ethology international journal of behavioural biology

Ethology

# An Experimental Study of Chick Provisioning in the Cooperatively Breeding Acorn Woodpecker

Walter D. Koenig*† & Eric L. Walters‡

* Cornell Lab of Ornithology, Ithaca, NY, USA
† Department of Neurobiology and Behavior, Cornell University Ithaca, NY, USA
‡ Department of Biological Sciences, Old Dominion University Norfolk, VA, USA

**Correspondence**
Walter D. Koenig, Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.
E-mail: wdk4@cornell.edu

Received: February 7, 2012
Initial acceptance: March 15, 2012
Final acceptance: March 23, 2012
(L. Ebensperger)

doi: 10.1111/j.1439-0310.2012.02043.x

## Abstract

Acorn woodpeckers (*Melanerpes formicivorus*) are cooperative breeders in which groups consist of a variable number of cobreeding males, joint-nesting females, and non-breeding helpers of both sexes that are offspring from prior nests. We temporarily manipulated brood size of nests to determine the feeding response of birds in relation to their status (breeder or non-breeding helper) and sex. All categories of birds responded similarly to brood size increases, adjusting their feeding rate upwards so as to maintain approximately the same per-nestling feeding rate. Breeders, however, exhibited more flexibility with respect to brood size reductions, decreasing their feeding rate while helpers did not. This suggests that the 'feeding rules' of helpers are less flexible than those of breeders, a result not previously detected in other cooperative breeders that have been studied to date. Particularly surprising was the finding that helpers maintain their feeding rates when brood demand is decreased rather than when it was increased, suggesting that the flexibility they exhibit is not a result of birds using the opportunity afforded by reduced brood demand to engage in other less cooperative activities.

## Introduction

Provisioning of offspring is an energetically expensive activity in altricial species (Drent & Daan 1980), forcing caregiving adults to balance potential trade-offs between additional investment in current reproduction and survival and/or future reproduction (Williams 1966; Stearns 1989). Although such provisioning is the most obvious and most readily quantified aspect of parental care in many species, much remains to be learned about both the proximate and ultimate factors affecting how species allocate parental resources (Winkler 1987). This is especially true in cooperatively breeding species, a situation in which there is more than a pair of caregivers, and thus the factors affecting expected investment in offspring are particularly complex (Wright & Dingemanse 1999; Heinsohn 2004; Johnstone 2011).

A basic question concerning offspring provisioning concerns the degree to which caregivers respond to the demands of offspring. Given that natural selection should favor individuals that maximize their reproduction and that the reproductive value of the current brood will generally be a positive function of brood size, a 'flexible investment' strategy should match changes in brood size by changes in investment (Johnsen et al. 1994). Alternatively, effort at a particular nest may be based on a cost-benefit analysis of survival relative to investment prior to breeding. If this is the case, current brood size should represent the optimal allocation of investment, and thus experimental changes in brood size would be expected to have little or no effect on the 'fixed-level' strategy of the caregivers (Sæther et al. 1993).

Proximately, whether feeding effort is flexible or fixed is an issue of cause and effect: do caregivers adjust their reproductive investment to match that of the demands of the current brood (the flexible investment strategy) or is the number of young in a nest adjusted (most obviously by brood reduction) to match the optimal fixed amount of investment that parents are able or willing to provide (the fixed-level strategy)? This issue is particularly cogent in cooperative breeders where caregivers may include both breeders and non-breeding helpers for which feeding a brood confers very different fitness benefits relative to other activities such as searching for reproductive vacancies.

Several recent studies of chick-feeding rules in birds have temporarily manipulated brood need, either by directly modifying brood size (Wright & Cuthill 1990; Komdeur et al. 2002; Magrath et al. 2007) or by manipulating begging signals using playback broadcasts near the nest (Kilner et al. 1999; Hinde & Kilner 2007). In general, these studies have demonstrated considerable flexibility in feeding, with provisioning rates changing in concert with experimentally altered (real or simulated) brood size. Moreover, the response of males and females in biparental care systems is often similar, with both sexes either increasing or decreasing their effort proportionate to experimental adjustments of brood need (Hinde & Kilner 2007; Magrath et al. 2007).

These results provide some basis for a preliminary understanding of intrafamily dynamics of biparental systems (Winkler 1987; Johnstone & Hinde 2006; Harrison et al. 2009) and, in one case, a system with more than two parents (Hatchwell & Davies 1990). Less progress has been made, however, in more complex cooperative breeders (MacColl & Hatchwell 2003). Such societies potentially involve a variable mix of multiple cobreeders and non-breeding helpers – individuals that may exhibit very different provisioning strategies (Baglione et al. 2010) – and the possibility (as yet unconfirmed) that feeding may in some cases be deceptive and act as a signal to other individuals within the group (Clutton-Brock et al. 2005; McDonald et al. 2007). Such behavioral complexity clearly complicates the expected feeding response of birds to nestling demands (Hatchwell 1999; Legge 2000; Heinsohn 2004).

To date, the most thorough study of chick-feeding rules in a cooperative breeder has been in the Arabian babbler (*Turdoides squamiceps*). In this species, experimental studies manipulating apparent brood demand using playbacks and food supplementation found that breeders and helpers exhibited statistically indistinguishable changes in provisioning with manipulation of perceived brood need as well as similar compensatory adjustments in feeding rates (Wright 1998; Wright & Dingemanse 1999). Other relevant studies include one on bell miners (*Manorina melanophrys*), which found that males increased their feeding rates during playbacks regardless of paternity in the nest (McDonald et al. 2009), and one on superb fairy-wrens (*Malurus cyaneus*), which found that males, whether dominant breeders or subordinate helpers, adjusted their feeding rates to increased perceived brood need whereas females did not (MacGregor & Cockburn 2002). Additional work investigating chick-feeding rules in cooperative breeders is clearly desirable.

We conducted experiments to investigate the sex- and status-related investment strategies of acorn woodpeckers (*Melanerpes formicivorus*), a cooperatively breeding species in which groups frequently contain both multiple cobreeders and non-breeding helpers of both sexes (Koenig & Mumme 1987; Koenig et al. 1995b). Helpers in this species are always offspring of the breeders in the group, and there is no extra-group parentage (Dickinson et al. 1995; Haydock et al. 2001). Thus, helpers are always closely related to the nestlings they help feed.

Our goal was to determine experimentally whether birds of different social status or sex exhibited different provisioning responses to changes in brood size. If responses were found to be variable – for example, if one category of birds reduced their feeding rate in response to decreased brood size while others did not – it would potentially indicate that birds of the reducing category take advantage of the behavioral inflexibility of other group members to minimize their own investment in feeding young in favor of engaging in other, potentially less cooperative, activities.

We envisioned several possibilities. One was that helpers, which are feeding non-descendant relatives rather than their own offspring, might be relatively quick to cut their investment in feeding when brood size was reduced and slow to feed more when brood size was increased, thus gaining more time to foray away from the territory and search for reproductive vacancies. Alternatively, helpers might be less accurate at judging brood need than breeders and hence less flexible than breeders in their feeding behavior, investing a set amount regardless of brood size. Breeders, on the other hand, might be quite adept at judging brood need and exhibit greater flexibility, adjusting their reproductive effort not only depending on brood size but potentially depending on whether they achieved paternity in the nest or not.

Alternatively, if all categories of birds responded similarly to changes in brood size, it would indicate that no category of individuals was trying to ‘cheat’ in their investment relative to other group members and that all categories exhibit similar chick-feeding rules, despite the different fitness benefits birds are gaining by helping to feed group offspring. Given the relatively high reproductive skew among male cobreeders (Haydock & Koenig 2002, 2003) and the fact that indirect fitness gains appear to be the primary benefit of feeding offspring for helpers in this species (Koenig & Walters 2011), equitable investment by all group members would be consistent with kin selection playing a key role in shaping provisioning behavior in this system.

## Methods

The study was conducted on 14 nests between May 3 and June 22, 1985, and May 16 and June 11, 2011, selected from a color-banded population studied since 1971 at Hastings Reservation, Monterey County, California. The protocol consisted of recording feeding visits from a blind during 3-h watches conducted at approximately the same time each day at nests with nestlings 8–29 d old. In all but one set of experiments, watches were conducted in the morning starting within 1.4 h ($\bar{x} \pm SD = 26 \pm 24$ min) of each other and were conducted during fair weather. Group composition varied considerably among the experimental groups, with breeder composition ranging from a single pair of birds to groups with both cobreeder males and joint-nesting females, and groups both with and without non-breeding helpers (Appendix 1). Both years in which experiments were conducted followed acorn crops that were near the long-term average (W. Koenig, unpubl. data), so results were not biased as a consequence of an unusually large or an unusually small amount of available food (Koenig et al. 2011).

Watches were followed immediately by the experimental brood manipulation in which we either added or subtracted one or two nestlings, depending on the original brood size. As controls, we compared feeding rates at the experimentally manipulated brood to those at the unmanipulated brood during watches conducted the day before (N = 5), the day after (N = 5) or on both the day before and the day after (N = 12) the manipulated brood. During all watches (N = 52), the identities of birds feeding were recorded onto tape along with the bolus size of the food items brought to the nest ranked in size from 1 (small; no food items seen in the bill) to 3 (large; bill significantly expanded by the presence of food items).

Even though all group members in our study were individually marked, a small proportion of feeding visits ($\bar{x} = 3.9\%$; range = 0–18.6%) were made by birds whose identity could not be confirmed, usually because the tarsus was obscured. To ensure that results were not biased by such incomplete data, we apportioned feedings by unidentified individuals among the birds observed to have fed during the watch according to the proportion of total feeds each bird was known to have contributed. That is, if known bird *x* was observed to have fed 10 times, while all known birds fed a total of 50 times and there were five additional feeding visits performed by unidentified birds, bird *x* was given a total of $10 + (5 \times 10/50) = 11$ feeds for that day's watch.

We calculated the feeding rate for all individuals combined and for each bird separately by dividing his or her feeding visits (including those apportioned to it by the above procedure) by the total length of the watch minus the length of time it took for the first feeding visit to take place following the start of the watch. We did not include the time to the first feed in order to control for the disturbance, primarily associated with setting up a blind, that accompanied the start of a watch (Koenig & Walters 2012). Time to first feed varied from 0 to 93 min ($\bar{x} \pm SD = 19 \pm 22$ min).

For each group, we calculated the mean feeding rate both per hour and per nestling per hour for each individual and for all birds combined for the relevant control day(s) and for the experimental day(s). Statistical tests for the effects of the experimental brood manipulations were made using generalized linear mixed-effects models (R Development Core Team 2011). For overall and individual feeding rates, feeding rate was the dependent variable, the experimental category and group size were fixed factors, and 'nest identity' was included as a random factor. For the analyses of individual birds, 'bird' was nested within 'nest identity' as a random factor. For the analyses of the difference in response by birds of different sex and status, we performed analyses involving both feeding rate per hour and feeding rate per nestling per hour. In all analyses, fixed factors included group size, mean bolus size, the experimental category (decreased, control, or increased brood size), sex (male or female), status (breeder or helper), and all two-way interactions between the experimental category, sex, status, and mean bolus size. Mean bolus size was not significant in any of the analyses either by itself or in two-way interactions and was eliminated from the analyses reported below. Group size was included to control for its influence on feeding rates (Koenig & Walters 2012).

We also examined the response of birds to the behavior of their cobreeders of the same sex in the same social group to determine whether birds responded differently to brood size manipulations depending on what their cobreeders did. Comparisons were made among cobreeder males and joint-nesting (cobreeder) females. We summarized the number of cases in which (1) all cobreeders responded as expected to the brood manipulation (increasing their feeding rate when brood size was increased or decreasing it when brood size was decreased), (2) all individuals responded opposite the direction expected (decreasing their feeding rate when brood size was increased or increasing it when brood size was decreased), and (3) at least one individual responded as expected and at least one did not.

## Results

Groups and individuals significantly adjusted their feeding rate to temporary changes in brood size (Fig. 1). Total feeding rates at nests paralleled changes in brood size when analyzed on either a nest-by-nest (Fig. 1a) or individual-bird (Fig. 1b) basis. Feeding rates per nestling did not change significantly when brood size was increased, but did increase significantly when brood size was decreased, again when analyzed on both a nest-by-nest (Fig. 1c) and individual-bird bases (Fig. 1d). Thus, overall feeding rates changed as expected, increasing with increased brood size and decreasing with decreased brood size, but birds did not reduce their feeding rate proportionately when brood size was decreased, resulting in an increase in the per-nestling feeding rate under this experimental regime.

When examining feeding rates by sex and status of group members, all categories generally increased their feeding rates when brood size was increased, whereas breeders, but not helpers, decreased their feeding rates when brood size was decreased (Fig. 2). These results were confirmed by the mixed-effects models (Table 1), in which feeding rate per nest per hour significantly declined when brood size was decreased, increased when brood size was increased, and there was a significant 'status × brood decreased' interaction indicating that breeders, but not helpers, reduced their feeding rate when brood size was decreased. There were no other significant interactions between the other factors tested or between any of the factors in the analysis of feeding rate per nestling per hour. Mean bolus size, which was excluded from the analyses presented, was not significant either by itself or in any interaction, indicating that there was no systematic change in bolus size across experimental categories that might explain the observed differences in feeding rates.

To test for whether cobreeders might be responding differently to brood size manipulations, we compiled cases in which all cobreeders of the same sex in a group responded similarly (regardless of whether it was in the direction expected or not) to brood size manipulations. Cobreeder males and cobreeder females both responded similarly in 10 of 12 cases

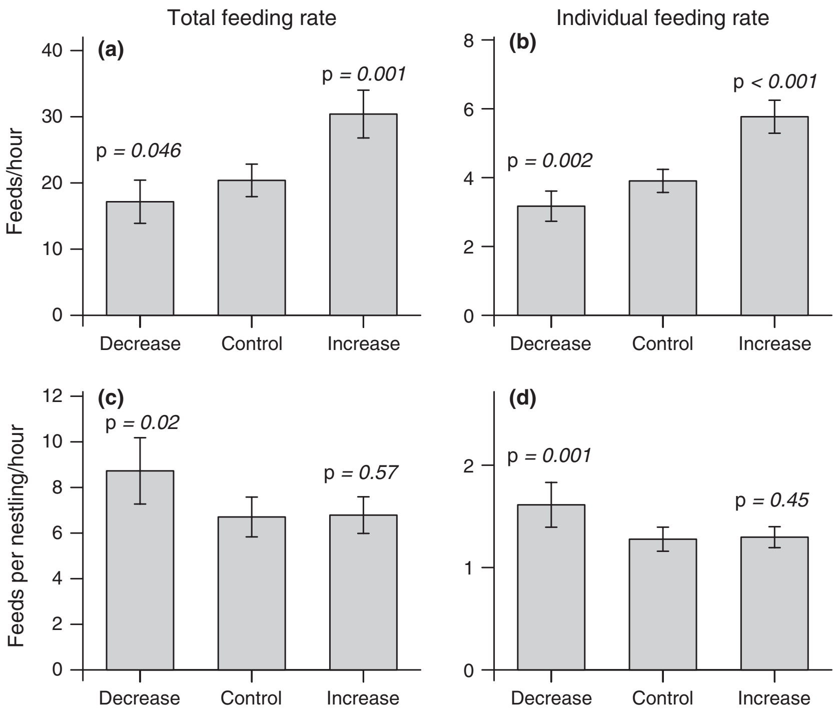

**Fig. 1:** Mean (±2 SE) feeding rate divided by the brood size manipulation (brood size decreased, control, or brood size increased). Top: (a) total feeding rate and (b) feeding rate per individual, both measured as feeds per nest per hour. Bottom: (c) total feeding rate and (d) feeding rate per individual, both measured as feeds per nestling per hour. Statistical significance of differences compared to controls based on generalized linear mixed models.

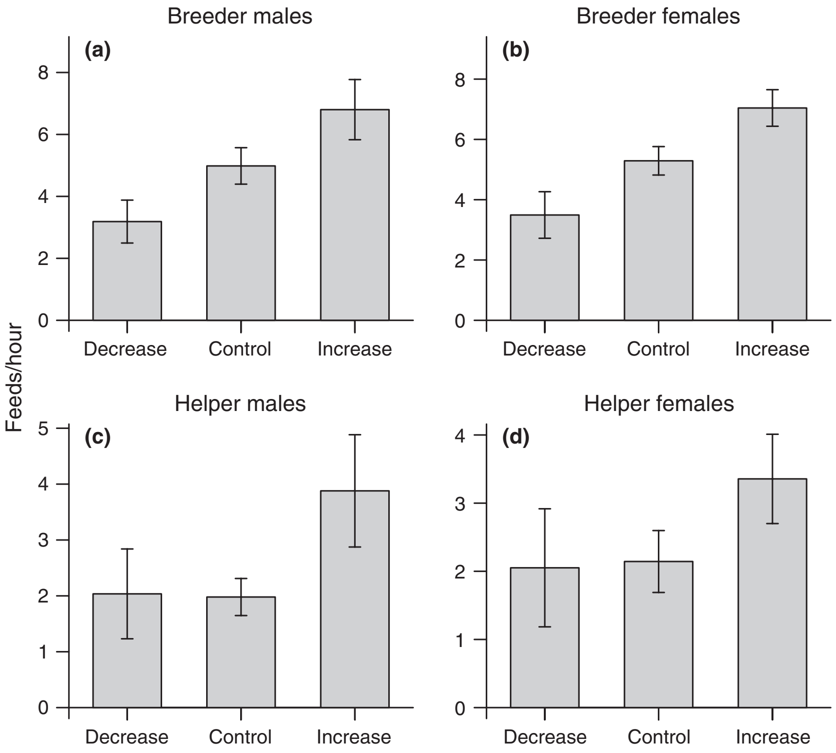

**Fig. 2:** Mean (±2 SE) feeding rate per nest (feeds per hour) divided by the brood size manipulation (brood size decreased, control, or brood size increased) for (a) breeder males, (b) breeder females, (c) helper males and (d) helper females.

**Table 1:** Summary of the mixed-effects models analyzing the experimental manipulation of brood size

| | Feeding rate per nest per hour | | | Feeding rate per nestling per hour | | |
|---|---|---|---|---|---|---|
| Factor | Effect size ± SE | *t*-value (df) | p-value | Effect size ± SE | *t*-value (df = 245) | p-value |
| Group size | −0.66 ± 0.30 | −2.21 (12) | **0.047** | −0.19 ± 0.10 | −1.96 (12) | 0.07 |
| Decrease | −1.47 ± 0.47 | −3.13 (187) | **0.002** | 0.39 ± 0.19 | 2.00 (187) | **0.047** |
| Increase | 2.19 ± 0.52 | 4.20 (187) | **<0.001** | −0.15 ± 0.21 | 0.68 (187) | 0.49 |
| Sex | 0.91 ± 0.58 | 1.55 (58) | 0.13 | 0.40 ± 0.23 | 1.76 (58) | 0.08 |
| Status | 1.85 ± 0.79<br>(Breeders > helpers) | 2.34 (58) | **0.02** | 0.58 ± 0.31<br>(Breeders > helpers) | 1.91 (58) | 0.06 |
| Sex × decrease | 0.02 ± 0.64 | 0.04 (187) | 0.97 | 0.06 ± 0.26 | 0.23 (187) | 0.81 |
| Sex × increase | 0.24 ± 0.68 | 0.36 (187) | 0.72 | 0.10 ± 0.28 | 0.38 (187) | 0.71 |
| Status × decrease | 1.63 ± 0.72<br>(Helpers > breeders) | 2.27 (187) | **0.02** | 0.00 ± 0.29 | 0.01 (187) | 0.99 |
| Status × increase | 0.46 ± 0.71 | 0.65 (187) | 0.51 | 0.32 ± 0.29 | 1.10 (187) | 0.27 |
| Sex × status | 0.46 ± 1.01 | 0.46 (58) | 0.64 | 0.31 ± 0.39 | 0.81 (58) | 0.42 |

Variables included were (1) experimental manipulation (enlarged or reduced relative to controls); (2) sex (male or female), (3) status (breeder or helper), and all two-way interactions. Direction of difference listed for significant effects. Decrease = experimental reduction in brood size; increase = experimental enlargement of brood size. BF, breeder females; BF, breeder males; BF, helper females; HM, helper males. Boldface values significant at $P < 0.05$.

(83%), usually in the expected direction (in six of 10 cases for males and eight of 10 for females).

## Discussion

All categories of acorn woodpeckers, regardless of the sex or status, exhibited at least some flexibility in the amount of parental care they provided to nestlings, significantly adjusting their feeding rate to the number of nestlings present on a day-by-day basis. Furthermore, all birds within the same category tended to respond similarly, at least among cobreeders. As a consequence, birds generally maintained about the same per-nestling feeding rate when brood size was altered, except that the decrease was not proportionate to brood size when it was reduced, resulting in increased per-nestling feeding rates under this scenario.

This latter result involved a significant difference between birds of different status, with breeders reducing their feeding rate when brood size was decreased significantly more so than helpers. That is, helpers exhibited less flexibility in their feeding behavior than did breeders. This finding could potentially indicate that helpers are less accurate at judging the needs of nestlings than breeders or that coercion on the part of breeders forces helpers to maintain their former feeding rate even when brood size, and thus need, is reduced. In any case, the direction of the difference in helper behavior was surprising. Helpers increased their feeding rate when brood size was increased but continued to provision at the original rate when brood size was decreased rather than using the extra time and energy to engage in alternative activities such as searching for reproductive vacancies (Koenig & Walters 2011). Thus, our results are not consistent with the hypothesis that helpers exhibit a fixed feeding strategy, nor that they are unwilling or unable to provide additional care when brood need increases. An additional possibility is that helpers reduced the amount of food fed to nestlings during each visit rather than the number of visits, but we found no evidence that mean bolus size changed across experimental treatments, thus failing to support this hypothesis.

Prior experimental results have generally not found significant differences in the feeding behavior of breeders and helpers, including studies of Arabian babblers (Wright 1998; Wright & Dingemanse 1999), bell miners (McDonald et al. 2009), superb fairy-wrens (MacGregor & Cockburn 2002), and analyses of compensatory feeding in our population of acorn woodpeckers (Koenig & Walters 2012). Surprisingly, studies of helpers in cooperative breeders have yet to find evidence that their chick-feeding behavior is in any way less cooperative than that of breeders, despite the fact that in most cases helpers appear to gain much lower fitness benefits from provisioning behavior (given that they are feeding non-descendant relatives) than do breeders (Dickinson & Hatchwell 2004). In the case of acorn woodpeckers, provisioning of nests appears to be a joint venture to which birds in a group generally all contribute, as found previously in several other aspects of their behavior including acorn storage, granary attendance and maintenance, and defense against both intraspecific and interspecific intruders (Mumme & de Queiroz 1985; Koenig et al. 2008).

This conclusion does not, however, imply that such contributions by different categories of birds are equal. Breeder females (BF), for example, feed more frequently than breeder males (BM) and breeders in general feed nestlings at over twice the rate of helpers (Koenig & Walters 2012; see also Table 1), while among helpers there are significant age effects with older helpers feeding more than second-year birds (Koenig & Walters 2011). Nor are the fitness consequences of provisioning behavior the same for all categories of birds in all years. Helper males, for example, have a much greater effect on reproductive success than helper females (HF), and their effect increases significantly with the size of the prior year's acorn crop (Koenig et al. 2011).

Moreover, although the majority of birds in a group contribute to provisioning of nestlings, such cooperation is clearly not observed in all acorn woodpecker activities. For example, they exhibit dramatic within-group competition over reproductive opportunities among both cobreeding males (Mumme et al. 1983a) and joint-nesting females (Mumme et al. 1983b; Koenig et al. 1995a). Understanding the conditions resulting in mutually beneficial cooperation rather than competition and conflict is clearly key to understanding the ecological basis for many of the more striking behaviors observed in social animals, including cooperatively breeding birds.

As is the case in most other systems that have been studied previously, feeding rates of acorn woodpeckers are adjusted largely, if not entirely, to the needs of the brood, as indicated here by brood size, rather than vice versa – that is, rather than feeding rates being fixed and thus potentially determining brood size through brood reduction. Apparently, birds in this population are typically not feeding as many young as they can, at least over the short term and within the range of brood sizes included in this study. Such flexibility renders the relatively high frequency of brood reduction observed in this population – nearly 60% of nests suffer at least some brood reduction as a result of apparent starvation, mostly during the early nestling stage when food demands are relatively small (Stanback 1991) – especially perplexing.

Finally, our results are consistent with the hypothesis that indirect fitness benefits play a key role in helping-at-the-nest in this species to the extent that patterns of provisioning behavior are generally the same (or in the direction of contributing more, rather than less, to provisioning activities) regardless of whether birds are relatively certain to have contributed genetically to the brood (as is the case for BFs), may have contributed genetically to the brood (as is the case for cobreeder males), or did not contribute genetically to the brood (as is the case for non-breeding helpers). That is, chick-feeding rules in acorn woodpeckers are generally similar regardless of whether the fitness benefits are direct, as is true for the successful breeders, or indirect, as is true for all other group members, including both helpers (Koenig & Walters 2011) and a substantial fraction of cobreeder males, among which reproductive skew is generally quite high (Haydock & Koenig 2002, 2003).

Although the indirect fitness benefits of feeding offspring by helpers in this species appears to be paramount (Koenig & Walters 2011), helpers may also gain direct fitness benefits as well through such mechanisms as 'group augmentation' (Kokko et al. 2001), forming associations with young in the nest, enhancing dominance or status, securing group membership ('pay-to-stay'; Mulder & Langmore 1993), or by gaining skills that enhance their future reproductive success (the 'skills' hypothesis), several of which also predict that helpers will exhibit similar chick-feeding rules as do breeders (Wright 1998). Such direct fitness benefits are apparently important in at least one cooperatively breeding species, the bell miner, where unrelated male helpers respond the same as genetic fathers to experimental manipulation of brood need (McDonald et al. 2009). Thus, although results from this study, as well as work on Arabian babblers (Wright 1998; Wright & Dingemanse 1999), are consistent with the hypothesis that kin-selected benefits are particularly important to helpers, the relative value of direct fitness benefits to the patterns of chick-feeding exhibited by helpers in cooperative breeders remains to be determined.

## Acknowledgements

We thank all the field assistants who conducted nest watches at the experimental nests included in this study and both the Museum of Vertebrate Zoology (UC Berkeley) and Hastings Reservation for logistical support. We also thank Janis Dickinson and the reviewers for comments and the National Science Foundation for support, most recently through grant IOS-0918944.

## Literature Cited

Baglione, V., Canestrari, D., Chiarati, E., Vera, R. & Marcos, J. M. 2010: Lazy group members are substitute helpers in carrion crows. Proc. Roy. Soc. Lond., Ser. B **277**, 3275—3282.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L. & Jordan, N. R. 2005: 'False feeding' and aggression in meerkat societies. Anim. Behav. **69**, 1273—1284.

Dickinson, J. L. & Hatchwell, B. J. 2004: Fitness consequences of helping. In: Ecology and Evolution of Cooperative Breeding in Birds. (Koenig, W. D. & Dickinson, J. L., eds). Cambridge Univ. Press, Cambridge, UK, pp. 48—66.

Dickinson, J. L., Haydock, J., Koenig, W. D., Stanback, M. T. & Pitelka, F. A. 1995: Genetic monogamy in single-male groups of acorn woodpeckers, *Melanerpes formicivorus*. Mol. Ecol. **4**, 765—769.

Drent, R. H. & Daan, S. 1980: The prudent parent: energetic adjustments in avian breeding. Ardea **68**, 225—252.

Harrison, F., Barta, Z., Cuthill, I. & Székely, T. 2009: How is sexual conflict over parental care resolved? A meta-analysis. J. Evol. Biol. **22**, 1800—1812.

Hatchwell, B. J. 1999: Investment strategies of breeders in avian cooperative breeding systems. Am. Nat. **154**, 205—219.

Hatchwell, B. J. & Davies, N. B. 1990: Provisioning of nestlings by dunnocks, *Prunella modularis*, in pairs and trios: compensation reactions by males and females. Behav. Ecol. Sociobiol. **27**, 199—209.

Haydock, J. & Koenig, W. D. 2002: Reproductive skew in the polygynandrous acorn woodpecker. Proc. Natl. Acad. Sci. USA **99**, 7178—7183.

Haydock, J. & Koenig, W. D. 2003: Patterns of reproductive skew in the polygynandrous acorn woodpecker. Am. Nat. **162**, 277—289.

Haydock, J., Koenig, W. D. & Stanback, M. T. 2001: Shared parentage and incest avoidance in the cooperatively breeding acorn woodpecker. Mol. Ecol. **10**, 1515—1525.

Heinsohn, R. G. 2004: Parental care, load-lightening, and costs. In: Ecology and Evolution of Cooperative Breeding in Birds (Koenig, W. D. & Dickinson, J. L., eds). Cambridge Univ. Press, Cambridge, UK, pp. 67—80.

Hinde, C. A. & Kilner, R. M. 2007: Negotiations within the family over the supply of parental care. Proc. Roy. Soc. Lond., Ser. B **274**, 53—60.

Johnsen, I., Erikstad, K. E. & Saether, B.-E. 1994: Regulation of parental investment in a long-lived seabird, the puffin *Fratercula arctica*: an experiment. Oikos **71**, 273—278.

Johnstone, R. A. 2011: Load lightening and negotiation over offspring care in cooperative breeders. Behav. Ecol. **22**, 436—444.

Johnstone, R. A. & Hinde, C. A. 2006: Negotiation over offspring care – how should parents respond to each other's efforts? Behav. Ecol. **17**, 818—827.

Kilner, R. M., Noble, D. G. & Davies, N. B. 1999: Signals of need in parent-offspring communication and their exploitation by the common cuckoo. Nature **397**, 667—672.

Koenig, W. D. & Mumme, R. L. 1987: Population Ecology of the Cooperatively Breeding Acorn Woodpecker. Princeton Univ. Press, Princeton.

Koenig, W. D. & Walters, E. L. 2011: Age-related provisioning behaviour in the cooperatively breeding acorn woodpecker: testing the skills and the pay-to-stay hypotheses. Anim. Behav. **82**, 437—444.

Koenig, W. D. & Walters, E. L. 2012: Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker. Behav. Ecol. **23**, 181—190.

Koenig, W. D., Mumme, R. L., Stanback, M. T. & Pitelka, F. A. 1995a: Patterns and consequences of egg destruction among joint-nesting acorn woodpeckers. Anim. Behav. **50**, 607—621.

Koenig, W. D., Stacey, P. B., Stanback, M. T. & Mumme, R. L. 1995b: Acorn woodpecker (*Melanerpes formicivorus*). In: Birds of North America (Poole, A. & Gill, F., eds). Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC, pp. 1—24.

Koenig, W. D., McEntee, J. P. & Walters, E. L. 2008: Acorn harvesting by acorn woodpeckers: annual variation and comparison with genetic estimates. Evol. Ecol. Res. **10**, 811—822.

Koenig, W. D., Walters, E. L. & Haydock, J. 2011: Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. Am. Nat. **178**, 145—158.

Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001: The evolution of cooperative breeding through group augmentation. Proc. Roy. Soc. Lond., Ser. B **268**, 187—196.

Komdeur, J., Wiersma, P. & Magrath, M. J. L. 2002: Paternal care and male mate-attraction effort in the European starling is adjusted to clutch size. Proc. Roy. Soc. Lond., Ser. B **269**, 1253—1261.

Legge, S. 2000: Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. Anim. Behav. **59**, 1009—1018.

MacColl, A. D. C. & Hatchwell, B. J. 2003: Sharing of caring: nestling provisioning behaviour of long-tailed tit, *Aegithalos caudatus*, parents and helpers. Anim. Behav. **66**, 955—964.

MacGregor, N. A. & Cockburn, A. 2002: Sex differences in parental response to begging nestling in superb fairy-wrens. Anim. Behav. **63**, 923—932.

Magrath, M. J. L., Janson, J., Komdeur, J., Elgar, M. A. & Mulder, R. A. 2007: Provisioning adjustments by male and female fairy martins to short-term manipulations of brood size. Behaviour **144**, 1119—1132.

McDonald, P. G., Kazem, A. J. N. & Wright, J. 2007: A critical analysis of 'false-feeding' behavior in a cooperatively breeding bird: disturbance effects, satiated nestlings or deception? Behav. Ecol. Sociobiol. **61**, 1623—1635.

McDonald, P. G., Kazem, A. J. N. & Wright, J. 2009: Cooperative provisioning dynamics: fathers and unrelated helpers show similar responses to manipulations of begging. Anim. Behav. **77**, 369—376.

Mulder, R. A. & Langmore, N. E. 1993: Dominant males punish helpers for temporary defection in superb fairy-wrens. Anim. Behav. **45**, 830—833.

Mumme, R. L. & de Queiroz, A. 1985: Individual contributions to cooperative behaviour in the acorn woodpecker: effects of reproductive status, sex, and group size. Behaviour **95**, 290—312.

Mumme, R. L., Koenig, W. D. & Pitelka, F. A. 1983a: Mate guarding in the acorn woodpecker: within-group reproductive competition in a cooperative breeder. Anim. Behav. **31**, 1094—1106.

Mumme, R. L., Koenig, W. D. & Pitelka, F. A. 1983b: Reproductive competition in the communal acorn woodpecker: sisters destroy each other's eggs. Nature **306**, 583—584.

R Development Core Team 2011: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org.

Sæther, B.-E., Andersen, R. & Pedersen, H. C. 1993: Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the Antarctic petrel *Thalassoica antarctica*. Behav. Ecol. Sociobiol. **33**, 147—150.

Stanback, M. T. 1991: Causes and consequences of nestling size variation in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*). PhD thesis, Univ. of California, Berkeley, CA.

Stearns, S. C. 1989: Trade-offs in life-history evolution. Funct. Ecol. **3**, 259—268.

Williams, G. C. 1966: Natural selection, the costs of reproduction and a refinement of Lack's principle. Am. Nat. **100**, 687—690.

Winkler, D. W. 1987: A general model for parental care. Am. Nat. **130**, 526—543.

Wright, J. 1998: Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behav. Ecol. Sociobiol. **42**, 423—429.

Wright, J. & Cuthill, I. 1990: Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. Behav. Ecol. **1**, 116—124.

Wright, J. & Dingemanse, N. J. 1999: Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. Anim. Behav. **58**, 345—350.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1:** Summary of the experiments performed to investigate the effects of brood size on feed rates.

## Appendix

Summary of the experiments performed to investigate the effects of brood size on feed rates. Group composition lists the number of breeder males (BM), breeder females (BF), helper males (HM), and helper females (HF) observed feeding at the nest during the experiment. Day 1 – Day 5 lists the number of young added to (+) or removed from (-)the original brood size during that day's watch; 0 = control days

| Group | First watch date | Last egg date | Group composition | | | | Brood size | Age (day 1) | Day 1 | Day 2 | Day 3 | Day 4 | Day 5 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | BM | BF | HM | HF | | | | | | | |
| *1985* | | | | | | | | | | | | | |
| Fanny Arnold | 3 May | 11 April | 2 | 1 | 0 | 0 | 3 | 11 | 0 | +2 | 0 | -2 | 0 |
| R1 (1st nest) | 11 May | 22 April | 1 | 2 | 2 | 0 | 4 | 8 | 0 | -2 | 0 | — | — |
| Finch | 12 May | 23 April | 3 | 1 | 0 | 0 | 3 | 8 | +2 | 0 | -2 | — | — |
| Lambert | 16 May | 14 April | 1 | 1 | 1 | 1 | 5 | 21 | 0 | -2 | 0 | — | — |
| UA2 | 16 May | 10 April | 1 | 1 | 0 | 1 | 3 | 25 | 0 | +2 | +2 | 0 | — |
| 1800 | 28 May | 1 May | 3 | 3 | 0 | 0 | 3 | 16 | 0 | +2 | 0 | -2 | 0 |
| Plaque Annex | 28 May | 1 May | 2 | 1 | 0 | 0 | 4 | 16 | 0 | -2 | 0 | +2 | 0 |
| R1 (2nd nest) | 20 June | 29 May | 1 | 2 | 3 | 2 | 2 | 11 | 0 | +1 | 0 | — | — |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *2011* | | | | | | | | | | | | | | |
| RE10 | 16 May | 14 April | 6 | 1 | 1 | 1 | 4 | 20 | 0 | -2 | +2 | 0 | — |
| Bradley | 25 May | 24 April | 1 | 1 | 1 | 5 | 4 | 19 | 0 | -2 | +1 | 0 | — |
| Horsetail | 25 May | 26 April | 1 | 4 | 2 | 1 | 3 | 17 | 0 | +2 | -1 | 0 | — |
| Low Haystack | 29 May | 30 April | 3 | 2 | 1 | 2 | 3 | 17 | 0 | -1 | +1 | 0 | — |
| Mike | 8 June | 9 May | 3 | 1 | 0 | 2 | 1 | 18 | 0 | +2 | 0 | — | — |
| Soto Springs | 8 June | 8 May | 1 | 2 | 1 | 1 | 5 | 19 | 0 | -2 | 0 | — | — |