avoidance. These attributes indicate that mate guarding is an expression of within-group competition rather than related to guarding against copulations by extra-group males (Mumme et al. 1983a). Meanwhile, competition between cobreeder females is expressed most dramatically by egg destruction whereby a breeder female laying an egg will have it removed from the nest by another breeder female in the group up until the latter is about to lay her first egg (Mumme et al. 1983b; Koenig et al. 1995). Eggs removed from a nest are taken to a horizontal limb where a crevice provides a suitable spot to hold it and then eaten by all group members, including the female that laid it.

Egg destruction by joint-nesting females is particularly detrimental in terms of delaying breeding, since it can take a week or more for two females to synchronize their egg-laying so as to produce a communal clutch, and even longer when there are three joint-nesting females. Moreover, a high proportion of eggs are

potentially lost; in one case in which three females attempted to breed together, 15 of 23 eggs (65%) were destroyed and only eight were eventually incubated (Koenig et al. 1995). Such competition reduces the relative benefit of female joint nesting compared to male cobreeding, presumably contributing to the greater incidence of the latter: 47% of 1,481 group-years involved two or more cobreeder males compared to 23% that involved two or more joint-nesting females. Overall, the mean (\pm standard error [S.E.]) number of cobreeding males per group is 1.73 ± 0.03 whereas the mean number of joint-nesting females per group is 1.22 ± 0.02 ; similarly, the proportion of males cobreeding with at least one other male is 71% compared to 41% of females that nest jointly with one (rarely more) other females.

Beyond influencing the relative costs and benefits of cobreeding, the outcome of these interactions is very different for the two sexes. Because of egg destruction, joint-nesting females share maternity more equally than expected by chance (Haydock and Koenig 2002, 2003). Breeder males, however, exhibit high reproductive skew, with one male monopolizing paternity of a brood approximately two-thirds of the time. Tests of reproductive skew versus estimates of ecological constraints on independent reproduction and on relatedness failed to find consistent support for transactional models of reproductive skew, whether assuming complete control on the part of a single dominant individual (“concessions” models) or assuming that dominants have limited or incomplete control (“restraint” models) (Haydock and Koenig 2003). This suggests that factors not necessarily considered in these models such as competitive interactions among potential breeders and mate choice are important determinants of parentage.

Between broods sired by the same set of males, however, there is frequent switching of paternity, raising the possibility that males share paternity equally on a brood by brood, rather than a nestling by nestling, basis. In other words, paternity of a brood may be a fair “winner take all” game in which the probability of winning is equal, rather than paternity of each chick being determined independently. If so, it explains the observation that male paternal care among cobreeders

Table 13.1. Behavior of cobreeder males vis-à-vis their realized paternity at nests

	Sex	Bird with more parentage did more	Bird with less parentage did more	<i>P</i> -value
Behavior at nests				
Provisioning	Males	31	19	0.12
	Females	12	12	1.0
Nest sanitation	Males	12	22	0.12
	Females	7	6	1.0
Brooding and incubation	Males	15	15	1.0
	Females	5	8	0.58
<i>Nocturnal roosting in the nest (males only)</i>		Male with some paternity	Male with no paternity	
Roosted	Males	9	7	1.0
Did not roost	Males	9	6	
		Male with majority of paternity	Male with minority of paternity	
Roosted	Males	4	11	0.14
Did not roost	Males	9	6	

None of the behaviors appear to correlate with paternity, consistent with the hypothesis that cobreeder males do not know whether they have paternity or not in a particular nest.

is uncorrelated with realized paternity. That is, the male who sires all or most of the young in any particular nest is often not the male that contributes the most paternal care at the nest or even one of the birds that spends the night in the nest incubating eggs or brooding young (Table 13.1). Apparently males do not have information on whether they have successfully sired young in a particular nest, but behave as if they may have done so regardless of the actual outcome.

One caveat to this conclusion may be when a large number of males – four or more – share breeding status in a group. In such cases, which typically result from helper males inheriting breeding status following the death and replacement of their mothers by one or more unrelated females, younger, subordinate males may have such a low probability of successfully siring young that for all practical purposes they are nonbreeding helpers. Such cases are not common, however; only 6.4% of groups contained four or more (maximum of eight) cobreeder males. A similar situation resulting in the exclusion of one or more individuals from

reproduction may apply to the rare cases when four females share breeder status, which has occurred in only <1% ($n = 10$) of group-years.

Characterizing the social mating system is thus problematic to the extent that a significant proportion of males considered to be “breeders” may not successfully sire offspring in any particular nest or within a given year. Furthermore, copulations are rarely observed, and thus there is little behavioral evidence to support assertions regarding which males are or are not “attempting” to breed. Because the breeding success of such birds is constrained by reproductive competition rather than incest avoidance, however, we consider them cobreeders rather than helpers, as explained in Chapter 20.

We tested this approach with experiments in which we removed eggs in nests with cobreeder males (i.e., males unrelated to the breeder female) shortly after laying in order to force groups to renest, and then compared paternity in the eggs artificially incubated from the first (experimental) nest with paternity

Table 13.2. Switching of majority paternity (the male siring the most young) across nests produced by the same coalition of cobreeder males within the same breeding season

Comparison		Switched	Did not switch	% switching
<i>N</i> cobreeder males	2	21	28	43
	2+	10	11	48
Relationship of male cobreeders	Father/son	7	9	44
	Siblings	24	30	44
<i>N</i> joint-nesting females	1	18	33	35
	2	13	6	68

There is no significant difference in the tendency for switching in relation to male coalition size or relationship of cobreeders (Fisher exact tests; $P > 0.05$). Switching is, however, significantly higher in groups containing two joint-nesting females compared to those with only a female ($P < 0.02$).

in the renesting attempt. Switching of paternity is common, regardless of male coalition size, whether cobreeders were brothers or a father and his son, or even the number of breeder females in the group, although switching is more common in groups with two joint-nesting females than those with only a single breeder female (Table 13.2). These results support the assumption that males unrelated to the breeder females in a group are all at least “hopeful breeders,” even if they fail to sire young during any particular nesting attempt.

One way in which the mating system of acorn woodpeckers is straightforward is in the absence of extra-group parentage. No offspring whose parentage has been determined thus far has been unambiguously identified as having been the result of intraspecific nest parasitism, quasiparasitism, or an extra-group mating on the part of a female. This is consistent with the conclusion reached from mate-guarding indicating that mate-guarding is a behavior directed toward cobreeder males within the group rather than against the unlikely possibility that females will attempt to mate outside their social unit (Mumme et al. 1983a; Dickinson et al. 1995).

In summary, the mating system of the acorn woodpecker is opportunistically polygynandrous, with groups consisting of between one and eight related, cobreeding males competing for matings with a lesser

number (usually one or two but rarely as many as four) joint-nesting females, plus their offspring (up to 10 of either sex) from prior years that participate in all group activities with the exception of mating. Joint-nesting females generally share maternity equally within nests; cobreeder males exhibit significant reproductive skew on a nest by nest basis, but switching is common and paternity is egalitarian across nests, except possibly for subordinate males and females in unusually large coalitions. Mating is always within the group; extra-group paternity or egg-dumping is at most rare.

Reproductive vacancies and incest avoidance

The close genetic relatedness combined with the opportunity for multiple individuals of both sexes to breed makes acorn woodpeckers ideal for investigating the importance of incest avoidance. Particularly key is the question of how groups persist through time, specifically when they are faced with a reproductive vacancy following the death or disappearance of all breeders of one sex. (The death of cobreeders does not result in a reproductive vacancy as long as at least one breeder of that sex is still present.)

Reproductive vacancies are of interest for several reasons. First, they are not generally filled by birds from within the group, but rather by coalitions of sibling helpers from elsewhere. Second, vacancies are often

not filled quietly, but rather following contests called “power struggles” involving helpers (often fighting in coalitions of same-sex siblings) from many territories away competing for the right to fill the vacancy (Koenig 1981; Hannon et al. 1985). Exactly how birds recognize vacancies is not known for sure; there is some evidence that surviving birds within groups advertise vacancies by means of increased rates of vocalization (Hannon et al. 1985), but vacancies are sometimes detected in less than an hour, even among groups still containing adult helpers of the missing sex, and it seems possible, albeit untested, that foraging birds are sufficiently familiar with the individuals in some groups that they are able to detect when a reproductive vacancy exists through some other means and act accordingly.

Power struggles end when one coalition of birds successfully drives off competing coalitions to the periphery of the territory, from where the losing birds eventually return home and resume their status as nonbreeding helpers. In general, the largest participating coalition wins power struggles, and after a victory, members of the coalition may all remain and become cobreeders in the new territory. This is not always the case, however, particularly among females, for which competition to fill vacancies is particularly intense, and sometimes large winning coalitions subsequently break up, leaving a smaller, more tractable number of females to breed in the new territory while the remaining coalition members fill a vacancy elsewhere or return home.

Reproductive vacancies are often filled very quickly, but exceptions occur when there are nonbreeding helpers of the missing sex present within the group. The presence of such helpers can significantly delay the filling of a vacancy, and if several are present, they can result not only in failure to fill the vacancy but also in failure of the group to subsequently breed. Because such groups contain adult, reproductively competent birds of both sexes that are all close genetic relatives, this loss of reproduction is directly attributable to incest avoidance, and is estimated to cost the population 9.2–12.1% in overall reproductive potential and decrease the population rate of increase by as much as 2.3% year⁻¹ (Koenig et al. 1999). Eventually, the helpers of the missing sex either find a vacancy elsewhere and disperse, after which the unfilled vacancy is quickly

filled, or the group breeds incestuously. The latter occurs approximately 4% of the time, a rate comparable to that observed in other cooperatively breeding species (Rowley et al. 1993; Haydock et al. 2001). Thus, incest occurs, but is avoided under most circumstances.

The most notable aspect of power struggles, however, is as an indication of the intense competition for breeding opportunities. Power struggles can last for days and involve dozens of birds; helpers are clearly willing to fight extensively for the possibility of gaining a reproductive position in the population, even one that they then must share with siblings. The duration of power struggles and the number of intruders competing are both positively correlated with the size of the territory’s granary (Hannon et al. 1985); thus, territory quality plays a role in determining the amount of competition to fill vacancies. Nonetheless, the fact that birds fight to such an extent for the chance to fill a vacancy is unambiguous evidence that breeding and cobreeding are preferred options compared to being a nonbreeding helper. It is unknown, however, why power struggles only take place when vacancies exist since it seems likely that large coalitions of siblings could displace smaller coalitions and enhance their breeding opportunities without waiting for an actual vacancy to arise.

Sexual conflict and sexual selection

Sexual conflict and sexual selection have yet to be studied in detail in acorn woodpeckers, but there is reason to believe that one or both may play an important role in their social behavior. Group reproductive success increases with all categories of birds, but breeders of both sexes gain by having as many breeders of the opposite sex help feed their young as they can and lose (on a per breeder basis) by sharing breeding status with cobreeders (Figure 13.2). Thus, as in the dunnock *Prunella modularis* (Davies 1992), this results in potential conflicts of interest between the sexes that may help explain the variability observed in the mating system.

Sexual conflict may also help explain why the act of mating is so secretive, with copulations almost never being observed during a female’s fertile period. Our current best guess is that copulation takes place within nest cavities in such a way that obscures potential

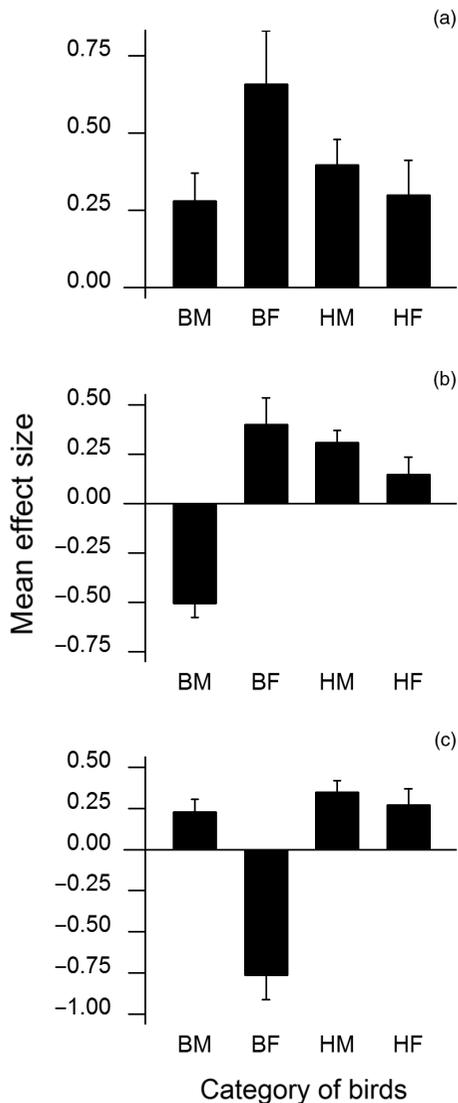


Figure 13.2. (a) Mean (± 2 S.E.) number of young fledged per group as a function of group composition (BM = breeder males; BF = breeder females; HM = helper males; HF = helper females). The effect size of each of the four categories is significant ($P < 0.001$). (b) Mean (± 2 S.E.) number of young fledged per breeder male as a function of group composition; all effects are $P < 0.001$ except that of helper females ($P = 0.004$). (c) Mean (± 2 S.E.) number of young fledged per breeder female as a function of group composition; all effects are $P < 0.001$. Analyses by linear mixed-effects models with “year” as a random effect. N group-years = 1,366; N years = 41.

paternity. Since males then have little or no information as to their success relative to their cobreeders, this sets the stage for male sharing of paternal duties that is uncorrelated with actual paternity (Table 13.1). Why acorn woodpeckers have evolved such a system rather than copulating frequently out in the open, as do, for example, red-cockaded woodpeckers *Picoides borealis* (Chapter 4), southern pied babblers *Turdoides bicolor* (Chapter 7), and lions *Panthero leo* (Schaller 1972) is unknown. In any case, it is important that all male cobreeders have had at least an opportunity to mate, since males denied mating access may subsequently destroy the nest and force re-nesting (Koenig 1990).

The role of sexual selection is even less well understood. Thus far we have detected no morphological, age-related, or behavioral correlates of paternity success, and thus whether any mate choice is taking place based on such characters seems unlikely. Given the significant reproductive skew among males at individual nests, female choice and sperm competition is possible, although the high frequency of paternity switching from one nest to the next would reduce variance in success among males, thus rendering it unlikely that significant sexual selection could result. Such findings, combined with the absence of extra-group mating, suggest that the greatest opportunity for sexual selection is likely to occur during power struggles and competition over the filling of reproductive vacancies.

Sex ratio evolution

The population sex ratio is slightly, but significantly, male biased. Over the 33 years from 1980 to 2012, the mean sex ratio (expressed as percent males) of breeders in the population during the breeding season was 58.1% (range 51.1 to 63.4%), while the mean sex ratio of helpers was an almost identical 57.7% (range 41.2 to 75.0%). The biased sex ratio of breeders can thus be explained in part by the sex-bias among helpers, but is in addition driven by the more destructive competitive interactions among joint-nesting females compared to cobreeder males, as discussed earlier. Also contributing to the bias is a higher mortality rate among breeder females, whose mean annual survivorship is 75.3% (range 61.0 to 95.2%) compared to 79.5% (range 70.0 to

93.5%) for breeder males (mean annual survivorship from 1 September to 31 August of all birds with complete data from 1979–1980 to 2011–2012). The higher mortality rate of females appears to occur mainly during the spring and summer, and thus is most likely related to the higher cost of reproduction incurred by breeder females, including costs of egg formation and nest care, the latter of which (except for nocturnal brooding, which, as in other woodpecker species, is primarily done by males) is performed disproportionately by breeder females (Koenig and Mumme 1987).

The biased sex ratio of helpers is also due to a combination of factors. First, the sex ratio of young birds surviving to independence (defined as the time of the postjuvencal molt about three months postfledging) is 54%, a significant male bias due to faster nestling growth and lower postfledging mortality of males, since the sex ratio of eggs appears to be either even or slightly female-biased (Koenig et al. 2001). Subsequently, there is a small bias toward male fledglings becoming helpers (59% of male fledglings become helpers compared to 53% of females), and males tend to remain slightly longer as helpers than females (the mean number of years males remain as a helper is 1.57 vs. 1.48 for females).

The ultimate cause of the male sex ratio bias among helpers is more difficult to determine. The major hypotheses for sex ratio variability all predict either a female bias or a male bias smaller than that observed (Koenig et al. 2001), including local resource competition, sexual size dimorphism, and the repayment model (Emlen et al. 1986; Koenig and Walters 1999), the last of which proposes that helpers repay part of the cost of their production by assisting their parents in subsequent breeding attempts. We have also yet to detect any evidence of facultative sex ratio manipulation within broods (Koenig et al. 2001), although producing broods of predominantly one sex or the other would seem to be potentially beneficial by increasing the size and competitiveness of sibling coalitions.

Helpers and provisioning behavior

Nonbreeding helpers make up a third of the population (33.8%) during the breeding season. Furthermore,

as mentioned previously, there are only minor differences in the proportion of fledglings of the two sexes that remain as helpers. There are, however, substantial differences in the proportion that attain breeding status in their natal territory (inherit), which is considerably more common for males than females (23.7% of males [$N = 577$] vs. 4.6% of females [$N = 482$]), and, conversely, in the proportion that disappear or leave the study area (57.8% of males vs. 76.1% of females). The former is a direct result of the greater incidence of female reproductive vacancies, which in turn is due to the greater size of male cobreeding coalitions and the lower survivorship of breeder females. The latter parallels the increased competition females experience for breeding vacancies and greater dispersal distance of females, whose root-mean-square dispersal distance is estimated at 0.53–9.57 km compared to 0.22–2.90 km for males (Koenig et al. 2000). As a result of these differences, acorn woodpecker groups are generally patrilineal; the mean (\pm S.E.) length of male lineages in groups present for at least six years between 1979 and 2012 was 4.95 ± 0.38 years (range 1–31), significantly greater than lineage length for females, which was 3.63 ± 0.38 years (range 0–20).

Helpers contribute to all aspects of group behavior, including acorn storage, granary defense, incubation, and feeding of young, although typically at lower levels than that of breeders (Mumme et al. 1990). The patterns of provisioning behavior are affected by a variety of variables, including not only sex and status (breeder or nonbreeding helper) but also nestling age, brood size, temperature, date, group size, and time of day (Koenig and Walters 2012a). Breeder females brood and feed nestlings more than do breeder males, and breeders brood and provision at higher rates than helpers. Helper males are more likely than helper females to feed nestlings overall, but in paired comparisons of male and female helpers at the same nest, helper females feed significantly more than helper males, contrary to the expectation that helper males should invest more in provisioning young because of the patrilineal nature of acorn woodpecker groups. There are no differences between helper males and helper females in their tendency to reduce provisioning rates with increasing group size (compensatory care), or to

adjust their provisioning rates to experimental changes in brood size (Koenig and Walters 2012b). Helpers do not adjust their feeding rates to changes in brood size to the same extent as breeders, however, a surprising result given that helpers might be expected to devote the extra time and energy afforded by reduced brood sizes to alternative activities such as foraging in search of reproductive vacancies.

Helpers exhibit a strong dominance hierarchy related to body size, which in turn is correlated with hatching order within broods (Stanback 1994). Overwinter survival of larger, dominant fledglings is greater than that of smaller subordinates, but among birds surviving their first winter, there are no differences related to dominance in the proportion that act as helpers or ultimately inherit their natal territory (Koenig et al. 2011a). Interestingly, in analyses of broods in which only one of two male broodmates became a helper instead of dispersing, the bird becoming a helper is more likely to have been the smaller, subordinate rather than the larger, dominant male, a result opposite that found in Siberian jays (*Perisoreus infaustus*; Chapter 1) and red-cockaded woodpeckers (Chapter 4).

Helpers help to raise birds that are related to them by an estimated mean $r = 0.45$ (Koenig and Mumme 1987), and thus, perhaps unsurprisingly, kinship is a particularly important aspect of helping behavior in this species. Of 1,366 helpers whose social parentage was known, 1,204 (88.1%) were helping birds that were breeding in the group when they were born, while 148 (10.8%) were helping stepparents of one sex or the other and were thus raising half-siblings, and only 14 (1.0%) were apparently provisioning unrelated offspring. Thus, virtually all helpers are offspring of the breeders they assist.

The effects of helpers on reproductive success of the group and survival of breeders vary depending on several factors. Overall, each helper at a nest contributes an average of 11% of the brooding time (10.6% for males; 10.9% for females) and about 15% of feeding visits (13.6% for males; 15.9% for females) (Figure 13.3), less than an average breeder but still a significant amount of effort (Koenig and Walters 2012a). The fitness effects of helping behavior vary significantly between the sexes and with the prior year's acorn crop (Koenig et al. 2011b).

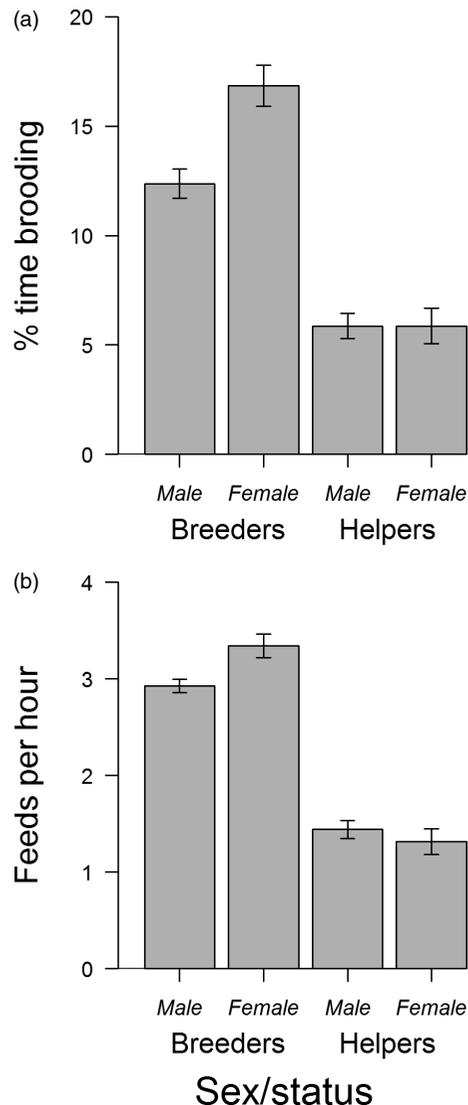


Figure 13.3. (a) Mean (\pm S.E.) brooding time and (b) mean (\pm S.E.) provisioning rates by sex and status. Brooding includes only watches conducted during the first 11 days of the nestling period. From Koenig and Walters (2012a).

The effect of helper females on reproductive success is positive but not statistically significant and is unrelated to the acorn crop (Figure 13.4b). In contrast, the effect of helper males is strongly dependent on the prior year's acorn crop: the better the acorn crop, the more beneficial

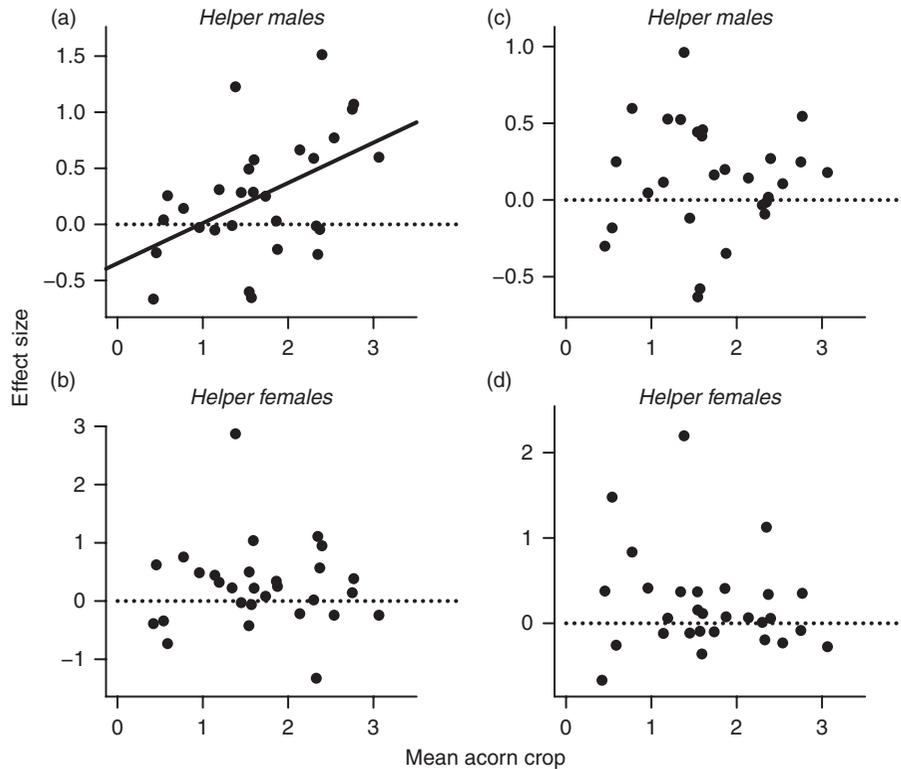


Figure 13.4. Effect size of (a) helper males and (b) helper females on mean annual reproductive success of groups as a function of the mean acorn crop based on linear regressions for individual years controlling for group composition and prior breeder experience; (c) and (d) are identical analyses using only data from first spring nests; thus, the positive effects of helper males in good acorn years are due entirely to additional nesting attempts rather than increased brood size. Correlations: (a) $r = 0.49$, $P < 0.01$; (b) $r = -0.03$, $P = 0.86$; (c) $r = 0.03$, $P = 0.88$; (d) $r = -0.17$, $P = 0.37$. $N = 29$ years.

a helper male is to group reproduction, whereas following a poor acorn year, each helper male correlates with a small reduction in group success (Figure 13.4a). This effect appears to be due almost entirely to an enhanced frequency of second nests in good years rather than increased brood size (Figures 13.4c, 13.4d).

Breeder male survivorship is increased when helpers of either sex are present, but again only when conditions are favorable, either in terms of a large acorn crop, on a high-quality territory, or among experienced breeders. Our data do not provide any evidence for “concealed” helper effects (Russell et al. 2007) such as, for example, females laying smaller eggs when assisted by helpers (Koenig et al. 2009).

In summary, helpers have a positive effect on the fitness of breeders – through increased survivorship and (at least for male helpers) increased fledging success – that is greater when ecological conditions are favorable. This pattern has not been described previously, and contrasts markedly from findings for other cooperative breeders that have been examined in which the effect of helpers is greater when conditions are poor (Magrath 2001; Covas et al. 2008). This latter, more common result is predicted by the hypothesis that cooperative breeding is an evolutionary response to ecological conditions that are so poor that cooperation among more than two individuals is required for success (the “hard life” hypothesis). Helpers in acorn

woodpeckers are clearly not necessary for successful reproduction. Instead, helpers, particularly males, provide significant benefits but only when conditions are favorable to begin with.

The overall fitness effects of helping are consequently not simple to estimate, since they vary depending on conditions, and particularly on the acorn crop, which itself varies greatly from year to year (Koenig et al. 1994). We approached this problem by performing a simulation estimating the lifetime fitness effects of a helper on breeders depending on the acorn crop and quality of the territory (Koenig et al. 2011b). Results suggest that on average, a bird delaying dispersal and helping for one year will increase the fitness of a breeder by 8–18% over the number of offspring the breeder would otherwise expect to produce over its lifetime (Table 13.3). Of these values, between 35 and 48% of the fitness benefits conferred by helpers are due to future indirect fitness; that is, increased fitness via enhanced survivorship of breeders (Mumme et al. 1989). The fitness benefits of helping are thus nontrivial, but are still much less than those gained by breeding.

There are at least two important caveats to this conclusion. First, helpers may gain direct fitness benefits from provisioning and other cooperative behaviors (Clutton-Brock 2002). These potentially include: maintaining access to resources on the territory (“pay-to-stay;” Mulder and Langmore 1993); gaining skills that allow them to be more successful when they become breeders later in life (the “skills” hypothesis; Selander 1964); enhancing their social status in a way that increases their future access to resources or mates (Zahavi 1995); or having their help reciprocated, either from the nestlings they help feed (Ligon and Ligon 1978) or by “group augmentation” – increasing the overall success of the group (Brown 1987; Kokko et al. 2001; Kingma et al. 2014).

Although we have not tested all these hypotheses in acorn woodpeckers, we have found no evidence to support those that we have examined (Koenig and Walters 2011). Helpers increase their provisioning rates with age, but in paired comparisons, helper males that fed young at higher rates had no greater reproductive success later in life than less helpful helper males, contrary to the key prediction

of the skills hypothesis that such experience should enhance future fitness. And although males that fed more as second-year helpers remained as helpers significantly longer and were more likely to inherit their natal territory than male helpers that fed less, this result is most likely a consequence of differences in dispersal behavior – specifically, that helpers devoting more time to searching for reproductive vacancies rather than provisioning offspring are more likely to find and fill a reproductive position in the population – rather than the birds’ prior feeding history, contrary to the key prediction of the pay-to-stay hypothesis. Thus, indirect, kin-selected benefits appear to provide the primary, if not the only, benefits gained by helpers through their provisioning behavior.

The second caveat to the conclusion that helpers gain primarily indirect fitness benefits is that we have no evidence that the positive effects they confer are causally related to their provisioning rather than some other cooperative behavior, a question that arises both because of the highly variable behavior of helpers and the lack of any obvious correlation between the overall fitness effects of helpers and their provisioning behavior (W. Koenig and E. Walters, unpubl. data). This problem, which arises in almost all cooperative breeders, is an important one: many helpers do not, in fact, provision at nests, and if their fitness effects are the same as those that do, it leaves wide open the question of “why helpers help?” We hope to address this problem in the future using new tracking technologies that will allow us to monitor the location of helpers as well as their behavior.

Endocrinology of helping

Neither sex nor breeding status (helper or breeder) affect pre-breeding season levels of luteinizing hormone, indicating that helpers are as capable of achieving breeding condition as are breeders (M. Stanback and J. Wingfield, unpubl. data). Breeding status, but not body weight or age, correlate with pre-breeding testosterone (T) levels in males, but although T levels are elevated and testes are larger

Table 13.3. Estimated lifetime number of young fledged (S = mean fitness) by a breeder living as a pair and as a consequence of the presence of a single male or female helper and whether the bird resides on a low- or a high-quality territory

	Helper male effect on				Helper female effect on			
	Breeder male		Breeder female		Breeder male		Breeder female	
	Low-quality territory	High-quality territory	Low-quality territory	High-quality territory	Low-quality territory	High-quality territory	Low-quality territory	High-quality territory
S_{nh} (mean fitness, no helper)	5.59	8.65	5.14	9.63	5.58	8.65	5.14	9.63
S_{ih} (mean fitness, 1 helper)	6.57	9.99	5.75	10.57	6.51	9.94	5.63	10.40
$S_{ih,R}$ (1 helper, effects on current reproduction only)	6.10	9.27	5.63	10.31	5.95	9.08	5.48	10.10
$S_{ih,S}$ (1 helper, effects on future survivorship only)	6.03	9.32	5.28	9.87	6.12	9.47	5.30	9.91
Combined benefit (% of S_{nh})	0.99 ± 0.27 (18%)	1.34 ± 0.31 (16%)	0.61 ± 0.25 (12%)	0.94 ± 0.28 (10%)	0.92 ± 0.07 (16%)	1.29 ± 0.08 (15%)	0.49 ± 0.02 (10%)	0.78 ± 0.03 (8%)
Current indirect fitness (% of combined benefit)	0.51 ± 0.23 (52%)	0.62 ± 0.25 (46%)	0.47 ± 0.23 (77%)	0.68 ± 0.26 (72%)	0.36 ± 0.01 (39%)	0.43 ± 0.01 (33%)	0.33 ± 0.01 (68%)	0.48 ± 0.01 (61%)
Future indirect fitness (% of combined benefit)	0.44 ± 0.05 (45%)	0.68 ± 0.06 (51%)	0.13 ± 0.01 (21%)	0.25 ± 0.02 (26%)	0.54 ± 0.06 (58%)	0.82 ± 0.07 (64%)	0.15 ± 0.02 (31%)	0.29 ± 0.02 (37%)

The mean effect of the helper (\pm S.D.) is divided into the fraction enhancing breeder reproduction (current indirect fitness) and the fraction increasing breeder survivorship (future indirect fitness).

Source: From Koenig et al. (2011b).

in breeders than helpers, helpers also have elevated T levels and larger testes during the breeding season compared to the nonbreeding season, indicating some degree of reproductive competence. Among males, body weight but not breeding status influence pre-breeding levels of corticosterone, indicating that their incomplete reproductive state is not due to glucocorticoid-mediated stress imposed by dominant breeders. Similarly, there are no direct effects of dominance status on corticosterone levels, pre-breeding T levels, or testis size.

These findings support the hypothesis that the absence of reproductive activity on the part of helpers is voluntary and not due to reproductive suppression by older, dominant individuals. This is consistent with the results indicating that reproductive roles are determined primarily by incest avoidance rather than reproductive competition, although the latter is still important in terms of the relative success of individual birds in cobreeding coalitions.

Evolution of cooperative breeding

Acorn woodpeckers at Hastings Reservation live under conditions of what has traditionally been referred to as habitat saturation. The clearest support for this statement is that birds fight to fill reproductive vacancies, unambiguously demonstrating that helpers value the opportunity to become a breeder in the population over helping. Indeed, competition is so fierce that birds often form coalitions in order to successfully win power struggles, implying that even a shared breeding position is a superior fitness option compared to serving as a helper.

Until recently, we believed that granaries were the resource most likely to be limiting territorial establishment and thus driving delayed dispersal in the Hastings population. We have now tested this hypothesis by means of an experiment in which we compared sets of four potentially useable sites not previously inhabited by acorn woodpeckers, experimentally adding artificial granaries with 1,500 storage holes to site 1, two artificial nest cavities to site 2, both artificial granaries and two nest cavities to site 3, and nothing to control site

4. After three years, the number of groups in the population increased by 17%, with artificial nesting cavities attracting more new groups than artificial storage facilities (E. Walters and W. Koenig, unpubl. data). As such, acorn woodpeckers are similar to red-cockaded woodpeckers in which nesting and roosting cavities are key ecological constraints driving delayed dispersal (J. Walters et al. 1992).

On the one hand, this is surprising in that acorn woodpecker cavities are not modified in any discernable way and are typically used communally for roosting, with up to 14 roosting in the same cavity, whereas red-cockaded woodpecker cavities are not only specially modified by the birds with a resin barrier to deter predators (Kappes and Sieving 2011) but also only used for roosting by one bird at a time. On the other hand, over 50% of acorn woodpecker nests are in previously excavated cavities (Wiebe et al. 2006), and we have observed groups apparently unable to nest when their nest cavity was taken over by European starlings (*Sturnus vulgaris*). In any case, these observations suggest that the excavation of new nesting holes is difficult and support the conclusion that cavities are an important resource to some extent driving cooperative breeding in this species.

In summary, the main proximate factors driving group living in acorn woodpeckers, both through delayed dispersal of offspring and coalition formation and mate-sharing among breeders, are the ecological constraints imposed by limited nesting cavities and the need for access to granary facilities in which to store acorns. Two predictions of this hypothesis are first, the number of groups should vary little from year to year relatively compared to the number of birds in the population, and second, there should be at best a modest relationship between the number of groups and key resources that vary from year to year – primarily the acorn crop. A factor confounding these tests is that the population size has not been constant throughout the course of the study: both the number of birds and number of groups within the core study area have increased, with the latter rising from 19 in 1980 to 54 in 2012 (Figure 13.5), at least in part because of an increase in canopy cover on the study area (McMahon et al. 2015). In contrast, group size has remained constant

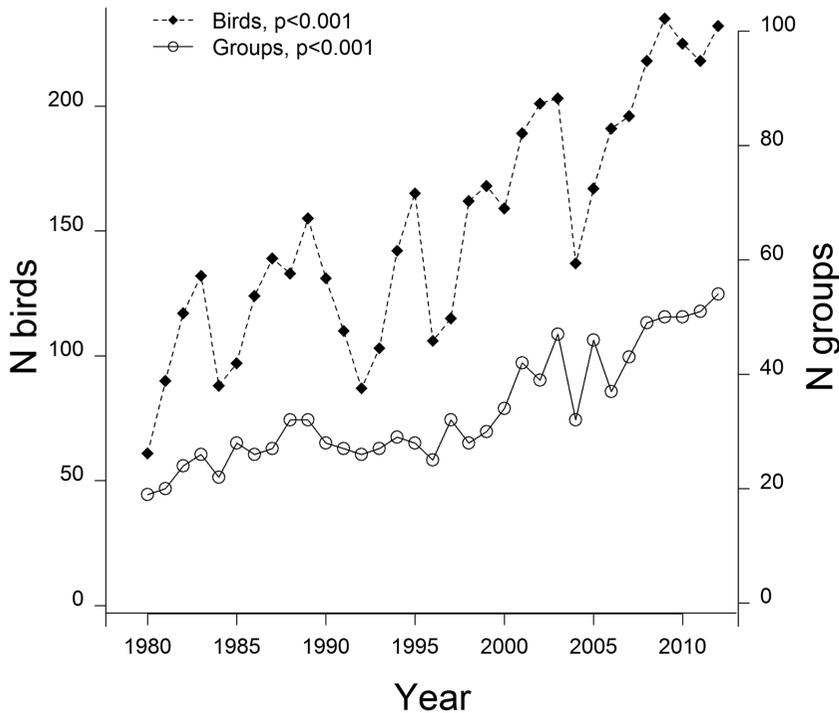


Figure 13.5. Population size through time at the Hastings Reservation study site. Correlations: $r = 0.86$ (N birds vs. year); $r = 0.92$ (N groups vs. year). $N = 33$ years (1980 to 2012).

(correlation between birds per group and year: $r = 0.12$, $P = 0.5$). In order to control for long-term changes in habitat we calculated the residuals from regressions of the number of groups and birds on year and used these values to estimate variability and the effects of the acorn crop.

Results support the first prediction: the variance in number of groups within the core study area between 1980 and 2012 was 20.4, significantly less than the variance in the number of birds in the population (580.7; variance test, $P < 0.001$) and variances of any of the four categories of birds (variance in breeder males = 119.8; breeder females = 86.2; helper males = 125.8; helper females = 90.4; paired variance tests, all $P < 0.002$).

Less clear are results regarding the second prediction: all components of population size, including the number of groups and group size, varied significantly and positively with either the acorn crop the prior year or (in the case of helpers and group size) with the acorn

crop two years earlier (Table 13.4). Thus, following large acorn crops, both the number of groups and the number of birds increase in the population, the latter primarily due to increased number of groups rather than changes in group size. With access to lots of acorns, groups are reproductively very successful, resulting in more helpers and larger groups the following year.

We can compare relative variation in the relevant parameters by log-transforming the number of birds and groups, thereby rendering their variances independent of scale (Lewontin 1966) and comparable to variance in the \ln -transformed acorn crop. The results confirm that variability in the (\ln -transformed) acorn crop (variance = 0.545) is several times greater than variance in the (\ln -transformed) number of groups (0.083) which in turn is less than variance in (\ln -transformed) overall population size (0.113).

The significant relationship between population size and resources raises a question regarding the

Table 13.4. Correlations between the residuals of regressions of group composition on year vs. the acorn crop in year $x-1$ (the prior autumn) and year $x-2$ (the year before that)

Category	Acorn crop year $x-1$	Acorn crop year $x-2$
<i>N</i> groups	0.46**	-0.26
<i>N</i> birds	0.35*	0.30
<i>N</i> birds per group	0.02	0.59***
<i>N</i> breeder males	0.36*	-0.16
<i>N</i> breeder females	0.56***	-0.32
<i>N</i> helper males	-0.01	0.60***
<i>N</i> helper females	-0.08	0.55**

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

habitat saturation hypothesis, which is predicated on the underlying fundamental processes restricting independent reproduction being relatively stable from year to year (Koenig and Pitelka 1981; Emlen 1982). Clearly this is not the case to the extent that both the number of birds and number of groups covary with the acorn crop. Specifically, conditions become more or less favorable depending on the acorn crop and in a good year a modest proportion of territories that would otherwise not be inhabited become suitable for colonization. Given this situation, it is possible that averaging across all years underestimates the importance of helping, particularly in years when the acorn crop is poor, and thus that helpers are not making the best of a bad job but rather choosing a situation that is either the best alternative when resources are unfavorable (Magrath 2001) or exercising a “bet-hedging” strategy designed to minimize variance in fitness under conditions of high spatiotemporal variation (Rubenstein 2011).

The first of these possibilities conforms to the “hard life” hypothesis discussed earlier, and is not supported by the finding that the fitness benefits of male helpers is greatest when the acorn crop is good rather than poor (Figure 13.4; Koenig et al. 2011). The second, bet-hedging hypothesis predicts that variance in fecundity decreases with increasing sociality. There are several approaches to addressing this question, but in general our analyses indicate that although relative fecundity variance (measured by the coefficient of

variation in the number of young fledged) is reduced in more social groups, the decrease is not enough to compensate for the decrease in mean fecundity as measured by the per capita number of young fledged (Table 13.5). Thus, in general, bet-hedging does not appear to play an important role in acorn woodpecker populations, although it is still possible that reduced fecundity variance may provide a significant benefit to some aspects of group living in years of poor acorn crops (Koenig and Walters 2015).

Because groups consist of close relatives, nonbreeding helpers gain indirect (kin) fitness benefits from helping, especially when the acorn crop is good. As discussed above, we have yet to demonstrate any significant direct fitness benefits of helping. One benefit that has frequently been proposed for helpers, however, is the potential for inheriting a high-quality territory (Stacey and Ligon 1991; Kokko et al. 2001; Clutton-Brock 2002; Covas and Griesser 2007). This is a potentially important phenomenon in acorn woodpeckers, particularly for males given their high rate of inheritance. Countering this hypothesis, however, is that a significant number of birds inheriting their natal territory (22% of males and 12% of females) did so after dispersing and assuming a breeding position elsewhere in the population (Haydock et al. unpubl. data). Thus, in our population, at least, inheritance of the natal territory is not dependent on delayed dispersal. Similar to species with redirected helpers (Chapters 1 and 2), birds apparently monitor their natal territory even *after* they have dispersed elsewhere and potentially return to breed there should a (nonincestuous) breeding opportunity arise. Such cases devalue the importance of delayed dispersal to helping and territorial inheritance, and increase the relative value of kin-selected benefits to the frequency of delayed dispersal and helping behavior.

Conclusion

Acorn woodpeckers do not live in a particularly stable environment, being dependent on a highly variable acorn crop. Thus, there is an argument for cooperative breeding in this system being an adaptation to cope

Table 13.5. Comparison of fecundity variance (CV) and mean estimated fitness for groups divided by an index of sociality measured by total group size, number of cobreeder males, number of cobreeder females, and the presence/absence of helpers

Index of sociality	Relatively nonsocial	Relatively social	Wilcoxon <i>V</i>	<i>P</i> -value
Fecundity variance (CV)				
Total group size ^a	77.7 ± 7.2	72.6 ± 4.6	205	0.04
Cobreeder males ^b	86.4 ± 7.5	71.2 ± 5.2	410	0.02
Cobreeder females ^b	78.9 ± 5.8	75.0 ± 5.9	332	0.37
Presence of helpers ^c	77.7 ± 8.7	58.8 ± 5.6	210	0.03
Estimated fitness^d				
Total group size ^a	0.67 ± 0.10	0.60 ± 0.05	285	0.48
Cobreeder males ^b	1.14 ± 0.18	0.86 ± 0.08	289	0.13
Cobreeder females ^b	1.24 ± 0.18	1.03 ± 0.12	132	0.04
Presence of helpers ^c	0.71 ± 0.10	0.64 ± 0.06	252	0.47

Values are means ± SE. Analyses by Wilcoxon paired signed-rank test. *N* = 33 years (except for presence of helpers, where *N* = 23 years for CV and *N* = 29 for fitness).

^a Pairs vs. groups, except for 10 years in which there were not enough pairs (or variance was undefined) where comparison is for pairs plus trios vs. groups of 4+ birds.

^b Groups with one breeder vs. two or more cobreeders; all groups had one breeder of the other sex and no helpers.

^c Pairs without vs. pairs with one or more helpers of either sex.

^d Estimated using the method described by Frank and Slatkin (1990); for details, see Koenig and Walters (2015).

Source: From Koenig and Walters (2015).

with highly variable and unpredictable conditions, as was proposed originally by Emlen (1982) and more recently expanded by Rubenstein and his colleagues (Chapter 11), and supported by the apparent reduction in fecundity variance exhibited by larger, more social groups (Koenig and Walters 2015). Nonetheless, the population generally lives under conditions of habitat saturation, with access to the key resources of nesting cavities and storage facilities acting as ecological constraints driving delayed dispersal on the part of offspring and coalition formation and subsequent polygyny on the part of breeders.

Thus, competition for territories sets the stage for delayed dispersal on the part of offspring and coalition formation on the part of helpers attempting to improve their chances of gaining a reproductive opportunity. But why help? For cobreeders, provisioning behavior appears to be driven by the direct fitness benefit of parentage, or at least the opportunity of parentage,

combined with the indirect fitness benefits of kinship with cobreeders. Both females and males share parentage relatively equitably, within individual nests (for females) and across nests (for males). We suspect that individuals that have copulatory access or have laid eggs in the nest have little information regarding their own parentage, but as we have shown, parentage is equally likely for all but the most subordinate of breeders. Given these circumstances, all breeders contribute to raising offspring, because they have a relatively equal chance of being a successful parent and, if not, gain the indirect benefits of assisting relatives.

The fitness benefits of provisioning offspring for non-breeding helpers appear to be primarily, if not exclusively, indirect through kinship. Not all possible routes to achieving direct fitness benefits have been tested, but thus far, our data do not support either the skills or the pay-to-stay hypotheses. Helper males gain significant indirect fitness benefits, particularly in good

acorn years; in contrast, male helpers do not appear to gain benefits in poor acorn years, and female helpers do not incur significant indirect fitness benefits from helping except by enhancing breeder survivorship. Several key questions remain, however: why do breeders allow helpers to remain in poor acorn years?; why do female helpers provision when they appear to confer little or no fitness benefit?; what, exactly, are male and female helpers doing differently that leads to these differences?; and are the observed benefits due to provisioning behavior per se or some other behavior on the part of helpers?

Also remaining is a thorough explanation for the differences among populations. Three populations have been studied in detail thus far, and each differs significantly from the others, resulting in strikingly different conclusions regarding the factors driving cooperative breeding (Koenig and Stacey 1990). With populations stretching through Mexico, Central America, and into Colombia, there is significant potential to further explore the existence and significance of variability in social behavior of this species, potentially yielding important new insights into the evolution and maintenance of complex social systems.

Acknowledgments

We are particularly grateful to Michael and Barbara MacRoberts, Ron Mumme, Sue Hannon, Mark Stanback, Philip Hooge, and Janis Dickinson for their many contributions to the study over the years, along with the help of the 139 field assistants that have assisted with the project since 1980. The study would not have been possible without the long-term support of the Museum of Vertebrate Zoology, UC Berkeley, Hastings Natural History Reservation, and the National Science Foundation. The manuscript was improved by the comments of Janis Dickinson and Bruce Lyon.

REFERENCES

- Bock, C. E. and Bock, J. H. (1974). Geographical ecology of the acorn woodpecker: diversity versus abundance of resources. *Am. Nat.*, 108, 694–698.
- Brown, J. L. (1987). *Helping and Communal Breeding in Birds: Ecology and Evolution*. Princeton, NJ: Princeton University Press.
- Clutton-Brock, T. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, 296, 69–72.
- Covas, R. and Griesser, M. (2007). Life history and the evolution of family living in birds. *Proc. R. Soc. London B*, 274, 1349–1357.
- Covas, R., Du Plessis, M. A., and Doutrelant, C. (2008). Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behav. Ecol. Sociobiol.*, 63, 103–112.
- Davies, N. B. (1992). *Dunnock Behaviour and Social Evolution*. Oxford: Oxford University Press.
- Dickinson, J. L., Haydock, J., Koenig, W. D., Stanback, M. T., and Pitelka, F. A. (1995). Genetic monogamy in single-male groups of acorn woodpeckers, *Melanerpes formicivorus*. *Mol. Ecol.*, 4, 765–770.
- Emlen, S. T. (1982). The evolution of helping. I. An ecological constraints model. *Am. Nat.*, 119, 29–39.
- Emlen, S. T., Emlen, J. M., and Levin, S. A. (1986). Sex-ratio selection in species with helpers-at-the-nest. *Am. Nat.*, 127, 1–8.
- Fajer, E. D., Schmidt, K. J., and Eschler, J. G. (1987). Acorn woodpecker predation on cliff swallow nests. *Condor*, 89, 177–178.
- Frank, S. A. and Slatkin, M. (1990). Evolution in a variable environment. *Am. Nat.*, 136, 244–260.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. I, II. *J. Theor. Biol.*, 7, 1–52.
- Hannon, S. J., Mumme, R. L., Koenig, W. D., and Pitelka, F. A. (1985). Replacement of breeders and within-group conflict in the cooperatively breeding acorn woodpecker. *Behav. Ecol. Sociobiol.*, 17, 303–312.
- Hannon, S. J., Mumme, R. L., Koenig, W. D., Spon, S., and Pitelka, F. A. (1987). Poor acorn crop, dominance, and decline in numbers of acorn woodpeckers. *J. Anim. Ecol.*, 56, 197–207.
- Haydock, J. and Koenig, W. D. (2002). Reproductive skew in the polygynandrous acorn woodpecker. *Proc. Natl. Acad. Sci. (USA)*, 99, 7178–7183.
- Haydock, J. and Koenig, W. D. (2003). Patterns of reproductive skew in the polygynandrous acorn woodpecker. *Am. Nat.*, 162, 277–289.
- Haydock, J., Koenig, W. D., and Stanback, M. T. (2001). Shared parentage and incest avoidance in the cooperatively breeding acorn woodpecker. *Mol. Ecol.*, 10, 1515–1525.
- Kappes, Jr., J. J. and Sieving, K. E. (2011). Resin-barrier maintenance as a mechanism of differential predation among

- occupants of red-cockaded woodpecker cavities. *Condor*, 113, 362–371.
- Kattan, G. (1988). Food habits and social organization of acorn woodpeckers in Colombia. *Condor*, 90, 100–106.
- Kingma, S. A., Santema, P., Taborsky, M., and Komdeur, J. (2014). Group augmentation and the evolution of cooperation. *Trends Ecol. Evol.*, 29, 476–484.
- Koenig, W. D. (1981). Space competition in the acorn woodpecker: power struggles in a cooperative breeder. *Anim. Behav.*, 29, 396–409.
- Koenig, W. D. (1990). Opportunity of parentage and nest destruction in polygynandrous acorn woodpeckers, *Melanerpes formicivorus*. *Behav. Ecol.*, 1, 55–61.
- Koenig, W. D. and Haydock, J. (1999). Oaks, acorns, and the geographical ecology of the acorn woodpecker. *J. Biogeogr.*, 26, 159–165.
- Koenig, W. D. and Mumme, R. L. (1987). *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton, NJ: Princeton University Press.
- Koenig, W. D. and Pitelka, F. A. (1981). Ecological factors and kin selection in the evolution of cooperative breeding in birds. In: *Natural Selection and Social Behavior: Recent Research and New Theory*, ed. R. D. Alexander and D. W. Tinkle. New York: Chiron Press, pp. 261–280.
- Koenig, W. D. and Stacey, P. B. (1990). Acorn Woodpeckers: group-living and food storage under contrasting ecological conditions. In: *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*, ed. P. B. Stacey and W. D. Koenig. Cambridge: Cambridge University Press, pp. 413–453.
- Koenig, W. D. and Stahl, J. T. (2007). Late summer and fall nesting in the acorn woodpecker and other North American terrestrial birds. *Condor*, 109, 334–350.
- Koenig, W. D. and Walters, E. L. (2011). Age-related provisioning behaviour in the cooperatively breeding acorn woodpecker: testing the skills and the pay-to-stay hypotheses. *Anim. Behav.*, 82, 437–444.
- Koenig, W. D. and Walters, E. L. (2012a). Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker. *Behav. Ecol.*, 23, 181–190.
- Koenig, W. D. and Walters, E. L. (2012b). An experimental study of chick provisioning in the cooperatively breeding acorn woodpecker. *Ethology*, 118, 566–574.
- Koenig, W. D. and Walters, E. L. (2015). Temporal variability and cooperative breeding: testing the bet-hedging hypothesis in the acorn woodpecker. *Proc. R. Soc. London B*, 282, 20151742.
- Koenig, W. D. and Walters, J. R. (1999). Sex-ratio selection in species with helpers at the nest: the repayment model revisited. *Am. Nat.*, 153, 124–130.
- Koenig, W. D. and Williams, P. L. (1979). Notes on the status of acorn woodpeckers in central Mexico. *Condor*, 81, 317–318.
- Koenig, W. D., Mumme, R. L., Carmen, W. J., and Stanback, M. T. (1994). Acorn production by oaks in central coastal California: variation in and among years. *Ecology*, 75, 99–109.
- Koenig, W. D., Mumme, R. L., Stanback, M. T., and Pitelka, F. A. (1995). Patterns and consequences of egg destruction among joint-nesting acorn woodpeckers. *Anim. Behav.*, 50, 607–621.
- Koenig, W. D., Van Vuren, D., and Hooge, P. N. (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol. Evol.*, 11, 514–517.
- Koenig, W. D., Stanback, M. T., and Haydock, J. (1999). Demographic consequences of incest avoidance in the cooperatively breeding acorn woodpecker. *Anim. Behav.*, 57, 1287–1293.
- Koenig, W. D., Hooge, P. N., Stanback, M. T., and Haydock, J. (2000). Natal dispersal in the cooperatively breeding acorn woodpecker. *Condor*, 102, 492–502.
- Koenig, W. D., Stanback, M. T., Haydock, J., and Kraaijeveld-Smit, F. (2001). Nestling sex ratio variation in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*). *Behav. Ecol. Sociobiol.*, 49, 357–365.
- Koenig, W. D., McEntee, J. P., and Walters, E. L. (2008). Acorn harvesting by acorn woodpeckers: annual variation and comparison with genetic estimates. *Evol. Ecol. Res.*, 10, 811–822.
- Koenig, W. D., Walters, E. L., and Haydock, J. (2009). Helpers and egg investment in the cooperatively breeding acorn woodpecker: testing the concealed helper effects hypothesis. *Behav. Ecol. Sociobiol.*, 63, 1659–1665.
- Koenig, W. D., Walters, E. L., and Haydock, J. (2011a). Fitness consequences of within-brood dominance in the cooperatively breeding acorn woodpecker. *Behav. Ecol. Sociobiol.*, 65, 2229–2238.
- Koenig, W. D., Walters, E. L., and Haydock, J. (2011b). Variable helpers effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. *Am. Nat.*, 178, 145–158.
- Koenig, W. D., Walters, E. L., Knops, J. M. H., and Carmen, W. J. (In press). Acorns and acorn woodpeckers: ups and downs in a long-term relationship. In: *Proceedings of the 7th California Oak Symposium: Managing Oak Woodlands in a Dynamic World*. Pacific SW Forest & Range Exp. Station Gen. Tech. Rep.
- Kokko, H., Johnstone, R. A., and Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. London B*, 268, 187–196.

- Leach, F. A. (1925). Communism in the California woodpecker. *Condor*, 27, 12–19.
- Lewontin, R. C. (1966). On the measurement of relative variability. *Syst. Zool.*, 15, 141–142.
- Ligon, J. D. and Ligon, S. H. (1978). Communal breeding in green woodhoopoes as a case for reciprocity. *Nature*, 276, 496–498.
- MacRoberts, M. H. and MacRoberts, B. R. (1976). Social organization and behavior of the acorn woodpecker in central coastal California. *Ornith. Monogr.*, 21, 1–115.
- Magrath, R. D. (2001). Group breeding dramatically increases reproductive success of yearling but not older female scrubwrens: a model for cooperatively breeding birds? *J. Anim. Ecol.*, 70, 370–385.
- McMahon, D. E., Pearse, I. S., Koenig, W. D., and Walters, E. L. (2015). Tree community shifts and acorn woodpecker population increases over three decades in a California oak woodland. *Can. J. For. Res.*, 45, 1113–1120.
- Michael, E. (1927). Plurality of mates. *Yosemite Nature Notes*, 6, 78.
- Mulder, R. A. and Langmore, N. E. (1993). Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.*, 45, 830–833.
- Mumme, R. L., Koenig, W. D., and Pitelka, F. A. (1983a). Mate guarding in the acorn woodpecker: within-group reproductive competition in a cooperative breeder. *Anim. Behav.*, 31, 1094–1106.
- Mumme, R. L., Koenig, W. D., and Pitelka, F. A. (1983b). Reproductive competition in the communal acorn woodpecker: sisters destroy each other's eggs. *Nature*, 306, 583–584.
- Mumme, R. L., Koenig, W. D., and Ratnieks, F. L. W. (1989). Helping behaviour, reproductive value, and the future component of indirect fitness. *Anim. Behav.*, 38, 331–343.
- Mumme, R. L., Koenig, W. D., and Pitelka, F. A. (1990). Individual contributions to cooperative nest care in the acorn woodpecker. *Condor*, 92, 360–368.
- Myers, H. W. (1915). A late nesting record for the California woodpecker. *Condor*, 17, 183–185.
- Rowley, I., Russell, E. M., and Brooker, M. G. (1993). Inbreeding in birds. In: *The Natural History of Inbreeding and Outbreeding*, ed. N. W. Thornhill. Chicago: University of Chicago Press, pp. 304–328.
- Rubenstein, D. R. (2011). Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proc. Natl. Acad. Sci. (USA)*, 108, 10816–10822.
- Russell, A. F., Langmore, N. E., Cockburn, A., Astheimer, L. B., and Kilner, R. M. (2007). Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science*, 317, 941–944.
- Schaller, G. B. (1972). *The Serengeti Lion: A Study of Predator-prey Relations*, Chicago: University of Chicago Press.
- Selander, R. K. (1964). Speciation in wrens of the genus *Campylorhynchus*. *Univ. Calif. Publ. Zool.*, 74, 1–305.
- Stacey, P. B. (1979a). Habitat saturation and communal breeding in the acorn woodpecker. *Anim. Behav.*, 27, 1153–1166.
- Stacey, P. B. (1979b). Kinship, promiscuity, and communal breeding in the acorn woodpecker. *Behav. Ecol. Sociobiol.*, 6, 53–66.
- Stacey, P. B. and Bock, C. E. (1978). Social plasticity in the acorn woodpecker. *Science*, 202, 1298–1300.
- Stacey, P. B. and Ligon, J. D. (1991). The benefits of philopatry hypothesis for the evolution of cooperative breeding: variance in territory quality and group size effects. *Am. Nat.*, 137, 831–846.
- Stanback, M. T. (1994). Dominance within broods of the cooperatively breeding acorn woodpecker. *Anim. Behav.*, 47, 1121–1126.
- Walters, J. R., Copeyon, C. K., and Carter, III, J. H. (1992). Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk*, 109, 90–97.
- Wiebe, K. L., Koenig, W. D., and Martin, K. (2006). Evolution of clutch size in cavity-excavating birds: the nest site limitation hypothesis revisited. *Am. Nat.*, 167, 343–353.
- Williams, G. C. (1966). *Adaptation and Natural Selection*, Princeton, NJ: Princeton University Press.
- Wynne-Edwards, V. C. (1962). *Animal Dispersion in Relation to Social Behaviour*, Edinburgh: Oliver and Boyd.
- Zahavi, A. (1995). Altruism as a handicap – the limitations of kin selection and reciprocity. *J. Avian Biol.*, 26, 1–3.