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Author for correspondence:

Walter D. Koenig

e-mail: wdk4@cornell.edu

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Temporal variability and cooperative breeding: testing the bet-hedging hypothesis in the acorn woodpecker

Walter D. Koenig^{1,2} and Eric L. Walters³

¹Cornell Laboratory of Ornithology, Ithaca, NY 14850, USA

²Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

³Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA

WDK, 0000-0001-6207-1427; ELW, 0000-0002-9414-5758

Cooperative breeding is generally considered an adaptation to ecological constraints on dispersal and independent breeding, usually due to limited breeding opportunities. Although benefits of cooperative breeding are typically thought of in terms of increased mean reproductive success, it has recently been proposed that this phenomenon may be a bet-hedging strategy that reduces variance in reproductive success (fecundity variance) in populations living in highly variable environments. We tested this hypothesis using long-term data on the polygynandrous acorn woodpecker (*Melanerpes formicivorus*). In general, fecundity variance decreased with increasing sociality, at least when controlling for annual variation in ecological conditions. Nonetheless, decreased fecundity variance was insufficient to compensate for reduced *per capita* reproductive success of larger, more social groups, which typically suffered lower estimated mean fitness. We did, however, find evidence that sociality in the form of larger group size resulted in increased fitness in years following a small acorn crop due to reduced fecundity variance. Bet-hedging, although not the factor driving sociality in general, may play a role in driving acorn woodpecker group living when acorns are scarce and ecological conditions are poor.

1. Introduction

What drives the evolution of complex animal societies? Perhaps most important is kin selection, suggested as a precursor to cooperation in many taxa [1–4]. Kin selection, however, is insufficient to explain the wide variability in social diversity found among taxa, much less individual differences in reproductive strategies. Besides kin selection, ecological factors have long been known to play a key role in shaping social behaviour and mating systems [5–7]. The manner in which ecological factors affect sociality is, however, frequently difficult to determine and in many cases controversial.

Nowhere is this controversy more apparent than in the study of cooperative breeding. This phenomenon is found in only about 9% of avian species but at least 45% of avian families [8]. Most frequently, cooperative breeding involves both delayed dispersal and helping-at-the-nest and is thought to be motivated by two very different kinds of environmental conditions [9]. The first of these occurs when the environment is inherently stable and predictable, selecting for delayed maturity, high survival, low dispersal and other demographic attributes that promote relatively high population densities in what has historically been referred to as the habitat saturation hypothesis [10,11]. Helpers in this scenario are usually offspring of the breeders and in many cases help primarily for indirect (kin-selected) benefits, but delay dispersal owing to some ecological constraint limiting their ability to obtain a suitable territory containing a mate and whatever other resources are critical for successful breeding [12,13].

The second situation thought to favour cooperative breeding occurs when the benefits of delayed dispersal are greater than those potentially achieved by independent breeding. According to this idea, often called the ‘benefits-of-philopatry’ hypothesis [14,15], cooperative breeding is hypothesized to enhance the direct

fitness of individuals by increasing the success of group foraging, territorial defence, predator deterrence or some other life-history character. A particularly likely scenario is that cooperative breeding enhances fitness when there is high variability in territory quality [15] or when successful reproduction by pairs is difficult or impossible [16], referred to as the 'hard life' hypothesis [17].

Both the habitat saturation and benefits-of-philopatry hypotheses involve ecological constraints and in some sense can be thought of as focusing on opposite sides of the same coin [18], or, perhaps more accurately, as endpoints on a continuum [19]. According to the habitat saturation hypothesis, however, helpers are individuals that have failed to gain a reproductive opportunity on their own, and are thus making the best of a bad job by helping to raise what are usually relatives. Under the benefits-of-philopatry hypothesis, helpers are potentially gaining greater fitness benefits by helping than they would by attempting to breed independently, and individuals are likely to experience poor or no success without such help.

An additional factor potentially favouring sociality is the variable distribution in time and space of resources [20]. Recently, Rubenstein [21] has built on this premise by proposing that helping behaviour maximizes fitness not by increasing the overall reproductive success of groups, but by reducing fecundity variance and thus minimizing the probability of reproductive failure. Such a bet-hedging strategy is particularly plausible when temporal or spatial variation in conditions is high, because such a situation is most likely to encompass years (or regions) when (or where) the probability of reproductive failure is also high [22–24]. Bet-hedging is a non-mutually exclusive alternative to both habitat saturation and benefits-of-philopatry in that it postulates a different function for cooperative breeding: specifically, minimizing variance in, rather than maximizing the number of, offspring produced. Bet-hedging is similar to benefits-of-philopatry, however, in that both hypothesize that cooperative breeding involves adaptations reducing variance under conditions of high spatial or temporal environmental variability [15,21].

Prior attempts to test the bet-hedging hypothesis have yielded mixed results. Reed & Walters [25] found that helpers were not associated with reduced reproductive variance in red-cockaded woodpeckers (*Picoides borealis*) or, based on a literature survey, eight other cooperatively breeding species. More recently, Gonzalez *et al.* [26] found that cooperative breeding in hornbills (Bucerotidae) was negatively related to climatic variability, opposite to the expectation of bet-hedging. By contrast, Rubenstein [21] supported the bet-hedging hypothesis as an explanation for cooperative breeding in the superb starling (*Lamprotornis superbus*) based on a correlation between the incidence of helping behaviour and environmental variation. Environmental variation driving fecundity variance has also been linked to the incidence of cooperative breeding in comparative analyses of both African starlings (family Sturnidae) and avian passerine taxa worldwide [27,28]. Thus, the evidence for the importance of bet-hedging in the evolution of cooperative breeding is mixed.

The cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*) offers a particularly appealing opportunity to test the bet-hedging hypothesis because its breeding behaviour has generally been considered to be a consequence of habitat saturation [11], yet this species is critically dependent on the acorn

crop, a resource that exhibits high temporal variation due to masting behaviour [29]. Here, we conduct analyses focusing on the question of whether reduced fecundity variance is sufficient to potentially select for increased sociality in this species, as proposed by the bet-hedging hypothesis.

2. Testing the bet-hedging hypothesis

Using acorn woodpeckers as our model system, our goals are fourfold. First, we consider two assumptions of the bet-hedging hypothesis: first, that temporal variation in ecological conditions is high, and second, that *per capita* fecundity declines with increasing sociality. If *per capita* productivity increases with group size, sociality is more parsimoniously driven by increased mean fecundity rather than by any reduction in fecundity variance and thus bet-hedging would not be applicable [30,31]. *Per capita* productivity rather than overall productivity is the relevant metric for this assumption since it provides the best single measure of the mean relative fitness of individuals in coalitions or in groups of a given size, regardless of whether individuals are breeders or closely related non-breeding helpers, as is the case in acorn woodpeckers [11,32]. In order to address the polygynandrous mating system of acorn woodpeckers, however, we also calculated success per breeder male and per breeder female. Because parentage is shared relatively equally among cobreeders [33], per breeder calculations provide a good approximation of relative fitness in these complex groups.

Our second goal is to test two key predictions of bet-hedging. First, that sociality is associated with reduced fecundity variance, and second, that reduced fecundity variance associated with sociality results in increased fitness.

Testing the bet-hedging hypothesis is complicated by the fact that there are multiple ways of parsing productivity data. Indeed, at least some of the conflicting conclusions reached by prior studies are potentially a consequence of how prior workers have partitioned their data [21,25]. Thus, our third goal is to compare different ways of analysing mean fecundity and fecundity variance. The four approaches we consider partitioning the data is as follows.

(a) By group size

Following Reed & Walters [25], we parsed the data according to group size and calculated mean fecundity and fecundity variance as a function of each group-size category. This approach makes the reasonable assumption that group size is an index of sociality, but ignores spatial variability (primarily differences among territories) and annual variation (differences among years), both of which can have significant effects on all aspects of group living [17,21].

(b) By years

Following Rubenstein [21], we parsed data by breeding seasons (years in our case) and calculated mean group size, mean fecundity and fecundity variance for each year. This analysis incorporates annually varying ecological factors but ignores differences related to variation in sociality or territory quality within years.

(c) By territory

This approach, also used by Rubenstein [21], involves calculating mean group size, mean fecundity, and fecundity variance

for each territory over the duration of the study. Consequently, it incorporates spatial variability, but obscures annual variation in conditions, differences related to group size within years and changes in territory quality over the duration of the study.

(d) By sociality within years

For this analysis, we compared the performance of relatively social versus relatively non-social groups within each year. This analysis ignores spatial variability, but combines a focus on both annual variation and the effects of group size.

Our fourth goal is to investigate the possibility that bet-hedging might be important, but only in years when conditions are poor. For these tests, we looked for a difference in the main ecological factor affecting reproductive success—the size of the acorn crop—dividing years into those in which relative fecundity variance and estimated mean fitness increased with increasing sociality versus those in which these variables decreased with increasing sociality.

3. Material and methods

(a) General

We studied a colour-banded population of acorn woodpeckers at Hastings Reservation, central coastal California ($36^{\circ}23'N$, $121^{\circ}33'W$), between 1972 and 2013, during which time the population was monitored continuously. Acorn woodpeckers are cooperative breeders that live in territorial groups of up to 15 individuals (mean \pm standard deviation (s.d.) = 4.54 ± 2.12 , $n = 1371$ group-years between 1981 and 2013). Groups consist of breeders and non-breeding helpers of both sexes. Non-breeding helpers are generally offspring from prior years, while cobreeding males and joint-nesting females (subsequently both referred to as ‘cobreeders’) are typically siblings or parents and their offspring, the latter of which have inherited breeding status following the death and replacement of their parent(s) of the opposite-sex by unrelated birds from elsewhere [34]. Consequently, cobreeder males are almost always unrelated to cobreeder females, but otherwise all group members are close genetic relatives. Extra-group mating does not occur, and thus, with the exception of territorial inheritance as described above and occasional cases of incest, helpers do not breed as long as they reside in their natal group [35,36].

Each social group defends a territory, typically an area 3–9 ha in size centred about a ‘granary tree’ in which groups store acorns. Stored acorns generally last for less than 1 year, although they sometimes persist into a second year. Granaries are relatively stable over time and represent the core of the defended territory. Analyses were generally either across years ($n = 33$, the number of years in which the acorn crop was monitored out of the 41 years that the acorn woodpecker population was monitored) and/or groups (mean \pm s.d. = 41 ± 9 ; range = 23–59).

Group composition is highly variable and includes groups with and without non-breeding helpers (of 1371 group-years, 61% had 1–10 helpers) as well as groups with and without cobreeders (38% of groups consisted of a monogamous breeding pair with or without helpers; 30% consisted of a polyandrous female along with at least two cobreeding males; 10% consisted of a polygynous male along with at least two cobreeding females and 14% were polygynandrous groups). All analyses were conducted in R v. 3.0.3 [37].

(b) Indices of sociality

As proxies of sociality, we used total group size, number of breeder males per group (using only groups with a single breeder female and no helpers), number of breeder females per group

(using only groups with a single breeder male and no helpers) and number of helpers (using only groups with a single breeder male and breeder female). Total group size combines all components of group composition but is confounded by differences between breeders and helpers, while the other indices focus on the number of cobreeders or the presence of helpers while controlling for other aspects of group composition.

For the analysis of sociality within years, we dichotomized the data so as to compare the performance of relatively social versus relatively non-social groups within each year. For total group size, we compared pairs versus groups. For sociality related to breeders, we compared groups with one breeder of the focal sex versus those with two or more cobreeders of that sex, in all cases using only groups with one breeder of the opposite sex and no helpers. For sociality related to the presence of helpers, we compared pairs without, versus pairs with, one or more non-breeding helpers of either sex. Sample sizes varied because there were not always enough groups of the requisite size and composition in a particular year to perform a test.

The main breeding season of acorn woodpeckers at Hastings Reservation begins in early April, peaks in early May, and extends through to late June or early July. Breeding can also take place in the autumn during years of large acorn crops [38], but such breeding constitutes less than 5% of overall population productivity and was thus ignored for the analyses conducted here.

(c) Reproductive success and fecundity variance

For mean fecundity, we calculated the *per capita* number of young fledged during the spring breeding season. Depending on the analysis, values were calculated based on the number of breeder males per group (for analyses of breeder males), the number of females per group (for analyses of breeder females) or total group size (all remaining analyses). For relative fecundity variance, we used the coefficient of variation (CV = s.d. $\times 100/$ mean) of *per capita* fecundity.

One approach to estimating fitness accounting for fecundity variance is to use the geometric mean [23]. Unfortunately, it is not possible to extrapolate from genotypic models based on geometric means to what will be favoured by selection, and in particular, it is necessary to consider the correlation in reproductive success among classes of individuals pursuing a particular strategy, referred to as ρ [4]. Consequently, we calculated the within-class and between-class correlations in reproductive success for each method of parsing the data described above; for details, see the electronic supplementary material.

For analyses in which the within-class correlations were sufficiently large to warrant further consideration, we used the method described by Frank & Slatkin [4] to compare estimated fitness of groups differing in degree of sociality. This method incorporates the mechanism driving variation in reproductive success to estimate the expected mean and variance of individual reproductive success. Details are provided in the electronic supplementary material.

(d) Ecological conditions

Annual rainfall, measured for the 1 July–30 June hydrological year, was monitored at Hastings Reservation headquarters, where data have been taken continuously since 1939. We estimated the overall size of the acorn crop, the main ecological variable influencing reproductive success, each autumn on 250 individually marked trees distributed among the five oak species commonly found within the study area [17]. Estimates were made by counting as many acorns as possible for 30 s on each tree; counts were ln-transformed ($LN30 = \ln[N \text{ acorns counted} + 1]$) in order to reduce the correlation between the mean and the variance [39,40]. The acorn crop exhibits a 1 year lag effect on woodpecker reproductive success; thus, analyses included acorn

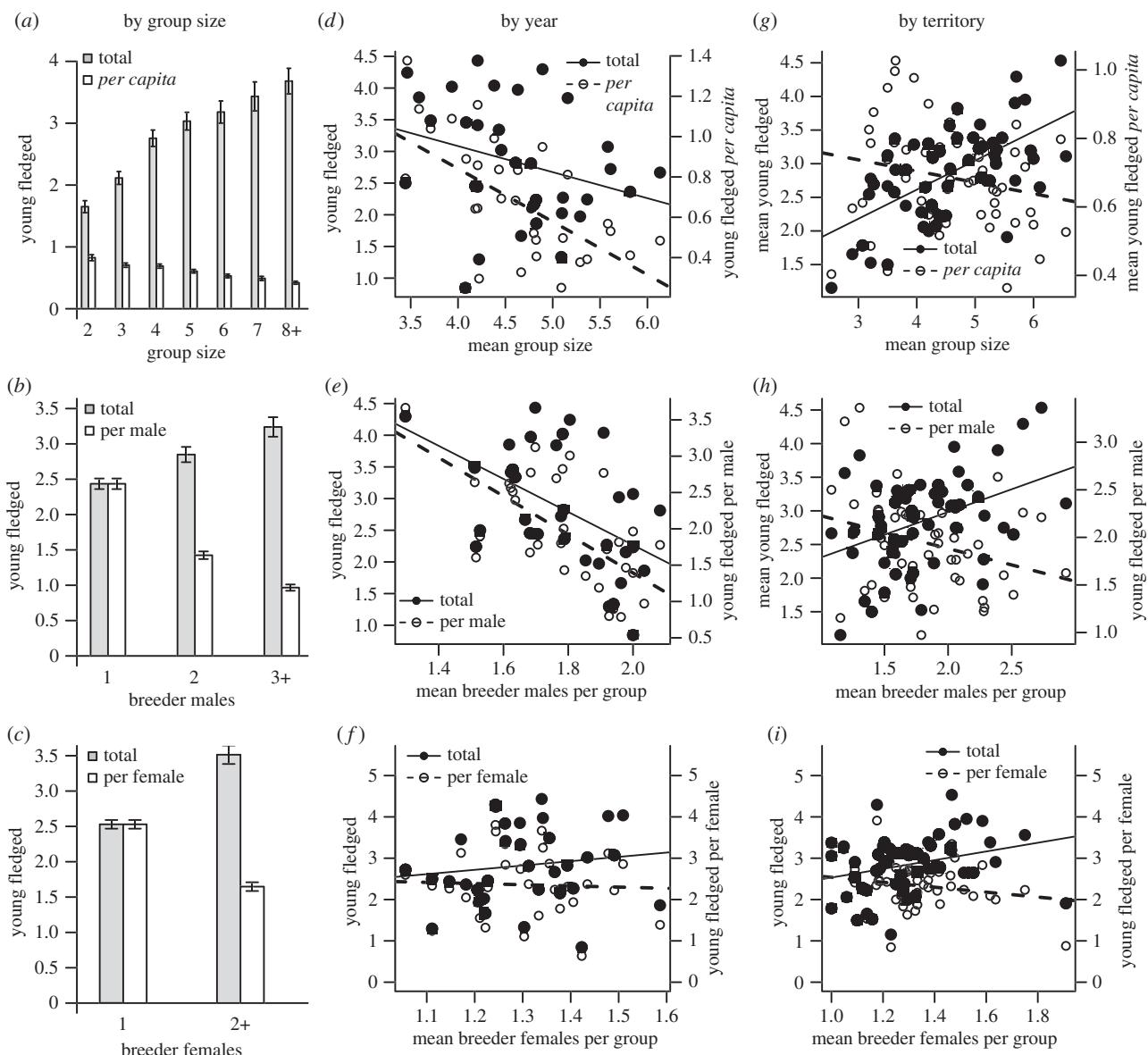


Figure 1. Mean young fledged and young fledged *per capita* versus sociality, where data are parsed by (a–c) group size (values plotted are mean \pm standard error (s.e.)), (d–f) year (each point is a year) and (g–i) territory (each point is a territory). Plots are of (a,d,g) total group size or mean group size, (b,e,h) number of cobreeding males or mean number of cobreeder males (including only groups with one breeder female and no helpers), and (c,f,i) number of cobreeder females or mean number of cobreeder females (including only groups with one breeder male and no helpers). Regression lines are drawn when statistically significant. Statistical tests by Spearman's rank correlations; correlations (total, *per capita*) are: (a) $r_s = 0.29^{***}, -0.17^{***}$, (b) $r_s = 0.14^{***}, -0.31^{***}$, (c) $r_s = 0.19^{***}, -0.21^{***}$, (d) $r_s = -0.32, -0.55^{***}$, (e) $r_s = -0.52^{**}, -0.59^{***}$; (f) $r_s = 0.18, 0.01$; (g) $r_s = 0.56^{***}, -0.23$; (h) $r_s = 0.33^*, -0.30^*$ and (i) $r_s = 0.35^{**}, -0.08$. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

data taken between 1980 and 2012, corresponding to acorn woodpecker data between 1981 and 2013.

In order to determine whether fecundity variance decreases or estimated fitness increases in relatively poor years, we compared the mean acorn crop in years in which these variables increased with sociality versus years when they decreased with sociality using Wilcoxon tests.

4. Results

(a) Assumptions of bet-hedging

Bet-hedging entails two assumptions: first, that temporal variation in ecological conditions is large, and second, that *per capita* reproductive success decreases with increasing sociality.

Regarding the first assumption, mean \pm s.d. annual rainfall (measured from 1939–1940 to 2012–2013) was 523 ± 195 mm (range 261–1113 mm). This is both sufficiently low

to qualify the habitat as semi-arid and likely to be limited by water availability [41], and highly variable ($CV = 40.8\%$) compared to even the 'extremely variable' environment of Kenya inhabited by the superb starlings studied by Rubenstein [21], where mean annual rainfall was identical (523 mm) but the s.d. was 138 mm [21], 41% lower than at our study site over the same time period. Annual variability of the acorn crop ($CV = 42.1\%$) paralleled that of rainfall.

As is typical for Mediterranean climates, seasonal variation in conditions was also considerable and CVs in monthly rainfall across years were high, varying from a low of 70% during the cold, wet month of December to 404% in the hot, dry month of July (data not shown). Thus, temporal variability in conditions was considerable at both the annual and within-year levels.

Regarding the second assumption, both total and *per capita* reproductive success are plotted as a function of sociality in figure 1. Total reproductive success generally increased

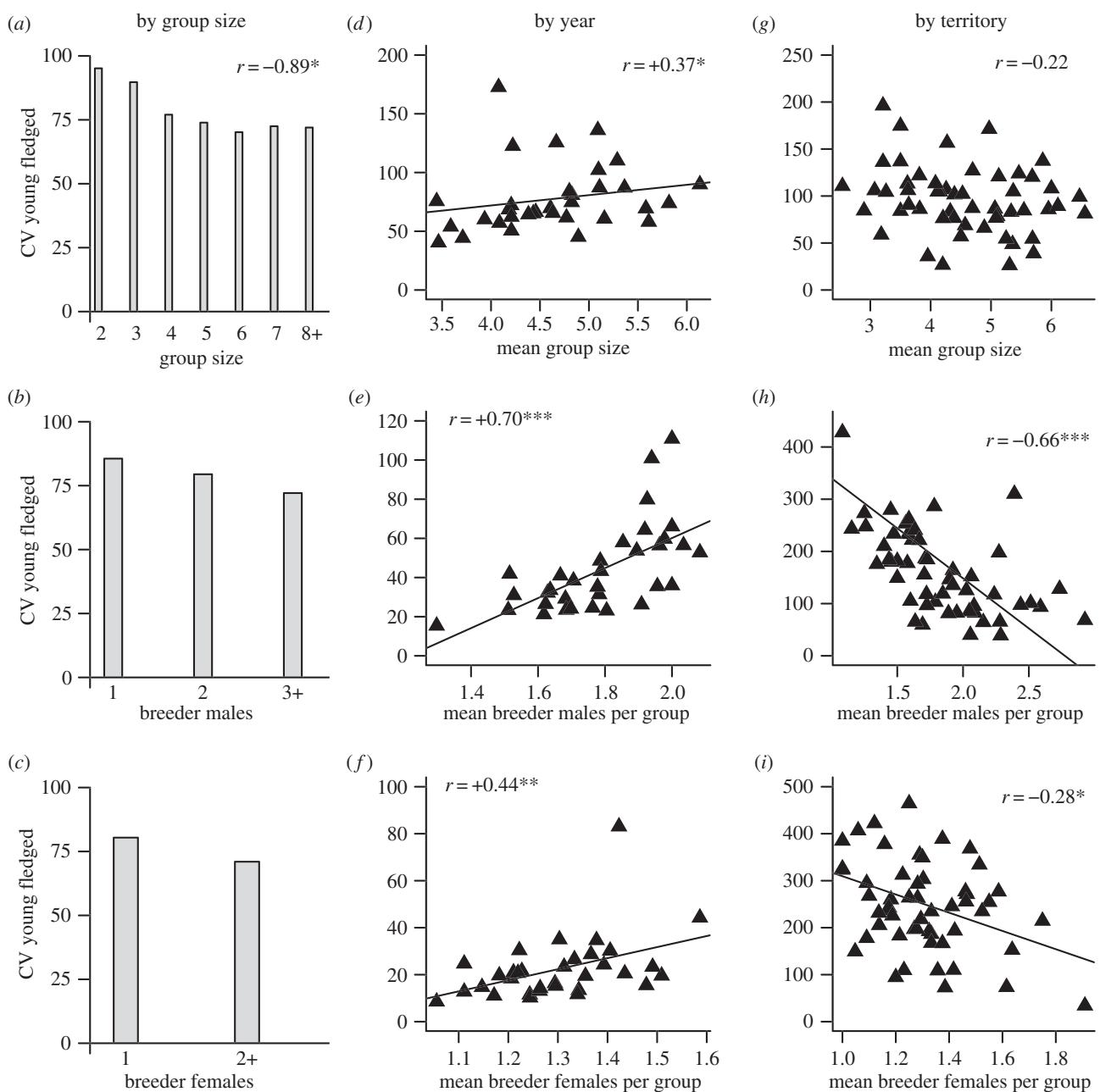


Figure 2. Coefficient of variation (CV) of young fledged versus sociality, where data are parsed by (*a–c*) group size, (*d–f*) year (each point is a year) and (*g–i*) territory (each point is a territory). Plots are of (*a,d,g*) total group size or mean group size, (*b,e,h*) number of cobreeding males or mean number of cobreeding males (including only groups with one breeder female and no helpers) and (*c,f,i*) number of cobreeding females or mean number of cobreeding females (including only groups with one breeder male and no helpers). Statistical tests by Spearman's rank correlations are listed and regression lines plotted (for (*d–i*)) when statistically significant. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

with mean group size when data were parsed by group size (column 1) or by territory (column 3), but decreased when parsed by year (column 2). *Per capita* success decreased with group size in all cases except when parsed by year and calculated per breeder female (figure 1*f*), where young fledged per female was essentially the same for groups with one versus two breeder females.

(b) Predictions of bet-hedging

The two main predictions of bet-hedging are first, that fecundity variance decreases with increasing sociality, and second, that this decrease compensates for the decrease in *per capita* reproductive success (assumption no. 2, above) to yield higher fitness among more social groups. A third prediction is that reduced fecundity variance and increased

fitness should be associated with harsh conditions, which for acorn woodpeckers follows a poor acorn crop.

When parsed by group size or territory, relative fecundity variance (CV) generally decreased with increasing sociality (figure 2*a–c* and *g–i*). Relative fecundity variance, however, increased with sociality when data were parsed by years (figure 2*d–f*). These latter results are, however, particularly susceptible to being confounded by differences in ecological conditions across years. In analyses in which relative fecundity variance was compared among groups partitioned by sociality within years, groups that were relatively more social exhibited lower fecundity variance, significantly so for total group size, the number of cobreeding males and the presence/absence of helpers (table 1, upper half).

To estimate fitness using fecundity variance, we calculated within- and between-class correlations among

Table 1. Comparison of fecundity variance (CV) and estimated mean fitness for groups parsed by sociality within years. (Indices of sociality include total group size (pairs versus groups), number of cobreeding males (groups with one breeder male versus two or more breeder males; all groups with one female breeder and no helpers), number of cobreeding females (groups with one breeder female versus two or more breeder females; all groups with one breeder male and no helpers) and the presence/absence of helpers (breeding pairs only). Analyses are by Wilcoxon paired signed-rank tests and values are means \pm s.e. across years. $n = 33$ years except for the 'presence of helpers' category, for which $n = 23$ (fecundity variance) and $n = 32$ (estimated fitness).)

index of sociality	relatively non-social	relatively social	Wilcoxon <i>V</i>	p-value
fecundity variance (CV)				
total group size	77.7 ± 7.2	72.6 ± 4.6	205	0.04
cobreeding males	86.4 ± 7.5	71.2 ± 5.2	410	0.02
cobreeding females	78.9 ± 5.8	75.0 ± 5.9	332	0.37
presence of helpers	77.7 ± 8.7	58.8 ± 5.6	210	0.03
estimated fitness				
total group size	0.67 ± 0.10	0.60 ± 0.05	285	0.48
cobreeding males	1.14 ± 0.18	0.86 ± 0.08	289	0.13
cobreeding females	1.24 ± 0.18	1.03 ± 0.12	132	0.04
presence of helpers	0.71 ± 0.10	0.64 ± 0.06	252	0.47

Table 2. Estimated correlations (ρ) among randomly chosen individuals from within and between classes, where classes are determined by group size/composition within years, restricted as in table 1, and dichotomized into relatively less social and relatively more social groups. (All correlations are significant at $p < 0.001$.)

group determined by	within-class ρ		mean	between-class ρ
	relative less social	relatively more social		
total group size	0.52	0.24	0.38	0.19
cobreeding males	0.52	0.33	0.43	0.17
cobreeding females	0.51	0.35	0.43	0.24
presence of helpers	0.52	0.36	0.44	0.32

randomly chosen individuals, where 'class' was determined based on how the data were parsed (i.e. by group size/composition, year or territory). Within-class correlations were invariably small when data were parsed by group size/composition, year or territory ($\rho < 0.2$; electronic supplementary material, table S1). Thus, in these cases the relative importance of fecundity variance is negligible (see the electronic supplementary material), and estimated fitness based on these alternative methods of data partitioning are effectively driven by mean *per capita* fecundity, which in no case favoured greater sociality (figure 1).

By contrast, ρ_i values were sufficiently high (mean within-class $\rho \sim 0.4$) when data were parsed by sociality within years (table 2) to warrant further consideration of the potential compensatory effects of fecundity variance. Results partitioning the data by group composition within years (table 1) indicated that in all analyses, estimated mean fitness decreased with increasing sociality, significantly so in the case of cobreeding females.

Finally, in order to test whether reduced fecundity variance or increased fitness is associated with poor acorn crops, we compared the prior autumn's acorn crop in years when fecundity variance or estimated mean fitness increased with sociality versus years when the variable decreased with sociality (table 3). No significant differences were detected vis-à-vis fecundity variance. Results were also largely non-

significant for estimated fitness, with the exception of total group size, for which the mean acorn crop was significantly smaller in years when fitness increased with sociality.

5. Discussion

The main question addressed here is whether cooperative breeding is a bet-hedging strategy designed to decrease fecundity variance in highly variable and unpredictable environments. The key concept behind this hypothesis is that high temporal unpredictability favours social variability that minimizes reproductive variability rather than maximizing the number of offspring. In the case of cooperative breeders, helpers and large group sizes are likely to be particularly important in years when conditions are poor or for young, inexperienced individuals for which successful breeding is difficult [42]. To the extent that sociality reduces fecundity variance, bet-hedging spreads the risk to which individuals are exposed [23] and is potentially important in populations of cooperative breeders that are subdivided into small, kin-based social groups [21,30].

Both key assumptions of the bet-hedging hypothesis are met in our woodpecker population. First, ecological conditions are highly variable both seasonally and annually. Moreover, acorn woodpeckers are dependent on a variable

Table 3. Mean \pm s.e. acorn crop (ln-transformed) associated with years when relative fecundity variance (CV) and estimated mean fitness increased or decreased with increasing sociality, measured as total group size, number of breeder males, number of breeder females and number of helpers, restricted as in table 1. (Analyses by Wilcoxon tests.)

mean \pm s.e. acorn crop (n years)				
index of sociality	variable increased with sociality	variable decreased with sociality	Wilcoxon V	p-value
fecundity variance (CV)				
total group size	1.66 \pm 0.74 (5)	1.96 \pm 0.45 (19)	33	0.33
cobreeding males	1.85 \pm 0.70 (7)	1.98 \pm 0.51 (15)	501	0.89
cobreeding females	1.82 \pm 0.82 (5)	2.38 \pm 0.79 (9)	10	0.11
presence of helpers	1.93 \pm 1.11 (3)	1.92 \pm 0.43 (20)	31	0.97
estimated fitness				
total group size	1.37 \pm 0.37 (14)	2.01 \pm 0.49 (17)	51	0.006
cobreeding males	1.36 \pm 0.45 (9)	1.92 \pm 0.43 (20)	57	0.13
cobreeding females	1.22 \pm 0.55 (5)	2.16 \pm 0.60 (13)	14	0.08
presence of helpers	1.69 \pm 0.45 (14)	1.86 \pm 0.48 (15)	84	0.38

food supply (the acorn crop), which drives highly varying annual reproductive success of the birds [17]. Second, *per capita* reproductive success declines with increasing group size, as is generally true for social species and as reported earlier for this population [32].

A key prediction of the bet-hedging hypothesis is that relative fecundity variance decreases with increasing sociality. Exactly how to measure sociality, however, is not obvious. If data are arranged on the basis of overall group size/composition or by territory, relative fecundity variance generally decreases with increasing sociality, as predicted by the bet-hedging hypothesis. By contrast, if data are parsed by year, fecundity variance *increases* with increasing sociality. These analyses, however, fail to consider at least one key source of variation, either differences in sociality within the population or annual variation in conditions.

We addressed this problem by comparing mean fecundity variance for relatively non-social versus relatively social groups within years. Results were in line with the bet-hedging hypothesis in that relative fecundity variance was generally smaller among more social groups. This decrease in fecundity variance was not, however, enough to compensate for lower overall mean fecundity, even when within-class correlations were fairly large, as was the case when parsing the data by sociality within years.

Nonetheless, by comparing the mean acorn crop in years when fecundity variance was smaller or the estimated mean fitness was greater among larger, more social groups, we found that the mean acorn crop was significantly smaller in those years when estimated fitness increased with total group size compared with years when it did not. This suggests that, despite the failure of bet-hedging across all years, bet-hedging may confer a fitness benefit in years when conditions are poor.

Additional analyses will be needed to determine the mechanisms by which fecundity variance is reduced among larger, more social groups [43]. Differences in such mechanisms are likely to play a key role in explaining apparent differences in the importance of bet-hedging across species. Careful scrutiny is also needed to avoid misinterpretation. For example, the inter-annual pattern found here is

potentially an artefact of differences in performance between established and newly formed groups; countering this possibility is prior work revealing no relationship between the acorn crop and new territory formation [17].

Our results offer several important lessons for future investigations of the role of bet-hedging to the evolution of sociality. First, it is important for analyses to consider the effects of variable conditions on sociality. A corollary of this result, and the second important conclusion stemming from our analyses, is that the method of data parsing can make a critical difference: in our case, fecundity variance did not decrease with sociality when data were parsed by years, but did when parsed by sociality within years.

The third lesson from our results is that although increased sociality may result in decreased fecundity variance, it does not necessarily compensate for decreased mean fecundity. In our case, even when within-class correlations were relatively large, estimated fitness was lower for more social groups.

Finally, although our results generally provided little support for the bet-hedging hypothesis, we found that bet-hedging may nonetheless favour sociality in years when conditions are poor. Thus, the fourth lesson is that an evolutionary benefit to a phenomenon such as bet-hedging may emerge only under occasional, potentially unusual ecological conditions. In our case, such conditions followed poor acorn crops, a conclusion that is to some extent unsurprising given the dramatic shifts in population demographics that take place during such years [44].

These conclusions add a new dimension to prior work indicating that delayed dispersal and helping behaviour in this population is a best-of-a-bad-job strategy, that helper males impart significant benefits to reproduction in good, but not bad, acorn crop years [17] and that cobreeding males, although not necessarily cobreeding females, gain significant fitness advantages in terms of enhanced survivorship and reproduction [29,45]. Decreased fecundity variance appears to be a potentially important benefit of increased group size and sociality in acorn woodpeckers when conditions are poor following small acorn crops.

Although the theoretical basis for bet-hedging has been emphasized by numerous authors [22–24,31], there has been

relatively little empirical work relating this phenomenon to social behaviour in general or cooperative breeding in particular. Whether cooperative breeding acts to spread risk over multiple generations by reducing the probability that a particular genetic lineage may go extinct, a phenomenon referred to as among-generation bet-hedging [23], remains to be tested. Clearly, however, the roles of temporal environmental variation and bet-hedging in the evolution of complex social behaviour deserve to be carefully investigated.

Ethics. This study was conducted under the auspices of the Animal Care and Use Committees of the University of California, Berkeley (protocol R010-0412), Cornell University (protocol 2008-0185) and Old Dominion University (protocol 12-001).

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