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Variable Helper Effects, Ecological Conditions, and the Evolution of Cooperative Breeding in the Acorn Woodpecker

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ABSTRACT: The ecological conditions leading to delayed dispersal and helping behavior are generally thought to follow one of two contrasting scenarios: that conditions are stable and predictable, resulting in young being ecologically forced to remain as helpers (extrinsic constraints and the habitat saturation hypothesis), or that conditions are highly variable and unpredictable, leading to the need for helpers to raise young, at least when conditions are poor (intrinsic constraints and the hard life hypothesis). We investigated how variability in ecological conditions influences the degree to which helpers augment breeder fitness in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*), a species in which the acorn crop, territory quality, and prior breeding experience all vary in ways that have important effects on fitness. We found that the relationship between ecological conditions and the probability that birds would remain as helpers was variable but that helpers generally yielded greater fitness benefits when ecological conditions were favorable, rather than unfavorable, for breeding. These results affirm the importance of extrinsic constraints to delayed dispersal and cooperative breeding in this species, despite its dependence on a highly variable and unpredictable acorn crop. Our findings also confirm that helpers can have very different fitness effects, depending on conditions, but that those effects are not necessarily greater when breeding conditions are unfavorable.

Keywords: experience effects, cooperative breeding, food supply, helping behavior, *Melanerpes formicivorus*, territory quality.

Introduction

Since the earliest studies of cooperative breeding, key questions have been why and to what extent helpers help (Woolfenden 1975; Brown 1978; Koenig and Pitelka 1981). The answers to these questions have often been ambiguous, partly because they can be addressed at both proximate and ultimate levels of analysis (Koenig and Mumme

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1990) and partly because there is variability among species in the apparent fitness consequences of helping (Dickinson et al. 1996; Cockburn 1998). Investigators have recently begun to focus on the significance of an additional complication, namely, that there is often considerable variability in the fitness consequences of helping not only among but also within populations (Baglione et al. 2010). Although the parameters contributing to such variability are potentially legion, a common finding has been that helping has greater fitness benefits when conditions are harsh—that is, when a pair is less likely to successfully raise young on its own (Canário et al. 2004; Covas et al. 2008). Factors potentially important in this context include number of helpers, sex of helpers, territory quality, food supply, and environmental conditions such as rainfall and temperature, all of which may affect both the probability of birds delaying dispersal and becoming helpers and the fitness effects of helpers once they decide to stay. A particularly strong case for helpers being important when circumstances are unfavorable for breeding has been made by Magrath (2001).

These prior studies demonstrate that variability vis-à-vis ecological conditions in the extent to which helpers affect breeder fitness is common and likely to play an important role in the evolution of cooperative breeding. More specifically, they support the hypothesis that the primary fitness benefit of helping behavior and of cooperative breeding in general is to provide assistance when conditions are poor or breeders are of inferior quality and thus unable to raise young successfully on their own. This hypothesis is important for two reasons. First, it provides one potential resolution to the dilemma posed by species in which there is no overall effect of helpers on reproduction when all data are considered (Magrath and Yezerinac 1997). Second, it raises the possibility that helping behavior—despite yielding relatively few fitness benefits

Table 1: Contrasting conditions for the ecological basis of delayed dispersal and their predictions vis-à-vis how reproductive success and the probability of delayed dispersal should change as conditions for breeding improve

Hypothesis	Conditions	Probability of delayed dispersal	Rationale	Reproductive success/survivorship	Rationale
Hard life	Constraints related to fluctuating, unpredictable environments/socially induced benefits	Less likely	Better conditions reduce constraints by making it easier to raise young independently; effect expected to be strong	Smaller benefit of helping	Helpers should have their biggest effect when independent breeding is difficult and their aid is most needed
Habitat saturation	Constraints related to stable, predictable environments/resource access benefits	No consistent effect expected	Little or no effect since conditions are inherently stable; more individuals will disperse when conditions are good only insofar as new territories are created, which should be uncommon	No prediction	No specific prediction since helpers are making the best of a bad job

overall, compared with independent breeding (Dickinson et al. 1996; Dickinson and Hatchwell 2004), and thus often considered a "best of a bad job" strategy pursued when ecological constraints restrict dispersal and independent breeding—might be so critically important when ecological conditions are poor that the "benefits of philopatry" (Stacey and Ligon 1991) are greater than the fitness benefits of dispersal and independent breeding. At the very least, this would indicate that the fitness benefits of helping are considerably more important than they appear to be when data are combined from both favorable and unfavorable ecological conditions. Here we refer to the hypothesis that helpers are important primarily to improve or make possible reproduction when conditions are unfavorable as the hard life hypothesis (Koenig and Mumme 1987).

The hard life hypothesis corresponds to the idea originally proposed by Emlen (1982) that an important ecological constraint leading to cooperative breeding is a harsh, variable, or unpredictable environment under which delayed dispersal and helping are likely to yield significant "intrinsic" (Koenig et al. 1992) or "socially induced" benefits (S.-F. Shen and S. T. Emlen, unpublished manuscript) related to "group augmentation" (Kokko et al. 2001)—that is, benefits emerging from being part of a social group—at least when conditions are poor. To the extent that such harsh or variable conditions are integral to cooperative breeding, fewer young should delay dispersal and remain as helpers when conditions improve and the constraints on independent breeding are reduced. Magrath's (2001) finding that this scenario applies to a wide variety of cooperative breeders thus raises the possibility that the hard life hypothesis is an important factor selecting for delayed dispersal and helping behavior in a much greater proportion of species than originally thought, a conclusion supported more recently by Jetz and

Rubenstein's (2011) finding that environmental variability correlates with the global incidence of avian cooperative breeding.

In contrast, if the ecological basis for delayed dispersal is based on extrinsic or "resource access" benefits (S.-F. Shen and S. T. Emlen, unpublished manuscript)—that is, benefits gained as a result of access to a localized or limited resource, such as might be the case under conditions of habitat saturation or shortage of mates (Koenig and Pitelka 1981; Emlen 1982)—the underlying fundamental processes restricting independent reproduction are assumed to be relatively stable from year to year. Consequently, there should be little effect of variable ecological conditions on the probability of delayed dispersal except insofar as new territories are created, in which case a moderate increase in dispersal and a concomitant decrease in delayed dispersal as conditions improve might be expected. Furthermore, there is no a priori reason to expect that helpers should be more effective or should influence the fitness of breeders more when conditions are poor. In fact, helpers might have a greater effect when conditions are favorable and food is more readily available (table 1).

A problem in testing these hypotheses is that the factors making for good versus poor conditions are often ambiguous. In the case of the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*), prior work has demonstrated a strong effect of acorn production by oaks (*Quercus* spp.) on the reproductive success and demography of this species both at a landscape level (Koenig and Haydock 1999) and within a single population (Hannon et al. 1987; Koenig and Mumme 1987). This results in considerable annual variability in size and success of populations, since acorn production by individual species of oak varies greatly from year to year (Koenig et al. 1994a). Furthermore, although annual variability in acorn abundance at any one site is to some extent mitigated by asyn-
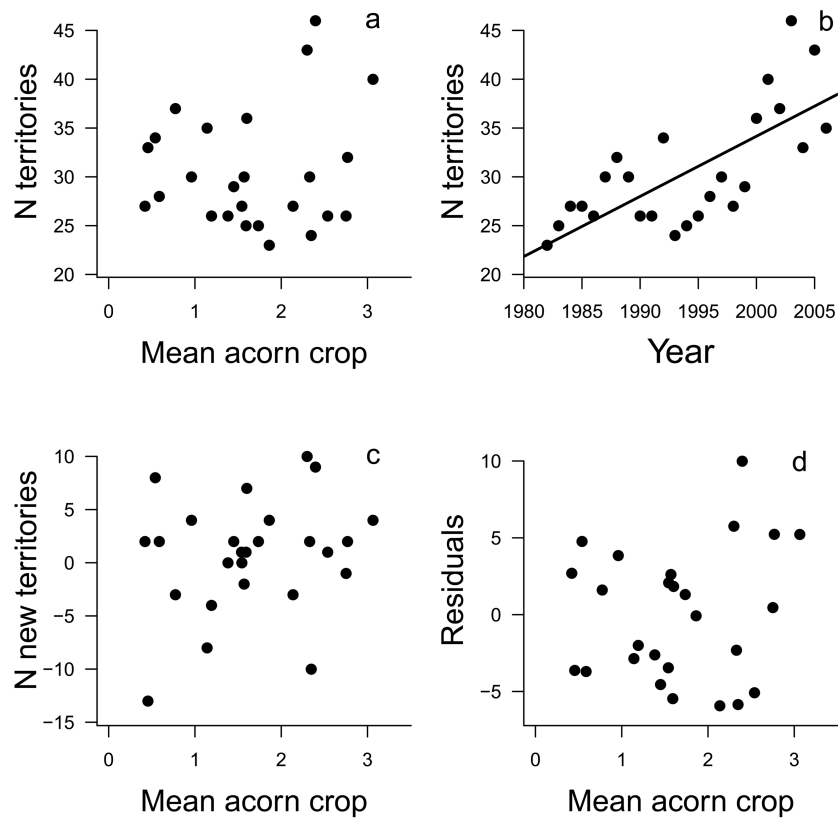
Figure 1: *a, b,* Relationship (1981–2006, $N = 26$ years) between the number of territories within the main study area and the mean acorn crop (*a;* $r = 0.12$, $t_{24} = 0.61$, $P = .55$) and year (*b;* $r = 0.74$, $t_{24} = 5.38$, $P < .001$). *c, d,* Relationship between the mean acorn crop and the number of new territories created in each year (*c,* (N territories in year x) − (N territories in year $x − 1$); $r = 0.21$, $t_{24} = 1.06$, $P = .30$) and the residuals from a regression of the number of territories on year (*d;* $r = 0.14$, $t_{24} = 0.71$, $P = .49$).

chrony among sympatric species (Koenig and Haydock 1999), crops tend to be spatially synchronized over large geographic areas of hundreds of kilometers (Koenig et al. 1999), making the effects of variable acorn production important to populations of acorn woodpeckers on a regional scale.

Other factors that have been shown to be important in prior analyses include breeder experience and territory quality, as indicated by the size of the facilities available to a group for storing acorns in the autumn (Koenig and Mumme 1987). Here, focusing on these three factors, we examine the relationship between delayed dispersal, helper effects, and conditions for breeding in order to examine the roles of habitat saturation versus the hard life hypothesis in the evolution of delayed dispersal and cooperative breeding in this species.

Preliminary analyses suggesting that the effects of helpers was greater in good, rather than poor, acorn years were performed recently in the context of testing for concealed helper effects by means of egg size variation (Koenig et

al. 2009). Conversely, a much earlier analysis concluded that helpers had a greater effect on reproduction when conditions were poor (Koenig and Mumme 1987), a result generally in accord with Magrath's (2001) analyses. These early analyses did not use an independent measure of ecological conditions, instead relying on overall reproductive success of the population as a proxy. Moreover, most used a potentially problematical measure of the relative effects of helpers—namely, the mean number of young fledged by groups without helpers divided by the mean number of young fledged by groups with helpers—and did not control for potentially confounding group composition. Here we address these issues in a more refined reanalysis of the fitness consequences of helpers in this species.

Material and Methods

Acorn woodpeckers are cooperative breeders that live in resident territorial groups of up to 15 individuals of all ages and both sexes. Group composition is highly variable
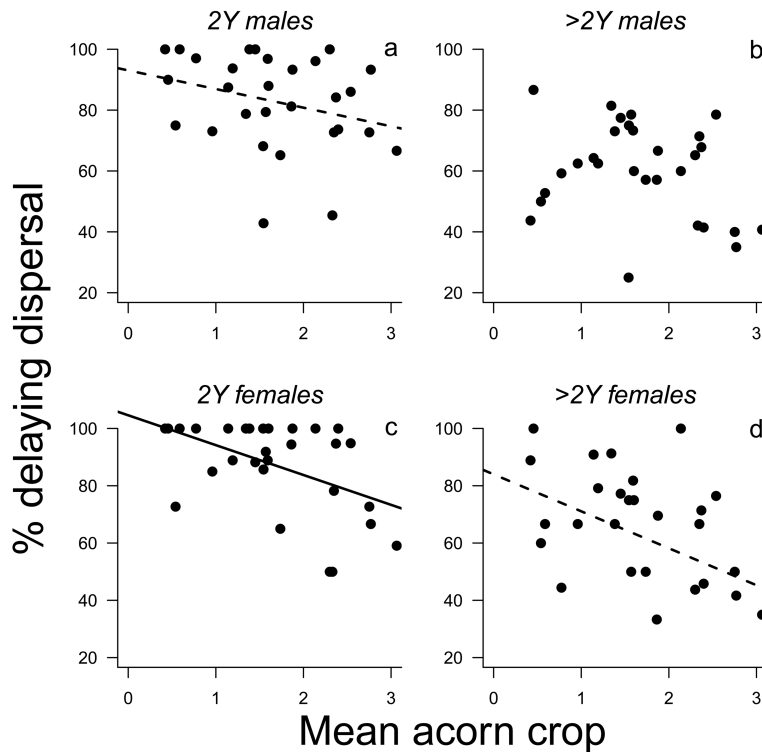
Figure 2: Relationship between the mean acorn crop and the percent of potential helpers that delay dispersal and remain as helpers on their natal territory during the breeding season. *a*, Second-year males surviving to their first February ($r = -0.33$, $t_{27} = -1.79$, $P = .09$). *b*, Males >2 years ($r = -0.25$, $t_{27} = -1.36$, $P = .19$). *c*, Second-year females surviving to their first February ($r = -0.49$, $t_{27} = -2.88$, $P = .008$). *d*, Females >2 years ($r = -0.35$, $t_{27} = -1.93$, $P = .06$). All correlations were calculated using arcsine-transformed proportions. *Solid line*, statistically significant; *dashed lines*, $.06 \leq P \leq .09$. *2Y*, second year.

but generally includes a breeding core of birds ranging from a pair to a cooperatively polygynandrous set of two to six cobreeding males competing for matings with one to two (rarely three) cobreeding (or joint-nesting) females plus their offspring from prior years that typically act as helpers. Thus, helpers are closely related to both the breeders they help and the nestlings they feed. Cobreeding males and females are generally siblings or parents and their same-sex offspring that have inherited their natal group following the replacement of the breeders of the opposite sex (Koenig et al. 1998). Thus, all group members are typically closely related, except that breeder males are generally unrelated to breeder females. All mating takes place within the group, and with the exception of rare cases of incest, helpers do not breed either within or outside their group (Dickinson et al. 1995; Haydock et al. 2001).

We report here on data from a color-banded population of birds at Hastings Reservation, central coastal California, studied between 1973 and 2009, during which time we continuously monitored the population and found all nesting attempts within the study area. For analyses in-

volving the acorn crop, we focused on the 29 years between 1981 and 2009, during which time we assessed the size of the acorn crop from the prior autumn each year by counting a sample of acorns on 250 marked trees distributed among the five common oak species present in the study area. The mean acorn crop was estimated as the mean of the ln-transformed number of acorns counted in 30 seconds (mean LN30 $=$ ln(N acorns counted $+ 1$)) across all trees surveyed (Koenig et al. 1994*b*). In all cases, we analyzed how the prior autumn's acorn crop (year $x -$ 1) affected the woodpeckers in year x. For simplicity, however, we refer to the prior autumn's acorn crop simply as the acorn crop without specifying that it is for the prior autumn. In some analyses, we divided years into those in which the acorn crop was poor to fair (mean ln-transformed number of acorns per tree <2.2; $N = 20$ years) and those in which the overall acorn crop was good to very good (mean ln-transformed number of acorns per tree >2.2; $N = 9$ years). For the analysis of the predicted number of young fledged for pairs versus groups with one male or one female helper vis-à-vis the acorn crop, we

Table 2: Variables influencing breeder survivorship based on generalized linear models

Variable	Breeder female survivorship (N = 1,166 bird years)			Breeder male survivorship (N = 1,764 bird years)		
	Mean effect size ± SE	z	P	Mean effect size ± SE	z	P
No. breeder males	−.004 ± .075	−.06	.95	−.050 ± .054	−.93	.36
No. breeder females	**−.245 ± .117**	**−2.09**	**.04**	−.116 ± .127	−.91	.36
No. helper males	.436 ± .326	1.34	.18	.473 ± .301	1.57	.12
No. helper females	−.084 ± .359	−.24	.81	−.051 ± .307	−.17	.87
(No. helper males)^2	−.039 ± .030	−1.27	.20	**−.086 ± .028**	**−3.05**	**.002**
(No. helper females)^2	−.068 ± .045	−1.51	.13	**−.150 ± .033**	**−4.52**	**<.001**
Acorn crop	.007 ± .173	.04	.97	**−.366 ± .134**	**−2.73**	**.006**
Territory quality	.131 ± .290	.45	.65	.159 ± .242	.65	.51
Prior breeder experience	−.324 ± .337	−.96	.34	−.312 ± .282	−1.11	.27
Acorn crop × helper males	.006 ± .086	.07	.94	.133 ± .080	1.66	.10
Acorn crop × helper females	−.042 ± .110	−.38	.70	.147 ± .097	1.51	.13
Territory quality × helper males	.059 ± .164	.36	.72	−.081 ± .161	−.50	.62
Territory quality × helper females	.141 ± .196	.72	.47	.065 ± .178	.37	.71
Prior breeder experience × helper males	−.348 ± .256	−1.36	.17	−.179 ± .226	−.79	.43
Prior breeder experience × helper females	.287 ± .241	1.19	.23	.368 ± .207	1.78	.08

Note: Boldface values indicate statistical significance.

used mean ln-transformed acorn crop numbers corresponding to a poor (0.5), fair (1.5), or good (3.0) crop.

The proportion of young remaining as helpers in year x was estimated as the proportion of second-year birds banded as nestlings in year $x − 1$ remaining in their natal group through the breeding season of year x (May through July) divided by the number known to have survived to February of year x, before which natal dispersal is rare (Koenig et al. 2000). The proportion of older birds remaining as helpers was calculated as the proportion of all helpers present during the breeding season of year $x − 1$ that were still helpers in their natal group in the breeding season of year x. Fledglings can be sexed visually when they are approximately 4 months old, and thus we considered males and females separately in most analyses.

For analyses of the effects of helpers, we performed generalized linear models with a binomial error term (for survivorship) and mixed-effects models (for reproductive success). We then examined the effects of the number of breeder males and breeder females, number of helper males and helper females, mean acorn crop, territory quality (a binary index based on the size of the storage facilities [low, <1,000 storage holes; high, >1,000 storage holes]), and a given bird's prior breeding experience on apparent survivorship of breeder males and breeder females. We hereafter refer to the three factors relevant to whether conditions were favorable for breeding (the acorn crop, territory quality, and prior breeding experience) as favorability factors. In order to consider key nonlinear effects, we included helpers in both linear and quadratic terms as well as interaction terms between the three favorability

factors and the total number of helpers. The analyses of reproductive success included group as a random effect.

The fitness consequences of helpers with respect to the three favorability factors were examined with the goal of determining the importance of the hard life hypothesis to acorn woodpeckers. If, for example, helpers increase breeder survivorship or reproductive success primarily when conditions are unfavorable (i.e., poor acorn crop, low territory quality, no prior breeding experience) and not when conditions are favorable, it would support the hypothesis that the ecological constraints in this system are intermittent and related to harsh and unpredictable conditions rather than constant and indicative of habitat saturation.

We started by quantifying the relationship between the acorn crop and the formation of new territories. In order to control for the temporal increase in territories that occurred during the study, we examined the relationship between the acorn crop and (1) the number of new territories created each year and (2) the residuals from a regression of the number of active territories on year. For these analyses, we used only the part of the study area monitored continuously during the entire study period (1981–2009) but excluded 2007–2009, during which time we were conducting experimental additions of granaries and nesting cavities that potentially affected the number and quality of territories available. We then examined the relationship between the acorn crop and the probability of delayed dispersal, followed by an investigation into the relationship between the three favorability factors and the effectiveness of helpers in terms of enhancing breeder sur-

Table 3: Effects of helpers on breeder male apparent annual survivorship

Variable	Poor conditions		Good conditions	
	Mean effect size $\pm$ SE	z	Mean effect size $\pm$ SE	z
Acorn crop:				
No. helper males	.231 $\pm$ .160	1.44	**.856 $\pm$ .225**	**3.80******
No. helper females	**.359 $\pm$ .172**	**2.09***	**.943 $\pm$ .269**	**3.51******
(No. helper males)^2	$-$.043 $\pm$ .033	$-$1.30	**$-$.156 $\pm$ .043**	**$-$3.66******
(No. helper females)^2	**$-$.107 $\pm$ .040**	**$-$2.63***	**$-$.202 $\pm$ .057**	**$-$3.51******
Bird years	1,254		679	
Territory quality:				
No. helper males	$-$.914 $\pm$ .508	$-$1.80	**.571 $\pm$ .145**	**3.94******
No. helper females	**1.026 $\pm$ .387**	**2.65***	**.440 $\pm$ .156**	**2.83***
(No. helper males)^2	.387 $\pm$ .199	1.94	**$-$.107 $\pm$ .028**	**$-$3.84******
(No. helper females)^2	**$-$.288 $\pm$ .104**	**$-$2.77***	**$-$.111 $\pm$ .034**	**$-$3.24***
Bird years	350		1,414	
Prior breeder experience:				
No. helper males	**1.550 $\pm$ .433**	**3.58******	**.329 $\pm$ .140**	**2.35***
No. helper females	.757 $\pm$ .421	1.80	**.573 $\pm$ .152**	**3.77******
(No. helper males)^2	**$-$.410 $\pm$ .130**	**$-$3.16***	**$-$.060 $\pm$ .028**	**$-$2.16***
(No. helper females)^2	**$-$.296 $\pm$ .127**	**$-$2.33***	**$-$.133 $\pm$ .034**	**$-$3.97******
Bird years	392		1,541	

Note: Groups are separated into those breeding under good versus poor conditions, on the basis of the three favorability factors. Boldface values indicate statistical significance.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

vivorship and reproductive success. The latter involved both performing mixed-effects models and looking in detail at the effects of helpers by comparing breeder survivorship and reproduction in groups with and without helpers when conditions were favorable versus unfavorable, using Fisher exact tests. Analyses of reproductive success were performed using both all groups and only groups that successfully fledged young. Results for the two sets of analyses were identical, however, and only the former are presented here.

We then estimated the overall fitness consequences of helpers by conducting a simulation to determine the effects of a helper on breeder lifetime fitness depending on the acorn crop and whether they were resident on a low- or high-quality territory. Values for reproductive output and survivorship were estimated from general linear models comparing hypothetical pairs with trios containing a breeding pair plus either a single helper male or a single helper female. Five hundred trials were run, each of which used a different set of acorn crop values chosen randomly (with replacement) from those measured at the site. For each simulation, we estimated the mean number of young fledged by breeding pairs with and without a helper on the basis of that year's acorn crop. We then used the next year's acorn crop to estimate survivorship and young fledged in year 2 and continued this process for 18 years

(the maximum observed life span thus far in the population), calculating the expected lifetime fitness of breeders by summing the proportion of individuals expected to survive to year x (m_x) times reproductive success in year x (l_x) over all years of the simulation. Fitness benefits of the helper to the breeder were first calculated for the combined effects of both survivorship and reproduction and then separately (i.e., first eliminating any survivorship effect and then eliminating any reproduction effect on the breeder), thus providing an approximation of both current and future (Mumme et al. 1989) indirect fitness consequences of the helper's presence to the breeders.

We determined the effects of the acorn crop experienced initially by birds in these simulations by correlating the difference in expected lifetime fitness among birds with and without access to a helper as a function of the acorn crop they experienced in their first year (affecting reproductive success of their group their first year) and the acorn crop in their second year (affecting survivorship to their second year of helping and reproductive success of their group the second year).

All analyses were conducted in R 2.10.0 (R Development Core Team 2009). Autumn nests, which are attempted occasionally in good acorn crop years (Koenig and Stahl 2007), were excluded from the analyses; however, young from such nests constitute <5% of the total productivity
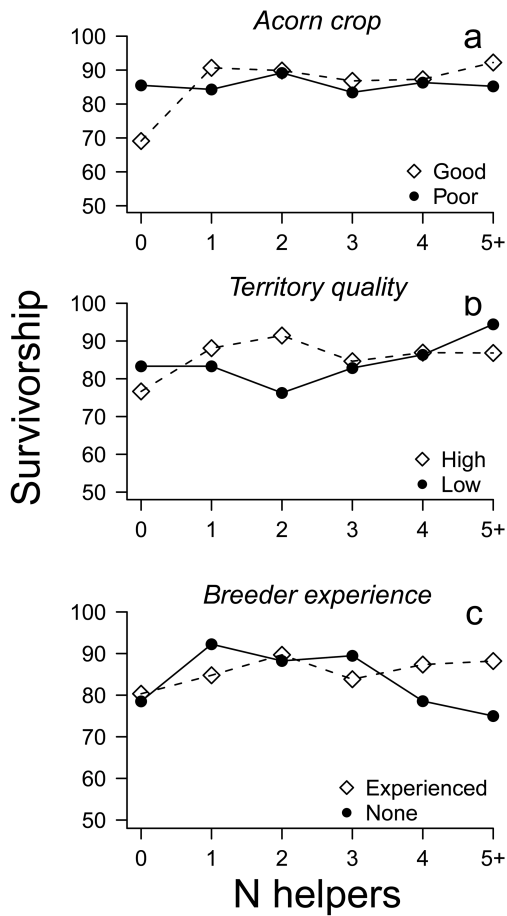
Figure 3: Comparison of the observed survival rates of breeder males as a function of the number of helpers of either sex present in their group divided according to the acorn crop (good, poor; *a*), territory quality (high, low; *b*), and breeder experience (experienced, none [no prior experience]; *c*).

of the population, and this omission does not alter the results. An α level of .05 was considered to indicate statistical significance.

Results

The Acorn Crop and New Territory Formation

We found no relationship between the number of active territories within the study area and either the previous year's acorn crop (fig. 1*a*) or the crop 2 years previously ($r = -0.12$, $t_{23} = -0.59$, $P = .56$). Examination of the data, however, revealed a potentially confounding linear increase in the number of active territories through time (fig. 1*b*). Although the cause of this increase is unknown, it was plausibly related to the maturing of trees and a

concomitant increase in habitat productivity during the study that, in turn, was the result of fire suppression and cessation of logging and agricultural activities in the study area beginning in the 1930s. Controlling for this temporal change by examining the relationship between new territories created and the residuals associated with a regression of the number of territories on year yielded no correlation with the mean acorn crop either the following year (fig. 1*c*, 1*d*) or 2 years later ($-0.31 < r < -0.26$, df $= 23$, $P \geq .14$). We conclude that despite a strong significant effect of the acorn crop on reproduction, there was no relationship between the acorn crop and the formation of new territories.
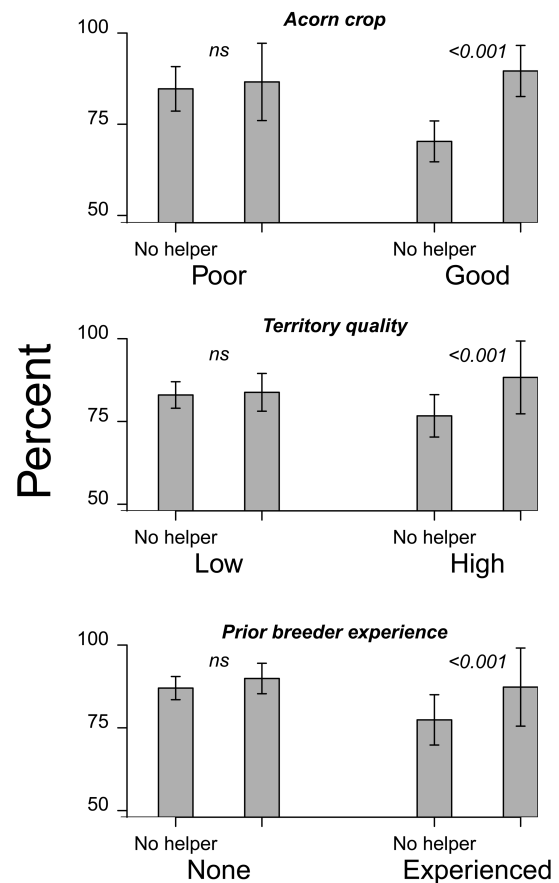

Figure 4: Observed mean ($\pm$ SD) survivorship of breeder males under poor and good ecological conditions, depending on whether the group contained helpers. Statistics are by Fisher exact tests; *ns*, not significant ($P > .05$). Number of individuals (in each case, the first value is for no helpers under poor conditions, the second for helpers under poor conditions, the third for no helpers under good conditions, and the fourth for helpers under good conditions): acorn crop, $N = 287, 966, 148, 528$; territory quality, $N = 112, 241, 227, 1,175$; prior breeder experience, $N = 108, 238, 327, 1,255$.

Table 4: Variables influencing reproductive success

Variable	Mean effect size ± SE	t	P
No. breeder males	**.155 + .074**	**2.08**	**.04**
No. breeder females	**.466 ± .150**	**3.11**	**.002**
No. helper males	−.187 ± .500	−.37	.71
No. helper females	1.190 ± .710	1.68	.09
(No. helper males)^2	.028 ± .033	.84	.40
(No. helper females)^2	.007 ± .059	.12	.91
Acorn crop	**1.095 ± .120**	**9.15**	**<.001**
Territory quality	**.609 ± .154**	**3.95**	**<.001**
Prior breeder experience	**.645 ± .196**	**3.29**	**.001**
Acorn crop × helper males	**.277 ± .084**	**3.29**	**.001**
Acorn crop × helper females	−.103 ± .114	−.90	.37
Territory quality × helper males	−.125 ± .166	−.75	.45
Territory quality × helper females	−.320 ± .230	−1.39	.17
Prior breeder experience × helper males	.133 ± .195	.68	.49
Prior breeder experience × helper females	−.008 ± .250	−.03	.97

Note: $N = 753$ group years. Boldface values indicate statistical significance.

The Acorn Crop and Delayed Dispersal

The relationship between the acorn crop and the percent of birds that delayed dispersal and remained on their natal territory as helpers partitioned by sex and age revealed that only one of the four relationships was statistically significant: the proportion of second-year females that delayed dispersal and remained as helpers significantly decreased ($P = .008$) as the acorn crop increased (fig. 2c). The relationships, however, for both second-year males and older (>2 years) females exhibited suggestive, albeit nonsignificant, negative trends ($.06 \leq P \leq .09$). Thus, the evidence that birds are more likely to delay dispersal when the acorn crop was poor was good for second-year females, poor for males >2 years, and equivocal for the other two categories of helpers.

Breeder Survivorship

A generalized linear model with group composition (including both linear and quadratic terms for the number of helpers), the acorn crop, territory quality, prior breeder experience, and interactions among the favorability factors and the number of helpers revealed that only the number of breeder females had a significant effect on annual breeder female survivorship (table 2). In contrast, the acorn crop and the quadratic effects of both helper males and helper females significantly impacted annual breeder male survivorship.

In order to investigate the effects of helpers on breeder male survivorship in more detail, we dichotomized the data on the basis of each of the three favorability factors and conducted general linear models of helpers, including both linear and quadratic terms on apparent survivorship

of breeder males. Results indicated that both sexes of helpers generally had highly significant positive effects on breeder male survivorship when conditions were favorable, whereas the fitness effects of helpers were much more variable and generally not significant when conditions were unfavorable (table 3).

Next, we plotted the survivorship of breeder males under favorable and unfavorable conditions as a function of the number of helpers (fig. 3), comparing the survivorship of breeders depending on whether helpers were present, using Fisher exact tests. Because the effects of helpers on breeder survivorship were generally similar regardless of helper sex (table 3), helper males and helper females were combined.

With respect to all three favorability factors, there was a relatively larger effect of helpers when conditions were favorable (fig. 4). In contrast, there was no significant difference in survivorship vis-à-vis helpers among groups when the acorn crop was poor or on low-quality territories or when birds did not have prior breeding experience. In general, differences in survivorship between breeder males with and without access to helpers did not differ whether they were breeding under favorable or unfavorable conditions, with the exception of males in groups without helpers whose apparent survivorship was (1) greater when the acorn crop was poor than when it was good and (2) greater when they were inexperienced than when they had prior breeding experience.

Reproductive Success

Mixed-effects models of group reproductive success, including all nests and only successful nests, indicated that the number of cobreeders, the acorn crop, territory quality,
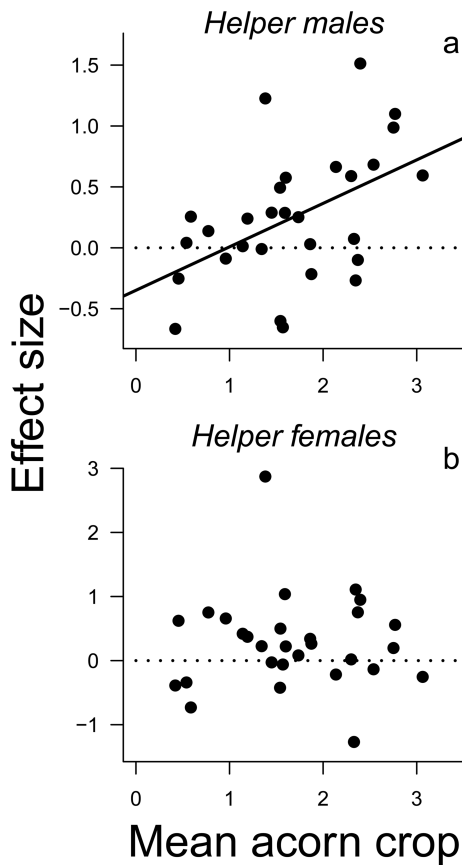
Figure 5: Effect size of helper males (*a*) and helper females (*b*) on reproductive success of all groups as a function of the mean acorn crop, on the basis of linear regressions for individual years. Regressions included group composition and prior breeder experience as covariates. Correlations: $r = 0.49$, $t_{27} = 2.90$, $P = .007$ (*a*); $r = -0.03$, $t_{27} = -0.17$, $P = .86$ (*b*). $N = 29$ years.

and prior breeder experience had significantly positive overall effects on reproduction. In neither case did the number of helper males or females have a significant effect on reproductive success (table 4). Differences in the relative effectiveness of helpers vis-à-vis the favorability factors were thus indicated by the interaction terms, none of which were significant, with the exception of that between the acorn crop and helper males. We focused on this interaction with analyses in which the effect size of helpers was determined for each year, confirming that helper males, but not helper females, had a highly significant positive effect on group reproductive success in good, but not in poor, acorn years (fig. 5).

We quantified this helper effect by comparing the predicted number and percent change in young fledged by a pair when the acorn crop was poor, fair, or good versus the values expected for groups consisting of a pair plus a

single helper (fig. 6). On average, helper males had a negative effect when the acorn crop was poor, decreasing the number of young fledged by 8% compared with the expected success of a pair. In contrast, helper males increased the reproductive success of pairs by 0.70 young when the crop was good, an increase of 21% over the expected fledging success of a pair. By comparison, helper females, whose effect was not statistically significant either by itself or in an interaction with the acorn crop (table 4), had a modest (but nonsignificant) positive effect on reproductive success whose absolute value did not vary with the acorn crop (fig. 6*d*).

Estimation of Lifetime Fitness

The effects of helpers, as described above, differed considerably depending on whether one considered their effects on breeder male or female survivorship or their effects on reproductive success of the group (table 5). In general, however, the effects, when present, were unambiguously positive when breeding conditions were favorable, either ecologically or demographically, and either not present or reduced when conditions were unfavorable. This pattern held for all three favorability factors in terms of breeder male survivorship and for the significant effects of helper males on reproductive success relative to the acorn crop.

In order to quantify the lifetime fitness consequences of having a helper, we conducted a simulation that estimated fitness effects of a helper on breeders depending on the acorn crop they experienced and whether they were resident on a low- or high-quality territory. Results yielded an estimated lifetime number of young fledged by a breeder male or female as a pair of between 5.14 and 9.63, while the fitness advantage of having a helper on a high-quality versus a low-quality territory (the difference in the combined benefits for the same helper/breeder combination) ranged from 0.29 to 0.37 fledglings (table 6). Dividing the indirect fitness benefits of helpers into current and future components, we found that the estimated future indirect fitness benefits provided by a helper male were generally lower (21%–51%; mean, 35%) than those provided by a helper female (31%–64%; mean, 48%), while those accruing to a breeder male were greater (45%–64%; mean, 55%) than those accruing to a breeder female (21%–37%; mean, 29%).

Examining the correlation between helper effects and the acorn crop experienced early in life, we found that the positive effects of a helper male were strongly and positively correlated with both the first year's and the second year's acorn crops (all correlations significant at $P < .001$), whereas for a helper female, all correlations with the first year's acorn crop were nonsignificant, while those with the second year's acorn crop were all significantly positive
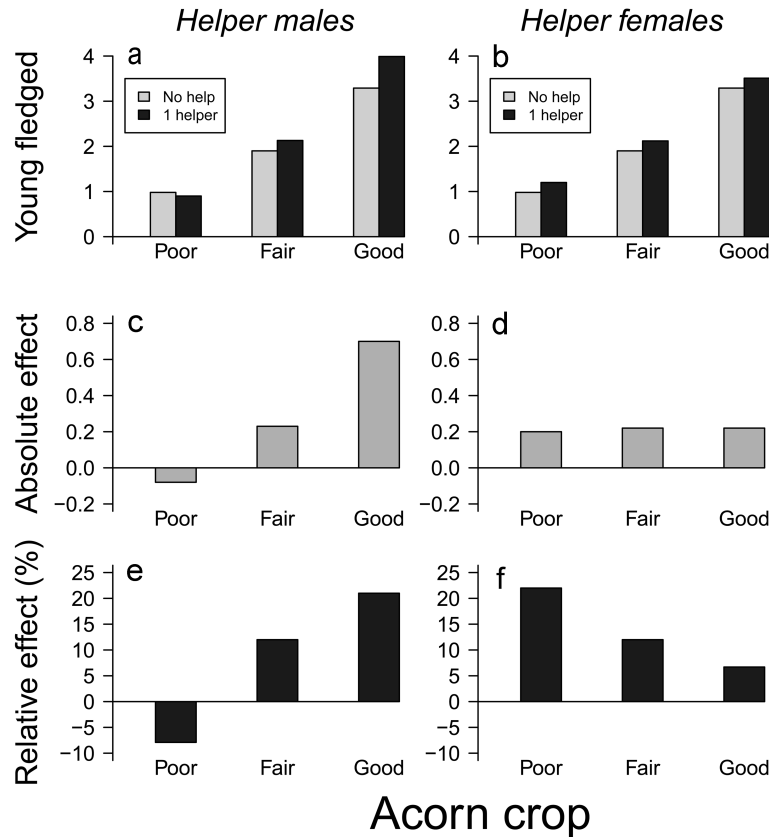
Figure 6: Predicted number of young fledged by pairs unaided and aided by a single male helper (*a*) and by a single female helper (*b*), in both cases as a function of whether the acorn crop is poor (mean of the ln-transformed number of acorns counted in 30 seconds [LN30] = 0.5), fair (mean LN30 = 1.5), or good (mean LN30 = 3.0). *c*, Absolute change in the number of young fledged as a consequence of a single male helper. *d*, Absolute change in the number of young fledged as a consequence of a single female helper. *e*, Relative change (compared with unaided) as a consequence of a single male helper. *f*, Relative change (compared with unaided) as a consequence of a single female helper. Values are based on a general linear model of young fledged including group composition, the acorn crop, and the acorn crop × helper male interaction.

($P < .001$). On average, a bird delaying dispersal and acting as a helper for 1 year can expect to augment the fitness of a breeder by 8%–18% over the number of offspring the breeder could otherwise expect to produce over its lifetime.

Discussion

Our results, although subject to the difficulties inherent in any observational study, cast a very different light on how ecological conditions shape the influence of helpers in cooperatively breeding systems than has been found in prior analyses. Particularly notable is the work of Magrath (2001), who proposed three potential models for the joint effect of conditions for breeding and presence of helpers on fitness in cooperatively breeding species and concluded that many cooperative breeders gain greater fitness benefits from helpers when conditions for independent reproduc-

tion are poor. The first important conclusion from our analyses is that this is not the case for acorn woodpeckers in central coastal California. Rather, the fitness consequences of helpers in this population, when they differ depending on conditions, are significantly greater when conditions are favorable.

This was clearly the case for helper males as a result of their significantly greater effect on reproduction during good acorn crop years, when each helper male resulted, on average, in the fledging of 0.7 additional young, whereas the effect of a helper male on reproduction in poor acorn years was nil or slightly negative. Combined with survivorship effects, the overall estimated lifetime fitness benefits of a helper averaged 0.75 additional fledglings on a low-quality territory versus 1.09 additional fledglings on a high-quality territory. In general, future indirect fitness benefits stemming from enhanced breeder survivorship

Table 5: Summary of the overall fitness effects of helpers on breeder survivorship and reproductive success under favorable versus unfavorable ecological conditions, with reference to the three favorability factors

	Acorn crop		Territory quality		Prior breeder experience	
	Poor	Good	Low	High	No	Yes
Effect of helpers on survivorship:						
Breeder males	+	++	+	++	+	++
Breeder females	0	0	0	0	0	0
Effect of helpers on reproductive success:						
Helper males	0	++	0	0	0	0
Helper females	0	0	0	0	0	0

Note: 0, no overall effect; +, moderately or variably positive effect; ++, strong positive effect.

were considerable, ranging up to 51% of the benefits accruing to breeder males and 64% of those accruing to breeder females. Future indirect fitness benefits are clearly important in this system, as previously suggested by Mumme et al. (1989).

The second important conclusion from our analyses has to do with the indirect fitness gained by helpers as a result of their help compared with the benefits of breeding. In a good acorn year, the predicted number of young fledged as a consequence of a helper male increased 21% over the number that a pair could expect to produce on its own (fig. 6). If we assume, on the basis of the results of the simulation (table 6), that this current indirect fitness benefit constitutes approximately half the total combined benefit to a breeder male of having a single helper male, then the total fitness benefit to the breeder male of a helper male can be estimated to eventually result in the fledging of up to 42% more offspring compared with an unassisted bird. Given the close relatedness of helpers to the birds they help, this is a substantial fitness benefit to both the breeder and the helper. The fitness gained by the helper, however, is still less than what he might have achieved as an unassisted breeder, assuming that he had been able to acquire a territory or otherwise gain breeding status in the population. It is also an upper bound; in most years, the fitness benefits of helping will be considerably less.

Thus, helpers—although of greater fitness consequence when conditions are favorable—do not gain sufficient fitness benefits to compensate for the failure to breed themselves and can be considered to be "making the best of a bad job" when compared with the alternative of independent breeding (Dickinson and Hatchwell 2004). This supports the hypothesis that ecological constraints in this system are based on resource-access benefits related to obtaining breeding opportunities, as previously proposed by Koenig and Pitelka (1981) and Koenig and Mumme (1987).

This hypothesis predicts that the probability of delayed dispersal should not vary in any clear way with ecological conditions because it assumes that conditions are relatively constant and predictable (table 1). The highly variable acorn crop on which acorn woodpeckers depend directly contradicts this view, as does the inverse correlation between the probability of delayed dispersal and the acorn crop among second-year females (fig. 2). For all other categories of helpers, however, the proportion of birds remaining as nonbreeders was not significantly correlated with the acorn crop. Thus, the pattern of delayed dispersal by helpers in our population did not provide strong support either for or against the hard life hypothesis.

One potential complication with these analyses is the inevitable dispersal/survival confound: because the study area is finite, some unknown fraction of birds that disappear will have died rather than dispersed (Koenig et al. 1996, 2000). The effects of this problem are difficult to predict. To the extent that there is a correlation between ecological conditions and helper survivorship, birds are more likely to survive when conditions are good, potentially enhancing rather than countering the patterns shown in figure 2. Alternatively, the generally negative correlation between the acorn crop and the proportion of birds delaying dispersal means that a greater absolute number of birds are potentially dying when conditions are good, reducing the strength of the correlations. Thus, the relationship between ecological conditions and the probability of remaining a helper remains equivocal.

A third conclusion from our study relates to the hypothesis that female helpers, when present, provide greater fitness benefits to breeders than do male helpers in cooperative breeders (Cockburn 1998). In acorn woodpeckers, male helpers exhibited a strong, significant effect when the acorn crop was good, whereas female helpers had no significant effect, regardless of the acorn crop (table 5). Thus, this hypothesis was not supported in our population.

Table 6: Estimated lifetime number of young fledged 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 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}	5.59	8.65	5.14	9.63	5.58	8.65	5.14	9.63
S_{1h}	6.57	9.99	5.75	10.57	6.51	9.94	5.63	10.40
$S_{1h.R}$	6.10	9.27	5.63	10.31	5.95	9.08	5.48	10.10
$S_{1h.S}$	6.03	9.32	5.28	9.87	6.12	9.47	5.30	9.91
Combined benefit	.99 ± .27	1.34 ± .31	.61 ± .25	.94 ± .28	.92 ± .07	1.29 ± .08	.49 ± .02	.78 ± .03
% of S_{nh}	18	16	12	10	16	15	10	8
Current indirect fitness	.51 ± .23	.62 ± .25	.47 ± .23	.68 ± .26	.36 ± .01	.43 ± .01	.33 ± .01	.48 ± .01
% of combined benefit	52	46	77	72	39	33	68	61
Future indirect fitness	.44 ± .05	.68 ± .06	.13 ± .01	.25 ± .02	.54 ± .06	.82 ± .07	.15 ± .02	.29 ± .02
% of combined benefit	45	51	21	26	58	64	31	37

Note: The mean effect of the helper (±SD) is divided into the portion enhancing breeder reproduction (current indirect fitness) and the portion increasing breeder survivorship (future indirect fitness). S, mean fitness; nh, no helper; 1h, one helper; 1h.R, one helper, current reproduction effects only; 1h.S, one helper, future survivorship effects only.

Several other counterexamples are summarized by Doerr and Doerr (2007), who found that male helpers frequently have positive effects on reproductive success when analyzed using more refined statistical methods. Whether there is a difference in the fitness consequences of male versus female helpers remains a tantalizing possibility, but the difference is clearly not as consistent as hypothesized by Cockburn (1998).

Our results suggest the desirability of models of helping behavior alternative to those proposed by Hatchwell (1999) and Legge (2000), both of which are predicated on the assumption that the marginal effects of helpers will be lower when ecological conditions are good. The fitness consequences of helpers often vary significantly depending on prevailing ecological conditions, but exactly how and why remain to be determined. For example, here we have focused on the variable benefits of care, but clearly the costs associated with providing care vary with resource abundance, and how the costs and benefits interact may have important implications for the benefits helpers confer under differing ecological conditions. At the very least, the relationship between the fitness effects of helpers and ecological conditions is clearly complex. For example, even under a model proposing that helpers have a greater effect when conditions are unfavorable, one might not expect helpers to have an effect when conditions are extremely poor because under such conditions even the contributions of helpers may be insufficient to allow for successful breeding (Magrath 2001). In the case of acorn woodpeckers, not only is reproduction minimal following a poor acorn crop but also birds will abandon their territories altogether if they are unable to acquire enough stored acorns to survive through the winter (Hannon et al. 1987).

Several additional questions are raised by our results. For example, in populations where helpers are more effective when conditions are unfavorable, it is generally unlikely that there will be a conflict between whether subordinates should remain as helpers or whether they should attempt to breed independently, because the greatest fitness benefits of helping accrue when independent reproduction is the most difficult. This is not the case in our population, where the greatest fitness benefits of helping come in good acorn crop years that provide the same favorable conditions for at least some potential helpers to disperse and breed independently. Whether this results in a conflict among some potential helpers as to whether they should delay dispersal remains to be determined.

It would also be of considerable interest to compare and contrast the benefits of helpers as determined by comparisons of fitness, as performed here, with analyses more directly focused on their behavior. In acorn woodpeckers, for example, we would expect to find that helpers provide relatively little help feeding offspring when conditions are unfavorable, such as years of poor acorn crops, but that helper males in particular feed a lot when the acorn crop is large. Of similar interest would be to examine the rate of nestling starvation and tendency for helping behavior to be compensatory rather than additive under different ecological conditions. Hatchwell (1999), again assuming that helpers would have a greater effect when conditions were unfavorable, found interspecific evidence that the feeding of nestlings tended to be additive when nestling starvation was frequent, as one would expect when conditions were unfavorable, whereas helping was compensatory when conditions were favorable and starvation was

rare. Whether this is true in acorn woodpeckers is currently under investigation.

Acknowledgments

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An adult male acorn woodpecker. This species lives in family groups including helpers, who are young from prior nests. Helpers increase group survivorship and reproductive success but only in years following large acorn crops when conditions are good, indicating that the advantage to living in families is not tied to harsh, unpredictable conditions. Photograph by Walter Koenig.