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Original Article

Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker

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We analyzed reproductive investment in parental care (brooding and the provisioning of nestlings) in the acorn woodpecker (*Melanerpes formicivorus*), a cooperatively breeding species in which both polygynandry and helping-at-the-nest are common. As predicted based on the strategies pursued by birds of different sex and status, breeders generally invested more in parental care than helpers, and breeder females invested more than breeder males. Contrary to expectations, however, the degree to which individuals reduced their effort with increasing group size (i.e., patterns of load lightening or compensatory care) did not match overall investment. Instead, as group size increased, there was no significant difference in compensation in either brooding or provisioning among the different categories of birds. Compensation, at least by breeders, was significantly lower during the first week of the nestling period than later on, supporting the hypothesis that compensatory reduction in care is less likely when brood reduction is more common and was not affected by the acorn crop, which had no significant effect on the incidence of brood reduction despite being important to overall reproductive success. Our results offer support for the hypothesis that levels of compensation are influenced by the relative importance of brood reduction. More theoretical work, however, will be needed in order to understand the basis for patterns of compensation among individuals of different sex and status. *Key words:* acorn woodpecker, compensation, compensatory care, cooperative breeding, helping behavior, load lightening, parental care. *[Behav Ecol 23:181–190 (2012)]*

INTRODUCTION

Caregivers should invest in their offspring in a way that optimizes the trade-off between current and future reproduction (Williams 1966; Stearns 1989). This trade-off is relatively simple in uniparental care systems. It becomes considerably more complex in biparental systems where the optimal investment of each caregiver depends on not only its own costs and benefits but also on the outcome of negotiations with its partner (Johnstone and Hinde 2006; Hinde and Kilner 2007). Such interactions typically result in "load lightening" (Brown JL and Brown ER 1981)—that is, a system in which individuals compensate, at least in part, for a reduction in care by their partner or other group members (Chase 1980; Winkler 1987; Hatchwell 1999). Despite extensive study, primarily in biparental systems, our understanding of the ecological and evolutionary factors affecting patterns of load lightening and compensation are notably incomplete (Harrison et al. 2009).

Understanding the relative amount that individuals should invest in brooding and provisioning young becomes even more difficult in cooperative breeders where caregivers may include nonbreeding helpers and, in some cases, coalitions of same-sex cobreeders, each of which may exhibit not only a different probability of kinship to the young but also have its own suite of costs and benefits affecting its pattern of optimal investment in the current brood relative to other group members (Crick 1992). At least 2 general issues are of interest: first, how and why does provisioning behavior (and other forms of reproductive investment such as brooding) differ among individuals of different sex and social status, and second, how and why do individuals adjust provisioning behavior in response to help provided by other group members? Both issues focus on investment strategies, the first being the more static measure (brooding or provisioning rate) and the second—referred to here as compensatory care or compensation—being a more dynamic measure of the response of individuals to aid provided by other group members (i.e., the change in care provided with increasing group size).

There have been but a handful of attempts to interpret variation in these measures of reproductive investment by cooperative breeders. In the dunnock (*Prunella modularis*), a species in which cobreeder males are unrelated but often share paternity, a male's opportunity of parentage was found to be a good predictor of paternal investment (Hatchwell and Davies 1990; Davies and Hatchwell 1992). In the long-tailed tit (*Aegithalos caudatus*), a species in which helpers are generally failed breeders that differentially choose to help close relatives, both helpers and breeders responded similarly to differences in ecological conditions, but helpers generally did not feed nestlings as much as breeders, a result attributed to the lower relatedness between helpers and the nestlings they feed than between breeders and their offspring (MacColl and Hatchwell 2003).

Similar results, with helpers investing less in parental-like behaviors than breeders, have been reported for numerous other cooperative breeders (Brown et al. 1978; Stallcup and Woolfenden 1978; Doerr ED and Doerr VAJ 2007). This includes an earlier analysis of acorn woodpeckers (*Melanerpes formicivorus*) by Mumme et al. (1990), who attributed this

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reduction in provisioning to the time and effort helpers devote to foraying in search of breeding opportunities outside their natal territory, an activity that precludes helping at the nest (Mumme and de Queiroz 1985). In some species, however, helpers do not appear to invest less than breeders, an example being Arabian babblers (*Turdoides squamiceps*) (Wright 1998).

With respect to the dynamic response of individuals to changes in group size, the situation is more complicated and considerably less explored theoretically. Similar to biparental systems in which one parent typically reduces its effort when aided by a mate, many, but not all, studies of cooperative breeders have found that breeders reduce their provisioning rates (i.e., exhibit compensatory feeding) when aided by helpers, as opposed to maintaining the same provisioning rate when aided by helpers (i.e., exhibit additive feeding). In an attempt to understand this variability, Hatchwell (1999) performed a comparative analysis of 27 cooperatively breeding species and found that the investment strategies of breeders compared with helpers varied considerably between being compensatory and being additive, sometimes even within the same species (Komdeur 1994; Hatchwell and Russell 1996). Hatchwell proposed that a major determinant of this difference was whether brood reduction by nestling starvation was common, hypothesizing that care was more likely to be compensatory when nestling starvation was rare. In contrast, he hypothesized that when nestling starvation is common, additional aid would be more valuable, and care was more likely to be additive.

Heinsohn (2004) developed a detailed model for how much aid helpers should provide and to what extent breeders should respond to helper provisioning based on comprehensive consideration of the life-history consequences to both parties. Results predicted by the model were highly variable, but in general, breeders were expected to benefit more from compensatory care than helpers and to gain more from reducing their effort when more closely related to the helper.

Although these studies offer insights into the complex factors potentially influencing provisioning patterns in cooperative breeders, much remains to be learned. Here, we present an analysis of brooding, provisioning patterns, and compensatory care in the acorn woodpecker, a cooperative breeder in which both polygynandry and nonbreeding helpers of both sexes are common. In contrast to dunnocks, however, cobreeders of the same sex are generally first-order relatives—siblings, parents and offspring, or a combination. Cobreeders also share parentage relatively equitably, although for males, this appears to be true only across multiple nesting attempts (Haydock and Koenig 2002, 2003). Because group composition varies considerably within and among years, it is possible to compare and contrast patterns of provisioning by breeders and helpers relative to both group size and the acorn crop, a key food resource for this species.

Predictions

Based on the fitness consequences of helpers and the demography of acorn woodpeckers, we made the following predictions vis-à-vis reproductive investment in brooding and provisioning of nestlings:

1) Investment should decline seasonally.—In common with many avian populations (Rowe et al. 1994), there is a highly significant seasonal decline in clutch size and fledging success in acorn woodpeckers (Figure 1a). Although to some extent, this may be due to variation in female quality (Christians et al. 2001); in general, this pattern indicates that the value of a nesting attempt declines seasonally, leading to the prediction that, all else being equal, caregivers should put less effort into later broods (Winkler 1987).

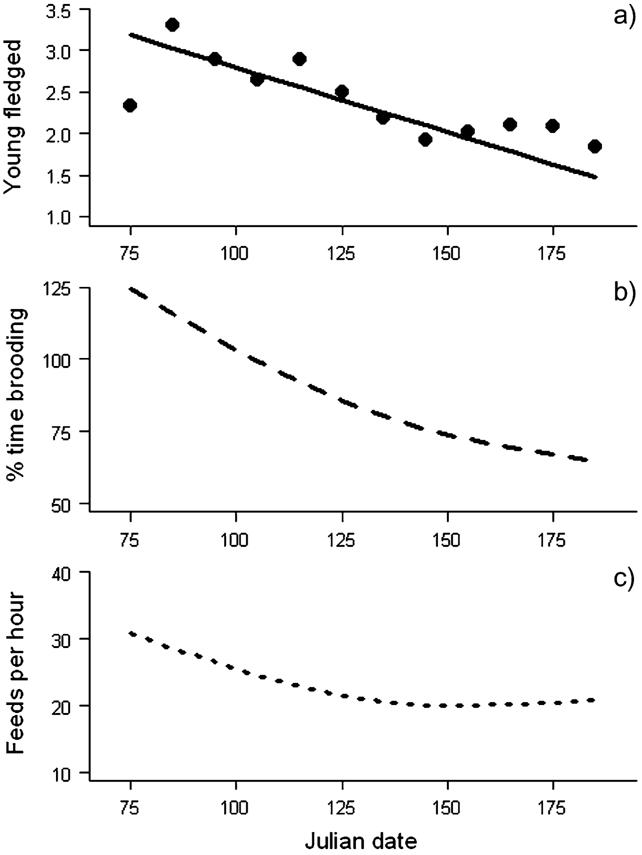

Figure 1
(a) The relationship between the number of young fledged and Julian date. The points are means for nests divided into 10-day periods; the line is the predicted regression line from a linear model including group size and Julian date. (b) The predicted nonlinear relationship between total percent time brooding at nests on nest day 5 and Julian date based on the best-supported model summarized in Table 1. (c) The predicted nonlinear relationship between overall provisioning rate and Julian date based on the best-supported model summarized in Table 1.

2) Breeders (whether cobreeding or not) should invest more than helpers.—Same-sex cobreeders are almost always closely related, appear to share reproduction relatively equitably, and do not engage in extra-group mating (see below). Furthermore, both cobreeders and helpers are closely related to the nestlings they feed; specifically, the estimated mean r between cobreeders and offspring is 0.443 compared with 0.449 between siblings within a group (Koenig and Mumme 1987). Consequently, helpers potentially gain significant indirect fitness benefits by provisioning offspring. Helpers, however, also stand to benefit by behaviors other than provisioning nestlings. In particular, they devote a significant amount of time to "forays" off their natal territory during which they search for reproductive opportunities. Such forays are common during the breeding season, and as a result, helpers contribute less than breeders not only to provisioning of nestlings but also to other cooperative behaviors, including territory defense and acorn storage, even though their effort when present can be comparable to that of breeders (Mumme and de Queiroz 1985). Thus, although the benefits to provisioning may be

similar for breeders and helpers, the fitness costs are certainly greater for helpers in terms of lost opportunities for finding reproductive vacancies. We therefore predicted that breeders should expend more effort brooding and provisioning nestlings than helpers and that helpers should be more likely to take advantage of aid provided by other group members—either breeders or helpers—to reduce their own provisioning efforts and to devote more time searching for reproductive opportunities outside their natal group.

3) Breeder females should invest more than breeder males.—Because of a higher frequency of cobreeding among males, the estimated mean relatedness between breeder females and nestlings is 12.7% greater ($r = 0.469$) than the estimated mean relatedness between breeder males and nestlings ($r = 0.416$; Koenig and Mumme 1987). Moreover, joint nesting among females is considerably less common than cobreeding by males and breeder females have lower survivorship than breeder males. Although the reduced survivorship of breeder females could be a result of higher reproductive investment rather than a cause, the overall result is that there is higher variance in reproductive success among females in the population than among males (Koenig et al. 1983; Koenig and Mumme 1987). Consequently, an individual reproductive event is relatively more valuable to a breeder female than to a breeder male, leading to the prediction that breeder females would invest more in each reproductive event than breeder males.

4) Helper males should invest more than helper females.—Acorn woodpecker groups tend to be patrilineal, with 23.7% of helper males inheriting their natal territory compared with only 4.6% of helper females (Koenig et al. 2000). Furthermore, helper males are more likely to disperse in sibling coalitions, often but not always consisting of same-aged birds, than helper females, and thus stand to benefit more by the production of siblings, some of which will be males (Koenig et al. 1983). Conversely, when they disperse, helper females move farther than helper males (Hannon et al. 1985; Koenig et al. 2000) and fight more aggressively for reproductive vacancies (Koenig 1981; Koenig et al. 1983), implying that females stand to gain relatively more by dispersing from their natal groups than do helper males. These factors led us to predict that helper males should invest more in each reproductive event than helper females, a prediction that would be consistent with the observation that helper males have a larger positive effect on breeder survivorship and reproductive success than helper females (Koenig et al. 2011a).

The above 4 predictions plausibly apply to both reproductive investment and to patterns of compensatory care. Specifically, the birds that invest the most in reproduction are also likely to be those that reduce their effort the least when other birds are contributing to the overall reproductive effort. Thus, we predicted that provisioning rates should decline seasonally and that the amount of investment in parental care should be in the following order for the 4 categories of birds: breeder females > breeder males > helper males > helper females. That is, breeder females should exhibit the greatest investment and the least decrease in investment with increasing group size (i.e., least compensation), whereas helper females should exhibit the least investment and greatest decrease in investment (i.e., most compensation) with increasing group size.

5) Compensation with increasing group size should be small or nonexistent during the first week of the nestling period and subsequently increase.—Brood reduction, the vast majority of which takes place within the first week of the nestling period, is relatively common regardless of territory quality or the size of the acorn crop (Stanback 1991). Following Hatchwell (1999), this suggests that investment should be primarily additive during the first week of the nestling period and compensatory at later nest stages when brood reduction is relatively rare.

6) Provisioning rates, but not compensation, should increase with the acorn crop.—Acorn woodpeckers are much more likely to breed and are far more successful in years following good acorn crops (Koenig and Mumme 1987; Koenig and Stahl 2007). With food being more plentiful, we predicted that overall provisioning rates should increase when the acorn crop is large, particularly among helper males, whose beneficial fitness effects are significantly greater during good acorn years (Koenig et al. 2011a). Surprisingly, however, brood reduction is not significantly affected by the acorn crop (Stanback 1991), and thus, we did not predict any change in compensatory care in conjunction with larger acorn crops.

Prior analysis of reproductive investment in this population based on 4 years of data found that breeders brooded and fed more than helpers and that females brooded and fed more than males but found no significant effect of either number of breeders or group size on investment by breeders and concluded that parental care was primarily additive rather than compensatory in this population (Mumme et al. 1990). Here, we use a more extensive 32-year data set, more recent statistical techniques, and data on the acorn crop to reevaluate these earlier conclusions and to measure patterns of compensation in both brooding and provisioning among different categories of birds and under different ecological conditions.

MATERIALS AND METHODS

Study population

Acorn woodpeckers, common in southwestern US oak woodlands, live in permanently territorial groups of up to 15 individuals of all ages and both sexes (Koenig et al. 1995). Group composition is highly variable, ranging from simple breeding pairs to a polygynandrous core of breeders along with their offspring from prior years that act as nonbreeding helpers at the nest. Extra-group parentage does not occur, and incest is rare; thus, helpers, as defined here, are exclusively nonbreeding (Dickinson et al. 1995; Haydock et al. 2001) and are almost always closely related to the breeders they help and the offspring they feed.

We studied a color-banded population of 18–56 groups (mean = 37) at Hastings Reservation, central coastal California, between 1973 and 2010. The analyses performed here are based on nest watches conducted between 1979 and 2010 during which observers sat in blinds located a discrete distance from active nests and, with the aid of spotting scopes, recorded all feeding visits during what was typically a 3-h period. For each feeding visit, the identity of bird, size of bolus being fed (small, medium, and large), whether the food bolus consisted of insects or acorns, and whether the bird removed a fecal sac or not were recorded on tape and later transcribed and summarized. Also recorded were both the time birds spent inside the hole and not looking out of the cavity (potentially brooding) and the time birds spent inside the hole and looking out of the cavity (not brooding). The proportion of time spent in the latter activity was small (~6% of total time spent inside the nest during the nestling period) and thus was added to the time spent brooding in the analyses performed here. We analyzed 3597 nest watches at 971 nests of 85 social groups for a total of 10 543 h of observation conducted throughout the season and the 30- to 34-day nestling period (Weathers et al. 1990). The number of different marked individuals included in the analyses was 472 breeder males, 364 breeder females, 498 helper males, and 385 helper females.

For analyses involving the acorn crop, we restricted analyses to the 30 years between 1981 and 2010, during which time we assessed the size of the crop the prior autumn by counting a sample of acorns on 250 marked trees distributed among the 5 major oak species (*Quercus* spp.) present in the study area. The mean acorn crop was estimated by the mean of the ln-transformed number of acorns counted in 30 s (xLN30 = ln[N acorns counted + 1]) across all trees surveyed (Koenig, Knops, et al. 1994; Koenig, Mumme, et al. 1994). In all cases, we analyzed how the prior autumn's acorn crop (year $x - 1$) affected behavior in year x. For simplicity, however, we refer to the prior autumn's acorn crop as "the acorn crop" without specifying when it was produced. In some analyses, we divided years into those in which the acorn crop was fair to poor (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, $N = 10$ years).

Data analysis

Statistical comparisons between breeders and helpers were made by paired Wilcoxon signed-ranks tests using the mean total brooding time or mean total number of feeding visits averaged for all individuals within a given status and/or sex category across all watches made at the same nest. Analyses of brooding were restricted to watches made during the first 11 days of the nestling period because this is when most brooding takes place (see below). We also calculated the proportion of watches during which each category of birds failed to participate in brooding and/or provisioning.

A parallel set of analyses was conducted with linear mixed-effects models. Although Cockburn (1998) recommended fitting such models using restricted maximum likelihood, this method is not valid when using model selection (Pinheiro and Bates 2000), and thus, we used maximum likelihood instead. Fledgling success was determined using spring nests (March–July) and was analyzed using a set of 5 candidate models: 1) group size; 2) Julian date; 3) group size and Julian date; 4) group size, Julian date, and their interaction; and (5) both linear and quadratic terms for group size and Julian date. In all cases, territory identity ("territory") was included as a random effect. We ranked models based on their Akaike information criterion (AIC)c values, considering any model whose ΔAICc < 2 as receiving competing support (Burnham and Anderson 2002; Anderson 2008). Autumn nests, which are attempted irregularly when the acorn crop is good, contribute <5% of fledglings to the population (Koenig and Stahl 2007) and were excluded from the analyses.

Overall provisioning rate as a function of nestling age was modeled using a third-order polynomial regression. For analyses of individual investment, the dependent variable was the arcsin-transformed proportion of time individual birds spent inside the nest (brooding) or the provisioning rate per hour. In order to control for the disturbance associated with the commencement of a watch, the length of a watch was measured as the total length minus the amount of time until the first visit to the nest to brood or feed. Independent variables included sex (male or female), status (breeder or helper), number of nestlings in the nest at the time of the watch (brood size), age of nestlings (days since hatching), total group size, time of day the watch began (Pacific Standard Time), maximum temperature for that day (measured at Hastings Reservation headquarters), Julian date, and the mean acorn crop from the prior autumn (ln-transformed). Quadratic terms for nestling age, Julian date, and the mean acorn crop were also included to test for nonlinear effects. As a random factor, we included the three-way nested factor of "bird" within "nest" within territory.

We tested the predictive value of these variables along with 7 potentially biologically relevant two-way interactions (sex × status, acorn crop × group size, time of day × Julian date, nestling age × number of young, nestling age × time of day, nestling age × maximum day temperature, and Julian date × maximum temperature for the day) by calculating AICc values and model probabilities as robust Bayesian posterior probabilities, starting with a series of variables that were likely to be important (sex, status, nestling age, total group size, maximum temperature, and Julian date) and then testing all combinations of the remaining variables using the multimodal inference package (MuMIn) in R (R Development Core Team 2011). When more than one model received competing support (ΔAICc < 2), we averaged their results using the "model.avg" function. Variables included in any of the models for which competing support was obtained were summarized by their standardized coefficients (±the unconditional standard error [SE]) and their *z*-score (standardized effect size divided by their SE).

In order to quantify compensatory care, we divided brooding time and provisioning visits by unidentified individuals within each watch (amounting to 8.1% of brooding time and 4.9% of provisioning visits) among those birds that were successfully identified during the watch proportionate to the amount of time (brooding) or number of visits (feeding) recorded for each known individual. We then analyzed compensatory behavior using linear mixed-effects models that included the independent variables listed above for the individual investment analyses and, as above, bird within nest within territory as a random factor. Compensation was then quantified by the effect of the variable "group size" in the analyses, with negative effect sizes representing a decrease in investment with increasing group size.

For the next set of analyses, we divided watches into relevant groups. That is, to compare compensation by breeders versus helpers, we divided brooding and provisioning data according to status, whereas for analyses focusing on age of nestlings (agecat), we divided watches according to whether nestlings were $\leq$7 days old or $>$7 days old because the majority of brood reduction takes place during the first week after hatching (Stanback 1991). We then recalculated the top-performing mixed-effects model as determined from the earlier analyses twice, once including the variable of interest and a second time without the variable. For example, to test whether helper males exhibited compensatory care, we compared models for the investment of helper males that included and that did not include the variable group size. To compare compensatory care by birds in different categories, by birds early versus late in the nestling period, or vis-à-vis the acorn crop, we compared models that did and did not include an interaction term between total group size and the variable of interest ("status" for comparisons between breeders and helpers, "sex" for comparisons between males and females, "agecat" for comparisons early vs. late in the nestling age, and "xLN30" for the acorn crop). We then compared the results of the 2 models based on their AICc values and considered compensation to have occurred if the model that included the term or interaction with total group size received competing support (ΔAICc < 2) compared with the model without the term or interaction with total group size.

All analyses were conducted in R version 2.12.2 (R Development Core Team 2011).

RESULTS

Seasonal patterns of fledging success, brooding, and provisioning

Of the 5 candidate models for fledging success, only the one that included group size and Julian date but not their interaction or quadratic terms received competing support (ΔAICc for the other 4 candidate models >10). Thus, both relationships were linear, and no interaction between the 2 variables was indicated. Fledging success was positively related to group size (mean ± SE effect size = 0.14 ± 0.03, $t = 5.2$, $P < 0.001$) and negatively related to Julian date (mean ± SE effect size = −0.015 ± 0.002, $t = -6.1$, $P < 0.001$; Figure 1a). Similar seasonal declines were observed in both percent time brooding and overall provisioning rates, although in both these cases, the effects were nonlinear and leveled off late in the season (Figure 1b,c).

Patterns of brooding and provisioning

Early in the nestling period, groups brooded an average of 60–65% of the time during the day, decreasing to 10–15% by the time nestlings were 12 days old (Figure 2a). Our analyses yielded support for only a single model of brooding time that included sex, status, nestling age, brood size, maximum day temperature, date, and the "nestling age × maximum day temperature" interaction as predictors (Table 1), with breeder females brooding significantly more than breeder males and breeders brooding significantly more than helpers (Figure 3a). In terms of the proportion of watches during which individual birds brooded, values ranged from 42.8% to 67.4% of watches conducted during the first 11 days of the nestling period, with helper females at the low end and breeder females at the high end of this range (Figure 4a).

Overall provisioning rates increased with nestling age until day 24, after which they decreased until fledging, a pattern matched well by a third-order polynomial of provisioning rate on nestling age (Figure 2b). In the analysis of the factors influencing provisioning rates, 2 mixed-effects models received competing support differing only with respect to which acorn crop term (linear or squared) they included. Model-averaged parameters in the supported models included nestling age (Figure 2b), brood size (provisioning increased overall but decreased per nestling as brood size increased; Figure 2c), group size (Figure 2d), sex, status, maximum temperature, date, and time of day, as well as several interaction terms (Table 1). Although the acorn crop was included in both models, it did not have a strong effect as judged by its *z*-score.

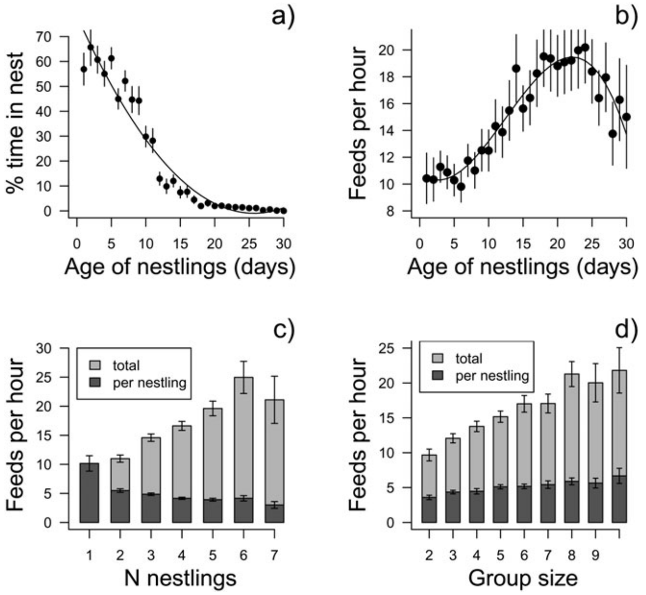

Figure 2
(a) Mean (±95% confidence interval [CI]) total percent of time spent in the nest (back-transformed from arcsin-transformed values) plotted against the age of nestlings in days since hatching. Fitted line based on quadratic regression ($F_{2,27} = 233$, $R^2 = 0.94$, $P < 0.0001$). (b) Mean (±95% CI) total provisioning rate (feeds·hr^{-1}) plotted against the age of nestlings. Fitted line based on cubic regression ($F_{3,26} = 84$, $R^2 = 0.90$, $P < 0.0001$). (c) Mean (±95% CI) provisioning rate (total and per nestling) as a function of the number of nestlings in the nest. (d) Mean (±95% CI) provisioning rate (total and per nestling) as a function of group size.

Comparing birds at the same nests using paired Wilcoxon signed-ranks tests (Figure 3b,d), breeders brooded ($N = 394$, $P < 0.001$) and fed ($N = 596$, $P < 0.001$) more than helpers, and breeder females brooded ($N = 587$, $P < 0.001$) and fed ($N = 912$, $P < 0.001$) more than breeder males. There was no significant difference in brooding between helper males and helper females ($N = 199$, $P = 0.9$), whereas helper females fed significantly more than helper males ($N = 293$, $P < 0.001$), a result not found in the analysis that included all data (Figure 3c). The probability of individual birds being observed feeding during a watch varied depending on their sex and status (Figure 4b), with helper females again at the low end of the range (65.4%) and breeder females at the high end (91.9%), and all classes of birds being significantly different from each other (χ^2 contingency tests; $P \leq 0.002$).

Patterns of compensation

We first tested the effect of group size on brooding and provisioning by comparing mixed-effects models that did and did not include total group size as an independent variable. For all 4 categories of birds, the model predicting brooding behavior that included total group size was less strongly supported than the model that did not include group size. For models that included helper males, however, ΔAICc = 1.6, whereas models containing the other 3 categories of birds had ΔAICc values ≥ 4.5, making helper males the only category of birds for which there was competing support for compensatory brooding behavior. Results for provisioning behavior were almost the opposite, with models that included total group size being more strongly supported for all categories of birds (ΔAICc ≥ 3.5 for the models not including total group size except for helper females, among which ΔAICc = 0.9 for the model not including total group size). Thus, in general, individuals decreased feeding but not brooding as group size increased.

Comparison of mixed-effects models for brooding effort that did and did not include the appropriate interaction term provided no support for the hypothesis that compensation differed among 1) breeders and helpers, 2) breeder males and breeder females, or 3) helper males and helper females (all ΔAICc ≥ 10.3 for the models including an interaction). Results were similar, although less dramatic, for provisioning rates (all ΔAICc ≥ 4.1 for the models including an interaction). Thus, our analyses provided no support for the hypothesis that there were differences in compensatory behavior among different categories of birds in terms of either their brooding (Figure 5a) or provisioning behavior (Figure 5b).

Next, we examined compensation in provisioning early versus late in the nestling period. Based on the ΔAICc values, compensation by both breeder males and breeder females was influenced by the stage of the nestling period (ΔAICc ≥ 9.4 for the models that did not include an interaction term), but there was no competing support for models that included the interaction term for helper males or helper females (ΔAICc ≥ 3.1 for the models that included an interaction). Thus, breeders, but not helpers, exhibited less compensation early in the nestling period (Figure 6a).

Table 1

AICc model-averaged parameter estimates (±SE) for time spent brooding (arcsin transformed) and provisioning rate (feeds·hr^{-1}) based on mixed-effects models

	Brooding time		Provisioning rate	
Variable	Model parameters (all ×10^{-3})	*z*-score	Model parameters	*z*-score
Sex	15.4 ± 3.7	4.1***	1.15 ± 0.20	5.9***
Status	83.8 ± 4.1	20.4***	0.86 ± 0.20	4.2***
Nestling age	−18.7 ± 1.0	18.9***	0.229 ± 0.016	14.6***
(Nestling age)^2	0.23 ± 0.02	11.4***	−3.37 ± 0.31(×10^{-3})	−11.0***
Brood size	−7.6 ± 2.1	−3.6***	0.189 ± 0.040	4.7***
Maximum temperature	−4.6 ± 0.6	−8.3***	−0.060 ± 0.024	−2.5*
Date	−6.5 ± 0.7	−8.8***	−2.80 ± 1.12(×10^{-2})	−2.5*
(Date)^2	0.016 ± 0.002	7.9***	1.31 ± 0.31 (×10^{-4})	4.2***
Group size	NA	NA	−0.20 ± 0.03	−7.7***
Time of day	NA	NA	4.17 ± 1.55 (×10^{-4})	2.7**
Mean acorn crop	NA	NA	−0.036 ± 0.058	−0.6
(Mean acorn crop)^2	NA	NA	−0.026 ± 0.025	−1.1
Nestling age × maximum temperature	0.17 ± 0.03	5.3***	NA	NA
Nestling age × brood size	NA	NA	9.51 ± 2.04 (×10^{-3})	4.7***
Date × maximum temperature	NA	NA	−5.82 ± 1.57(×10^{-4})	−3.7***
Sex × status	NA	NA	0.332 ± 0.136	2.4*
Nestling age × time of day	NA	NA	−6.98 ± 0.90(×10^{-5})	−7.8***

Models averaged are those with ΔAICc < 2; only one model met this criterion for proportion of time brooding. NA = variable not included in any of the supported models. For a list of all interactions examined, see text. The *z*-score (mean model parameter divided by the SE) provides an estimate of the weighted significance of the variable in terms of a traditional hypothesis testing approach.

*$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.

Finally, we compared patterns of compensation in relation to the acorn crop. In none of the analyses did the model that included the interaction term between group size and the acorn crop receive competing support (all ΔAICc ≥ 3.8 for the models including an interaction term). That is, our analyses failed to support the hypothesis that birds exhibited differences in compensatory feeding depending on the size of the acorn crop.

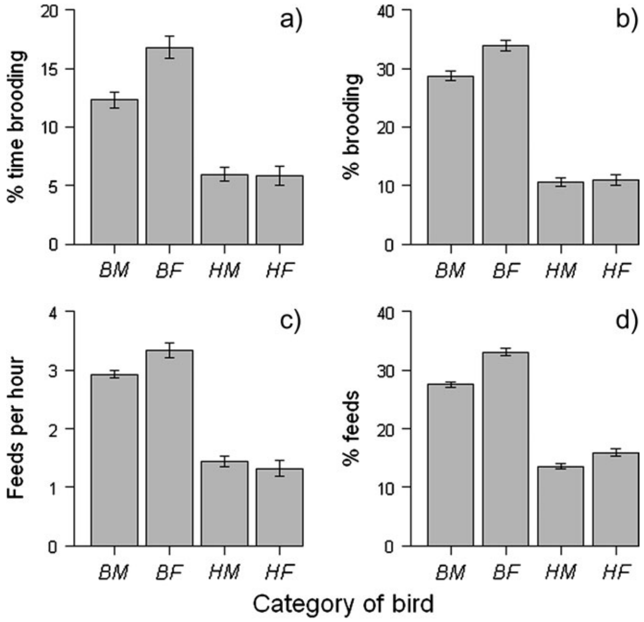

Figure 3

Top row: brooding by sex/status, including only watches conducted during the first 11 days of the nestling period. (a) Mean (±SE) percent time brooding including all data, and (b) mean (±SE) percent of brooding time contributed by birds of each category using watches included in the paired analyses. Bottom row: provisioning rate per hour by sex/status. (c) Mean (±SE) provisioning rate per hour including all data, and (d) mean (±SE) percent of total feeds contributed by birds of each category using watches included in the paired analyses. Categories of birds are: BM, breeder males; BF, breeder females; HM, helper males; and HF, helper females.

DISCUSSION

Brooding and provisioning of nestlings in the acorn woodpecker are influenced by a variety of variables. Several of these were expected based on energetic considerations. For example, brooding declined and provisioning rate increased with nestling age, patterns expected as nestlings grow larger and simultaneously require more food while becoming better able to thermoregulate on their own (Weathers et al. 1990). Similarly, brooding declined and provisioning rate increased with brood size, a pattern reflecting the increased energetic demands of greater numbers of chicks combined with the thermoregulatory benefits of larger broods (Royama 1966). Provisioning rate per nestling declined with increasing brood size, a pattern found in many other species again presumably due in part to the more advantageous thermal environment experienced by larger broods (Royama 1966) but also because caregivers eventually approach the physiological limits of their efforts. Both brooding and provisioning rates declined with increasing temperature, an effect that could be due to a variety of factors including the lower energetic requirements of nestlings and decreased need for brooding when ambient conditions are warmer. Such environmental influences on brooding and provisioning of nestlings are common in birds and have been reported in other cooperative breeders (Brown et al. 1978; MacColl and Hatchwell 2003).

Our primary interest here, however, was in understanding the variation in contributions to provisioning by breeders versus nonbreeding helpers and males versus females. Based on a priori knowledge of acorn woodpecker life-history traits, we made 6 predictions regarding how effort should vary among categories of birds and under different ecological conditions.

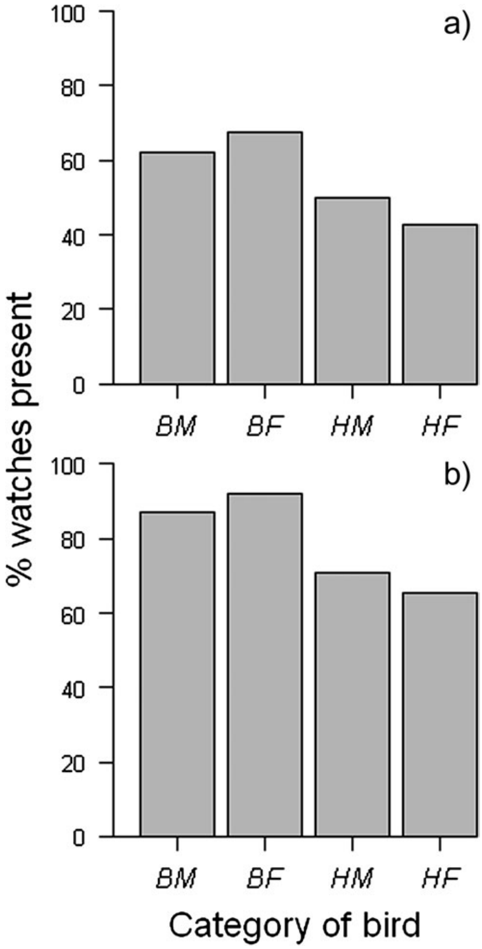

Figure 4
Mean percent of birds participating in watches of different sex/status categories in (a) brooding and (b) provisioning. Categories as in Figure 3. Sample sizes are: BM (brooding = 2275; feeding = 5752); BF (brooding = 1505; feeding = 3785); HM (brooding = 1372; feeding = 3256); and HF (brooding = 845; feeding = 2130). All proportions are significantly different from each other (χ^2 contingency tests; $P \leq 0.002$).

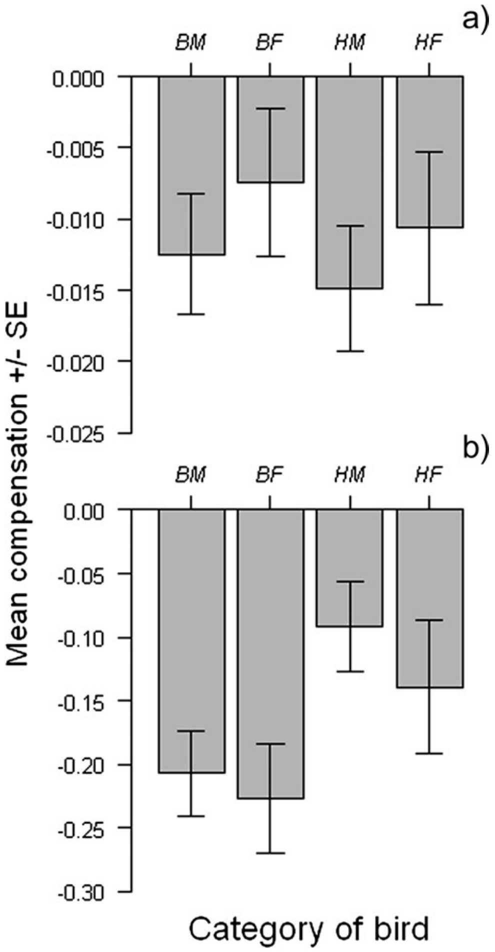

Figure 5
Mean (±SE) compensation by sex/status category as measured by the mean effect size in an analysis of total group size on (a) percent time brooding and (b) provisioning rate per hour. Categories as in Figure 3. For comparisons, see text.

The first prediction was that reproductive investment should parallel the seasonal decline in fledging success (Figure 1a). In support of this prediction, both percent time brooding and provisioning rates decreased seasonally, the only difference being that the decreases were nonlinear, particularly in provisioning rates, leveling off late in the season (Figure. 1b,c), contrasting somewhat with the statistically linear seasonal decline in fledging success. In general, however, our results supported the prediction that birds devoted less to reproduction as the season progressed and that the decline generally matched the observed seasonal decline in fledging success.

The next 3 predictions focused on the relative investment and compensatory behavior of different categories of birds. In terms of overall investment, we predicted that breeders should invest more than helpers, breeder females should invest more than breeder males, and helper males should invest more than helper females. These predictions were all borne out when considering the proportion of watches birds in each of the 4 different categories participated: For both brooding and provisioning, breeder females were present in the highest proportion and helper females the lowest (Figure 4). In terms of provisioning rates and the percent time brooding, the first 2 predictions were also generally upheld: breeders brooded and fed at higher rates than helpers and breeder females brooded and fed at higher rates than breeder males (Figure 3). Thus, investment in brooding generally paralleled that for provisioning. We found no significant difference in brooding between helper males and helper females, however, while in paired comparisons of birds at the same nest, helper females fed significantly more than helper males, contrary to prediction 4.

Our predictions were less successful when it came to predicting how parental care for different categories of birds should change as group size increased. We predicted that compensatory reduction in care should be inversely correlated with effort; that is, breeders should exhibit less compensation (that is, reduce their effort less) than helpers, breeder females less than breeder males, and helper males less than helper females. No significant differences in compensation, however, were found between any of these categories of birds in either brooding or provisioning. Thus, our evidence with respect to compensation failed to support predictions 2, 3, or 4.

Prediction 5 stems from Hatchwell's (1999) hypothesis that compensation should be significantly reduced during the first week of the nestling period when brood reduction is common compared with later in the nestling cycle when brood reduction is rare. Results supported this prediction in the case of breeder males and breeder females, both of which exhibited minimal compensation during the first week of the nestling

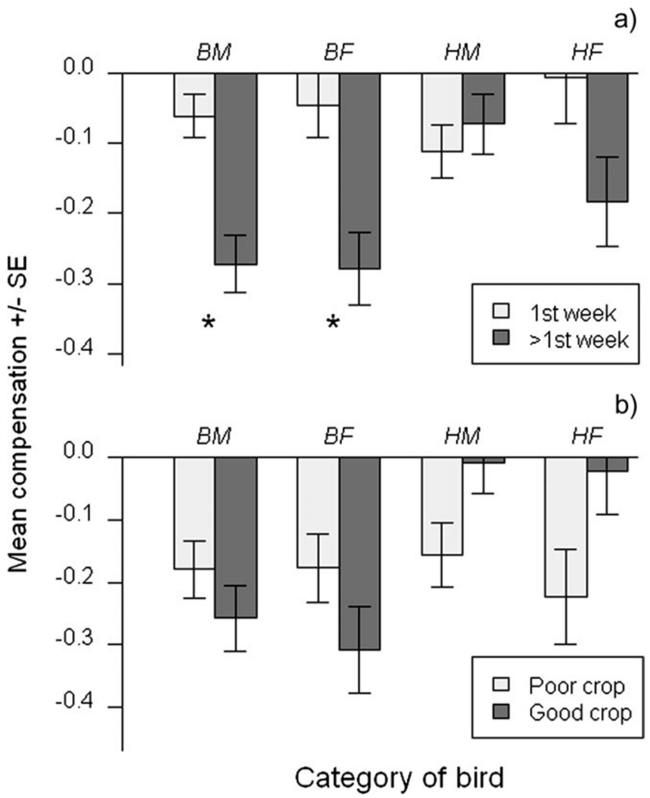

Figure 6
Mean (±SE) compensation by each sex/status category measured by the effect size of total group size on provisioning (a) early (≤7 days old) versus later (>7 days old) in the nestling period and (b) when the acorn crop was fair to poor (xLN30 < 2.2) versus good to very good (xLN30 > 2.2). Differences for breeder males and breeder females early versus late in the nestling period were significant and are marked with asterisks (see text); other differences, including comparisons vis-à-vis the acorn crop, were not.

period compared with when nestlings were older. In contrast, compensation by nonbreeding helpers did not differ between the 2 periods (Figure 6a).

Our last prediction was that provisioning rates, but not compensation, would be greater when the acorn crop was good. Both these predictions were upheld: The acorn crop was included in the supported models predicting total provisioning rates, with the rate being greater when the acorn crop was large (Table 1). In contrast, there were no significant differences in any of the 4 categories of birds in terms of the compensatory care they exhibited vis-à-vis the acorn crop (Figure 6b).

Except for differences between helper males and helper females, we were generally able to predict relative provisioning effort with respect to sex, status, season, and a critical food resource (i.e., the acorn crop) given a priori knowledge of the costs and benefits associated with variation in these factors. Matching our predictions particularly well was the probability that birds of different categories would be present and participating in nestling care during a watch, suggesting that this measure, which quantifies the relative value of nestling care compared with mutually-exclusive activities such as foraying away from the territory, is a good indicator of the relative value of nests to birds of different status and sex.

Less successful were our predictions of how birds should adjust their overall reproductive effort in response to increasing group size. Prior work has suggested several factors that may be important to understanding variation in compensatory behavior, including reproductive skew affecting the constraints on reproduction by helpers (the greater the skew, the less helpers stand to gain by reducing investment, and saving resources for future potential reproduction; Gilchrist and Russell 2007); uncertainty regarding brood need (the greater the uncertainty, the more likely it is that individuals will increase effort if they observe other group members investing more as a signal of brood need, thus reducing the likelihood of a compensatory response; Johnstone and Hinde 2006); the benefits of alternative behaviors such as attracting additional mates (Komdeur et al. 2002) or searching for reproductive vacancies (Mumme and de Queiroz 1985; Young et al. 2005); and the incidence of brood reduction (provisioning should be additive when brood reduction is common and compensatory when it is not; Hatchwell 1999). Our results indicating that compensation in provisioning behavior was less among breeders early in the nestling period when brood reduction is common is consistent with the "brood reduction" hypothesis. Despite the fact that the acorn crop has been shown to have numerous effects on both demography and behavior in acorn woodpeckers, we found no evidence that it affects either brood reduction or compensatory behavior in this population.

Less clear is how to interpret the lack of variation in compensation exhibited by different categories of birds. One key observation is that helper males are more likely to inherit and eventually breed in their natal group, whereas helper females are more likely to disperse (Koenig et al. 2000). This difference predicts that helper females should exhibit more compensation in parental behavior than helper males because females should benefit more by spending their time searching for vacancies, whereas males should benefit more by helping at their natal groups. Consistent with this idea, helper females were the category of birds least likely to participate in a given brooding and feeding watch (Figure 4). We did not, however, find evidence for a significant difference in compensatory behavior between helper males and helper females or, for that matter, in compensatory behavior between any of the other categories of birds considered in our analyses.

Prior studies have found wide variation in the compensatory behavior of cooperative breeders, including compensation by both breeders and helpers (Brown et al. 1978; Legge 2000), compensation by breeders but not helpers (Hatchwell and Russell 1996; Clutton-Brock et al. 2004; Gilchrist and Russell 2007), greater compensation by breeder males than breeder females (Stallcup and Woolfenden 1978; Meade et al. 2010), and greater compensation by helpers than breeders (Legge 2000). Moreover, at least 2 studies have provided evidence for variation in compensatory behavior among birds of the same class depending on the number of helpers (MacColl and Hatchwell 2003) and the ability of other group members to feed the young (Baglione et al. 2010). Clearly generating a comprehensive theoretical framework with which to understand such variation will be challenging, even more so than for simpler biparental systems where the factors influencing compensatory behavior remain unresolved (Schwagmeyer et al. 2002; Lendvai et al. 2009).

An additional complexity in interpreting patterns of investment is the various other activities that make up reproduction. Three obvious such behaviors in the acorn woodpecker system include incubation, nocturnal brooding during the nestling period, and removing fecal sacs (nest sanitation). As found by Mumme et al. (1990), patterns of incubation are generally similar to those of brooding, with breeders incubating more than helpers and breeder females incubating more than breeder males. Of greater interest are the other 2 behaviors, both of which are apparently performed far more frequently by breeder males than by either breeder females or nonbreeding helpers. For example, of 7470 fecal sacs we recorded being removed from nests, 4584 (61.4%) were removed by breeder males, while only 38.9% of the feeding visits were by breeder males, a highly significant difference (χ^2 test, $P < 0.001$; conversely, all other categories of birds engaged in nest sanitation significantly less frequently than expected). Although some fecal sacs may have been eaten and thus missed by our observations (Pechacek and Kristin 2004), breeder males appear to engage in this form of nest sanitation far more frequently than other classes of birds.

More cogent from the standpoint of a potentially dangerous activity is that of nocturnal incubation and brooding activities that are almost exclusively performed by breeder males (Koenig et al. 1983). The significance of these behaviors, however, is difficult to determine. The costs of egg laying have been suggested to result in male nocturnal incubation and be key to the evolution of joint-nesting avian systems (Vehrencamp 2000). Alternatively, male nocturnal incubation is a phylogenetically constrained trait found generally in the family Picidae (Jackson 1976; Mumme et al. 1990). Regardless, nocturnal incubation and brooding is a costly activity engaged in differentially by males, and consequently, the total time spent in the nest is biased toward breeder males, contrary to the pattern of greater female investment exhibited by diurnal brooding and provisioning behavior.

Beyond these issues are additional factors such as age, dominance, and parentage that may prove important to investment. Age effects were not found to be important in the earlier analyses by Mumme et al. (1990), but more recent analyses indicate that helpers increase their provisioning rates with age, at least until their third year (Koenig and Walters 2011). Dominance among individuals within a social group affects the likelihood of subordinate individuals remaining as helpers and, by extension, their propensity to help (Koenig et al. 2011b). As for the effect of parentage on investment, evidence thus far indicates that there is no reproductive skew among joint-nesting females within nests and that paternity among cobreeding males is relatively equitable across multiple nests despite relatively high skew within any particular nest (Haydock and Koenig 2002, 2003). Thus, to the extent that skew is low overall, there may be little or no bias in expected parental effort related to differences among cobreeders in confidence of parentage for either females or males. Testing this assumption, however, will have to await more detailed parentage data.

Possibly the only conclusion for which there is a consensus among the various studies thus far of alloparental care in cooperative breeders is that the variation in parental care reflects different solutions to the problem of optimal tradeoffs between current versus future reproduction. Given this, it is perhaps not surprising that the range of patterns in parental care among cooperative breeders is as diverse as their life histories, which involve both species faced with harsh, variable, and unpredictable environments and species living in stable, predictable environments, the unifying feature of which is the importance of ecological constraints to the evolution of delayed dispersal (Emlen 1982; Koenig et al. 1992). Whether species on opposite ends of this spectrum exhibit different patterns of parental investment strategies or not remain to be determined.

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