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RESEARCH ARTICLE

Load Lightening in the Cooperatively Breeding Acorn Woodpecker Depends on the Analysis

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Received: 9 March 2026 | **Revised:** 2 June 2026 | **Accepted:** 9 June 2026

ABSTRACT

Despite empirical and experimental work in a variety of taxa, a general understanding of investment strategies in cooperative breeders has proven difficult. Analysis of provisioning patterns in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*) reveals that whether birds reduce their investment when assisted by other individuals depends on the analytical approach, including the type of data used as an index of effort and the time span over which it is measured. Estimated by group composition over the course of a complete nesting effort, provisioning is compensatory, with birds reducing their feeding rates in larger groups. In contrast, when measured by the provisioning effort of other group members on a short-term, individual watch basis, provisioning is additive, with birds matching the feeding rates of other group members. Both the time frame over which patterns of parental and parental-like care are made and the type of data used need to be considered to understand investment strategies by individuals in social groups.

1 | Introduction

Load lightening and compensatory feeding are dynamic measures of the response cooperative breeders make to aid provided by other group members, conferring significant fitness benefits to individuals when receiving aid from helpers (Brown 1978; Crick 1992; Heinsohn 2004; Downing et al. 2021). Consider provisioning in a cooperative breeder that consists of a pair with or without a helper (Figure 1; only one of the breeders is illustrated). An indirect consequence of adding a helper to the group is that the breeder may feed less; this is "load lightening" whereby the breeder no longer needs to provision as much as when it did not have a helper (Figure 1a,b). Conversely, an indirect consequence of a helper disappearing or leaving a group is that the breeder is likely to feed more; this is "compensatory care" whereby the breeder makes up for some of the provisioning lost when the helper left (Figure 1c,d). If the breeder continues to feed at the same rate after gaining the aid of a helper, provisioning is "additive," resulting in increased total provisioning rate (Figure 1e). Alternatively, if the breeder reduces its provisioning to the same extent of a helper that joins the group, provisioning is "compensatory;" that is, the total feeding rate remains unchanged (Figure 1f). If the breeder reduces its provisioning (i.e., exhibits load lightening), but by less than the helper adds, provisioning is partly compensatory (or, alternatively, "partly additive"). This latter situation can, of course, be reversed; if help is lost, the breeder may exhibit compensatory feeding but not enough to fully make up for the loss. Additive and compensatory effects are thus not mutually exclusive (Hatchwell and Russell 1996; Kingma et al. 2010).

Note that "compensatory" can be used both as the opposite of "additive" (as in Figure 1e vs. Figure 1f) and as the flip side of "load lightening" (as in Figure 1b vs. Figure 1d). In the latter context, "compensatory care" and "load lightening" are interchangeable, referring in general to the ways individuals alter their provisioning based on the effort of other group members.

The degree to which provisioning is additive or compensatory depends on costs and benefits and is highly variable even in

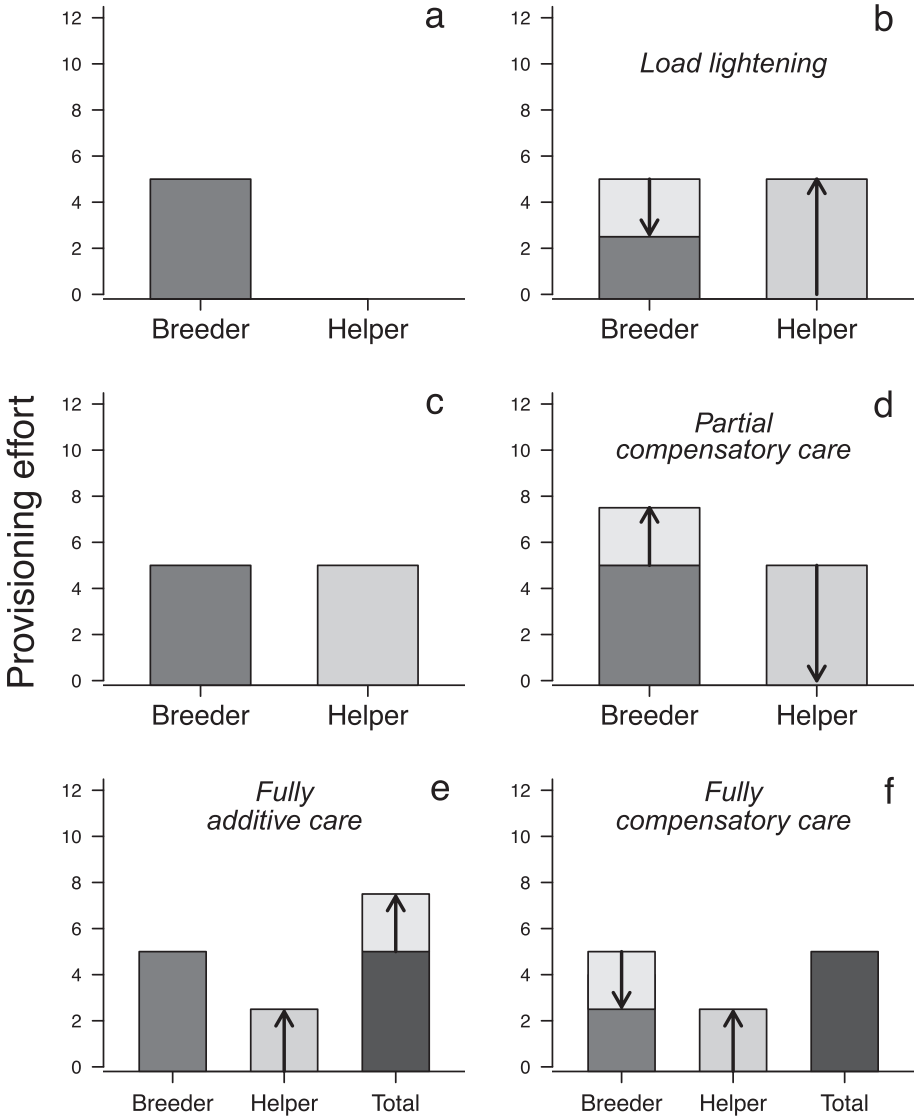

FIGURE 1 | (a, b) The breeder, initially without a helper (a), reduces its provisioning effort (exhibits load lightening) when a helper joins the group (b). (c, d) The breeder, initially aided by a helper (c), increases its provisioning effort (exhibits compensatory care partially making up for the lost provisioning of the helper) when the helper is no longer present (d). (e) Fully additive care. When the breeder is joined by a helper, the breeder continues to provision at the same rate resulting in the total provisioning effort increasing by the amount added by the helper. (f) Fully compensatory care. When the breeder is joined by a helper, the breeder reduces its provisioning rate such that the total provisioning effort remains the same.

relatively simple biparental care systems. Overall, however, the mean response to reduced partner effort is partially compensatory, in line with game-theoretical models of parental care (Harrison et al. 2009). The situation in cooperative breeders, where caregivers may include nonbreeding helpers, more than two breeding individuals, or both, adds additional complexity. It is therefore unsurprising that analyses of cooperative breeders have yielded variable results including partially compensatory, fully compensatory, additive, and even "super" additive care whereby breeders increased their feeding rate when they had helpers (Hatchwell and Russell 1996; Valencia et al. 2006; Liebl et al. 2016; Espinosa-Colín et al. 2026). A comparative analysis of 27 species by Hatchwell (1999) attempted to make sense of this variability, predicting that provisioning should be additive when nestling starvation is frequent and compensatory when starvation is rare.

Compensatory care and load lightening can be analyzed in two ways. First is in relation to group size or composition. In cooperative breeders, analyses based on group composition typically involve quantifying the provisioning rates of breeders in groups with and without helpers or in groups with different numbers of helpers over the course of a breeding effort. This observational approach has typically been used in empirical studies (van Boheemen et al. 2019), including one of our own (Koenig and Walters 2012a). In analyses involving group composition, the explanatory variable is usually the presence or number of helpers.

A second way compensatory care and load lightening can be analyzed is by what we refer to as "observed provisioning." In these analyses, the explanatory variable is the provisioning rate of the helper(s) rather than the number of helpers.

The observed provisioning approach has often been used in experimental studies focusing on short-term, individual effort expended over the course of one or a few days. The variety of modifications that have been performed are extensive and often ingenious (Harrison et al. 2009). For example, Liebl et al. (2016) found fully additive care following the temporary removal of helpers in chestnut-crowned babblers (*Pomatostomus ruficeps*), and Baglione et al. (2010) reported compensation by carrion crow (*Corvus corone*) helpers that had previously contributed little ("lazy helpers") when the provisioning of helpers that had previously fed a lot in the same group was impaired. Other studies have investigated short-term changes in observed provisioning when specific individuals were provided with extra food (Wright and Dingemanse 1999), the number of nestlings was altered (Koenig and Walters 2012b), or apparent brood demand was modified using playbacks of chick begging (Wright 1998; Hinde and Kilner 2007).

Note that the provisioning rate of an individual bird of the focal sex/status category is the response variable in both types of analyses. Their key difference, as already mentioned, is the explanatory variable, which is typically group composition or group size in the first set of analyses and the provisioning rate of other group members in the second. It is also noteworthy that group size and composition are generally assumed to remain constant during a nesting effort, whereas provisioning rates potentially differ from day to day or even from watch to watch.

Although examining effort of group members based on group composition versus observed provisioning over the course of one or a few days may yield similar results, there is no a priori reason for them to do so. One reason they might differ is that provisioning rates at any one time may be determined by short-term environmental or social factors that are of lesser importance over the course of an entire breeding attempt (Hinde 2006; Meade et al. 2011).

The acorn woodpecker (*Melanerpes formicivorus*) is a cooperative breeder that lives in family groups of 2–15 birds partitioned among 1–8 cobreeding males and 1–3 joint-nesting females along with nonbreeding helpers of both sexes (Koenig and Mumme 1987; Koenig et al. 2020). Helpers are offspring of the breeders, and cobreeders are close relatives—siblings, parents, and their offspring, or a combination of both. There is no extra-group parentage (Dickinson et al. 1995; Haydock et al. 2001). Thus, all birds within a group are close relatives, except that the cobreeding males are unrelated to the joint-nesting females with whom they mate (Koenig et al. 1998), except in rare cases of incest (Haydock et al. 2001).

A previous analysis of brooding and provisioning effort in acorn woodpeckers detected significant compensatory care among all four sex/status categories of birds (breeder males, breeder females, helper males, and helper females) as group size increased but compensatory care did not differ among the categories (Koenig and Walters 2012a). This countered predictions that compensatory responses should be inversely related to reproductive effort, which, based on the fitness consequences of helpers and the demography of the population, was expected to be greater for breeders than helpers, greater for breeder females than breeder males, and greater for helper males than helper females. That study did, however, find evidence that compensatory care by both breeder males and females was significantly less during the first week of the nestling period, when most starvation occurs, and increased later in the nestling period, providing support for Hatchwell's (1999) prediction that compensatory care should be reduced when nestling starvation is common.

In a parallel experimental study, we investigated how birds altered their provisioning rate when brood size was temporarily manipulated to investigate the short-term flexibility of observed provisioning behavior. We found that breeders increased and decreased their provisioning congruent with the direction of brood size manipulation, whereas helpers were less flexible, increasing their feeding rate when brood size was increased but not decreasing it when brood size was decreased (Koenig and Walters 2012b).

Here, we compare patterns of compensatory care for acorn woodpeckers analyzed based on group composition vs. observed provisioning rate. Analyses based on group composition add 13 years of data to our previous study. Analyses focusing on observed provisioning rates have not been conducted previously.

2 | Methods

This work is part of a long-term study of a completely color-banded population of acorn woodpeckers at Hastings Reservation, central coastal California, started in 1972 (MacRoberts and MacRoberts 1976; Koenig and Mumme 1987; Koenig and Walters 2012a). Analyses are based on 3-h nest watches conducted by observers in blinds using spotting scopes to record feeding visits; watches were generally spread out over representative intervals during the approximately 31-day nestling period (Weathers et al. 1990). In total, we analyzed data from 4587 watches at 1375 spring nests between 1979 and 2023. Analyses involved a total of 13,351 h of observation and 167,454 feeding visits. All analyses were conducted in R 4.4.2 (R Core Team 2024).

Quantifying compensatory care based on group composition generally followed the methods described in Koenig and Walters (2012a). Provisioning visits by unidentified individuals within each watch, amounting to < 5% of visits, were partitioned among birds that were identified during watches proportionate to the number of feeding visits recorded for each known individual.

To illustrate how provisioning changes with group size, we used two mixed-effects models [procedure *lme* in package *nlme* (Pinheiro and Bates 2025)], one with *total provisioning rate* and the other with *provisioning rate per bird* as the response variables. Explanatory variables were those known from prior analyses (Koenig and Walters 2012a) to affect feeding rates, including *nestling age* (linear and quadratic terms), *brood size, maximum daily temperature, time of day*, and the interaction of *nestling age* × *brood size*. In both models, *nest ID* within *group ID* was included as a random factor. In all cases, brood size was determined by direct nest examination and nestling age was either based on the known hatching date or estimated from growth data summarized in Weathers et al. (1990).

To quantify load lightening at the group level, four models were tested, one for each of the two sexes and the two status categories (breeders and helpers). In each model, the response variable was the feeding rate of an individual bird (i) of the focal sex/status category during a feeding watch, while the explanatory variables were the number of birds of each sex/status category in i's group and the variables known to affect feeding rates listed above. The number of birds of each sex/status category was scaled (mean = 0; standard deviation = 1) to allow comparison of effect sizes. *Bird ID* within *nest ID* within *territory* was included as a random effect in all four models. Load lightening was quantified by the effect sizes of the sex/status explanatory variables, with negative values indicating a decrease in the feeding rate by birds of the focal category as the number of birds in the relevant sex/status category increased.

Estimating compensatory care based on observed provisioning is more difficult. First, there is a potential confound between the provisioning rate of a bird and the total provisioning rate of all birds of the same sex and status. To avoid this issue, we did not include the total feeding rate of birds of sex/status j in the model for which the dependent variable was the feeding rate of birds of sex/status j. The second problem is the change in overall feeding rate as nestlings grow. To minimize this confound, we limited analyses to watches conducted when nestlings were 18–25 days old, during which time the overall feeding rate is relatively constant (Figure 2a). *Nestling age*, *brood size*, and *maximum daily temperature* were included as explanatory variables to account for potential confounding variables, including those of nestling growth. *Bird ID* within *nest ID* within *territory* was again included as a random effect. Other variables and interactions included in the group composition models described above were not statistically significant in any of the models examining observed provisioning rate and were excluded from the analyses.

As an additional test of compensatory care based on observed provisioning we considered only nests at which two or more watches were conducted when nestlings were 18–25 days old and computed the Pearson correlation between the total observed provisioning rate of breeders versus the total provisioning rate of helpers over the watches to ask the question: when birds of one sex/status category fed more, did birds of other sex/status categories feed less? We then summed the number of positive and negative correlations and used a binomial test to examine whether the direction of feeding rates between sex/status categories was inversely related more frequently than expected by chance, indicating compensatory care, or positively related more frequently than expected, indicating additive care.

3 | Results

Total provisioning rates increased linearly with group size (Table S1; a separate model in which the quadratic effect of total group size was added was not statistically significant) while provisioning rates per bird decreased nonlinearly with increasing group size (Table S1). Thus, provisioning is both (partially) additive and (partially) compensatory based on group composition. Representative provisioning rates for groups of different size are illustrated for nests containing three nestlings in Figure 2b.

Evidence for load lightening based on group composition was statistically significant for all sex/status categories, although not with respect to all categories of birds (Figure 3; Table S2).

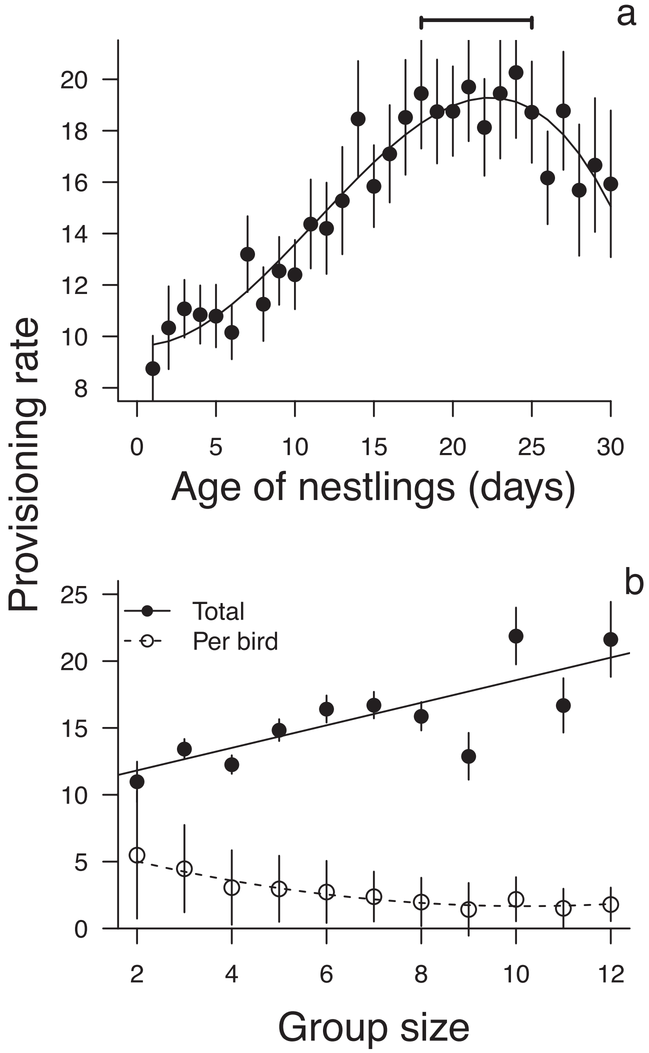

FIGURE 2 | (a) Mean (±95% confidence interval [CI]) total provisioning rate (feeds h^{-1}) plotted against the age of nestlings. Bar indicates the range of dates during which the overall feeding rate is essentially constant (Pearson correlation between age of nestlings 18–25 days old and mean daily feeds per hour = 0.13, $t = 0.31$, df = 6, $p = 0.76$). Fitted line based on cubic regression of daily means ($F_{3,26} = 96.9$, $p < 0.0001$). (b) Mean (±95% confidence interval [CI]) total provisioning rate (feeds h^{-1}) total and per bird plotted against total group size for groups with 3 nestlings.

Interestingly, the feeding rates of breeders of both sexes were significantly affected by the number of breeders of the same sex (Figure 3a,b), while the feeding rates of helpers of both sexes were significantly affected by the number of helpers of the opposite sex but not the same sex (Figure 3c,d).

In contrast, load lightening was not detected in models based on observed provisioning rates (Figure 4; Table S3). In all comparisons, provisioning rates were positively related to those of other group members, indicating additive rather than compensatory care. In general, breeders increased their feeding rates significantly in parallel with the feeding rates of other breeders (Figure 4a,b) while helpers increased their feeding rates in parallel with all other sex/status categories of birds (Figure 4c,d). Provisioning by different categories of birds matched each other rather than exhibiting compensation.

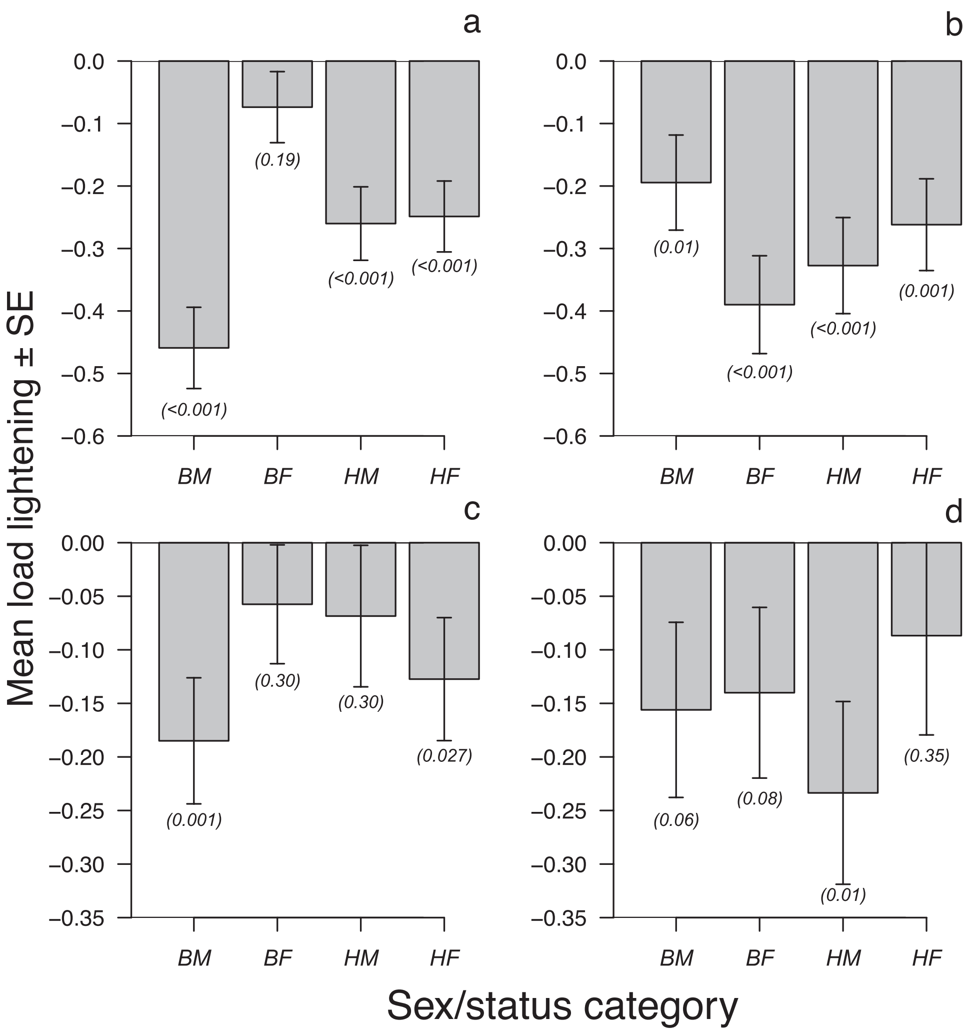

FIGURE 3 | Standardized effect sizes (±SE) of linear mixed-effects models testing the overall provisioning effort of a focal individual of a given sex/status category depending on group composition (the number of birds in the group of each sex/status category). (a) Breeder males (BM); (b) breeder females (BF); (c) helper males (HM); (d) helper females (HF). Sample sizes are 8616 (BM); 5603 (BF); 5109 (HM); and 3362 (HF) individuals. *p*-values listed for each sex/status category in parentheses. Model details in Table S1.

We also compared the provisioning rates of different sex/status categories at nests at which two or more watches were conducted while nestlings were 18–25 days old. In three of the four comparisons, the provisioning rates of different categories of birds were positively correlated more often than expected by chance (Table 1).

4 | Discussion

In cooperatively breeding species, load lightening is often thought to be an important benefit to breeders of having helpers and may also benefit the helpers themselves by enhancing their future indirect fitness (Heinsohn 2004; Meade et al. 2010; Downing et al. 2021). Prior studies have often focused on the effects of relatedness on load lightening and compensatory care, but the relationship between provisioning and nestling survival and differences between the sexes and how different family members respond to one another are also important (Hatchwell 1999; Johnstone 2011). Additional issues affecting these phenomena include the potential for helpers to substitute other behaviors for provisioning (Carranza et al. 2008; Kushnick 2012), variability in helper behavior (Baglione et al. 2010), differences vis-à-vis the risk of nestling starvation at different stages of the nesting cycle (Hatchwell 1999), food availability (van Boheemen et al. 2019), differences in the amount of food in each feeding bout, and even meteorological conditions (Nomano et al. 2019). Given these complexities, it is unsurprising that a general theory of parental investment in cooperative breeders has remained elusive.

Here, we focus on a relatively neglected dimension by which load lightening can be measured: the provisioning rate of helpers and other group members rather than group size. Analyzing observed provisioning rather than group size or group composition focuses attention on short-term adjustments in effort and considers differences among group members that are otherwise potentially obscured.

Prior analyses of provisioning by acorn woodpeckers found that both breeders and helpers benefited by load lightening as a consequence of increasing group size (Koenig and Walters 2012a), while experimental manipulation of brood size suggested that

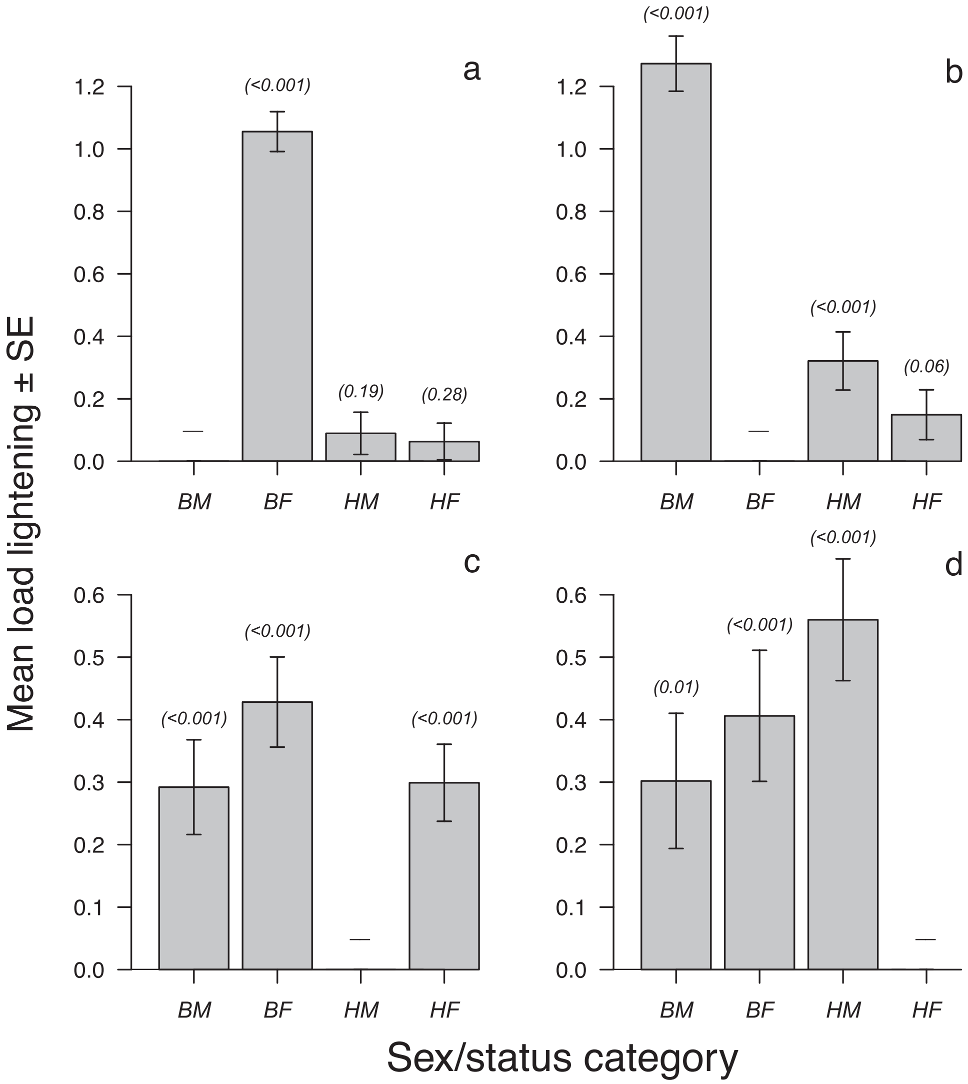

FIGURE 4 | Standardized effect sizes (±SE) of linear mixed-effects models testing the provisioning effort of a focal individual of a given sex/status category on the total provisioning rates by other sex/status categories of birds on a watch-by-watch basis. (a) Breeder males (BM); (b) breeder females (BF); (c) helper males (HM); (d) helper females (HF). *p*-values listed for each sex/status category in parentheses. Only includes watches made when nestlings were 18–25 days old. Model details in Table S2.

TABLE 1 | The mean Pearson correlation (*r*) between the total provisioning rates of breeders and helpers at nests across multiple watches using only nests with 18–25 day-old nestlings.

	Provisioning by breeder males				Provisioning by breeder females			
	Mean *r*	***N* positive**	***N* negative**	**Binomial *p***	**Mean *r***	***N* positive**	***N* negative**	**Binomial *p***
Provisioning by helper males	0.24	66	31	0.005	0.12	64	46	0.10
Provisioning by helper females	0.32	64	46	< 0.001	0.19	60	39	0.044

Note: Also listed are the number of *r* values that were positive and negative and the *p*-value of the difference based on binomial tests.

breeders were more flexible in their provisioning patterns than helpers (Koenig and Walters 2012b). With respect to the number of birds of each sex/status category, analyses conducted here yield comparable results: all sex/status categories of birds exhibited load lightening, with slight differences in which categories appear to have the greatest effects. For example, the provisioning rate of breeder males was strongly reduced (i.e., compensatory) in groups with additional cobreeding males but did not change relative to the number of joint-nesting females (Figure 3a), whereas the provisioning of breeder females was most strongly reduced in groups with an additional joint-nesting female (Figure 3b). Although helpers also fed less in larger groups, the effects were generally smaller than that of breeders, with helper males most strongly affected by the number of breeder males (Figure 3c) and helper females most strongly affected by the number of helper males (Figure 3d). The drivers of such differences remain to be investigated.

Our main goal, however, was to compare compensatory care when analyzed by group composition compared to observed provisioning behavior. Using provisioning rate is challenging because of changing brood energetic requirements during the nesting cycle. In acorn woodpeckers, as in many species, brood need increases as nestlings grow until they achieve adult body mass, after which growth plateaus or decreases slightly (Weathers et al. 1990). We attempted to circumvent this issue by restricting analyses to the short, eight-day period during which feeding rates are nearly the same, but even then the age of nestlings was an important predictor in some models (Table S3). Although investigations of load lightening focusing on observed provisioning rates have often involved experiments temporarily altering feeding by helpers or apparent brood need over a period of a few days, such studies may minimize but do not necessarily eliminate the confounding effects of nestling growth on provisioning patterns.

In our case, analyses based on short-term provisioning rates yielded results opposite those obtained using group composition. Based on provisioning, feeding rates of birds of different sex/status categories were positively rather than negatively related, indicating that group members matched each other's efforts. Provisioning by helpers of both sexes, for example, was positively correlated with the provisioning rates of all other sex/status categories of birds (Figure 4c,d). Provisioning by breeders was significantly positively correlated with the provisioning rate of breeders of the opposite sex but generally not with the provisioning rate of helpers, although mean correlations were all positive (Figure 4a,b). Quantified using observed provisioning rate, feeding rates were additive rather than compensatory.

Findings based on observed provisioning rates during short-term manipulations may help explain differences in provisioning based on group composition. In acorn woodpeckers, for example, brood size manipulations indicated that helpers exhibit less flexibility in provisioning than breeders (Koenig and Walters 2012b). This suggests that provisioning by helpers is likely to be less sensitive to group composition and exhibit less load lightening than breeders, which generally matches the results found here (Figure 3). Why birds are differentially sensitive to the sex and status of other group members remains to be determined.

More importantly, these results demonstrate that analyses based on observed provisioning data, even if based on experimental manipulations, should be interpreted cautiously. For example, Liebl et al. (2016) reported fully additive care in natural and experimentally reduced groups of chestnut-crowned babblers based on short-term (<2 days) provisioning rates. Their results do not, however, necessarily demonstrate that load lightening would not be detected if measured over the course of a nesting effort based on differences in group size. Provisioning effort may be additive on a short-term, provisioning basis but compensatory based on group composition.

Why are observed provisioning rates over the short term positively correlated, even though they are sensitive to group size and composition over the course of a nesting effort? Possibilities include differences in food availability or decisions made over short time scales (Hinde 2006). Birds feed less overall when living in larger groups, but there is more food on some days than others. When food is abundant, all birds can find more food and increase their provisioning rates. Alternatively, the amount of information available to birds about brood value or need likely varies, resulting in a matching response in provisioning among birds when information is low and partial compensation when information is high (Johnstone and Hinde 2006; Meade et al. 2011).

In summary, we show that load lightening by acorn woodpeckers differs depending on whether it is measured based on relatively long-term group composition or short-term observed provisioning behavior. Comparisons of patterns of parental and parental-like care need to be conducted using comparable analyses. Only then will it be possible to understand patterns of investment by individuals in both cooperatively breeding and non-cooperatively breeding groups.

Author Contributions

Eric L. Walters: funding acquisition, writing – review and editing, investigation, supervision. **Walter D. Koenig:** conceptualization, methodology, funding acquisition, project administration, writing – original draft, writing – review and editing, data curation, investigation, supervision.

Acknowledgments

We thank for reviewers for their comments and Ron Mumme, Mark Stanback, Joey Haydock, and the 250+ field and laboratory assistants who assisted with the project over the years gathering much of the data on which this study is based.

Funding

This work is supported by National Science Foundation grants IOS-1455881 to W.D.K. and IOS-1455900 to E.L.W.

Ethics Statement

This study was conducted under the auspices of the University of California, Berkeley's Animal Care and Use Committee, Cornell University's Institutional Animal Care and Use Committee (Protocol number 2008-0185), and Old Dominion University's Institutional Animal Care and Use Committee (most recently by protocol 24-010).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at https://datadryad.org, Reference number 10.5061/dryad.4j0zpc8t3.

References

Baglione, V., D. Canestrari, E. Chiarati, R. Vera, and J. M. Marcos. 2010. "Lazy Group Members Are Substitute Helpers in Carrion Crows." *Proceedings of the Royal Society B* 277: 3275–3282.

Brown, J. L. 1978. "Avian Communal Breeding Systems." *Annual Review of Ecology and Systematics* 9: 123–155.

Carranza, J., V. Polo, J. Valencia, C. Mateos, and C. de La Cruz. 2008. "How Should Breeders React When Aided by Helpers?" *Animal Behaviour* 75: 1535–1542.

Crick, H. Q. P. 1992. "Load-Lightening in Cooperatively Breeding Birds and the Cost of Reproduction." *Ibis* 134: 56–61.

Dickinson, J. L., J. Haydock, W. D. Koenig, M. T. Stanback, and F. A. Pitelka. 1995. "Genetic Monogamy in Single-Male Groups of Acorn Woodpeckers, *Melanerpes formicivorus*." *Molecular Ecology* 4: 765–769.

Downing, P. A., A. S. Griffin, and C. K. Cornwallis. 2021. "Hard-Working Helpers Contribute to Long Breeder Lifespans in Cooperative Birds." *Philosophical Transactions of the Royal Society B* 376: 20190742.

Espinosa-Colín, M., C. de la Cruz, and J. S. Gutiérrez. 2026. "Experimental Evidence for Flexibility in Provisioning Behavior in a Cooperatively Breeding Bird." *Behavioral Ecology* 37: arag021.

Harrison, F., Z. Barta, I. Cuthill, and T. Székely. 2009. "How Is Sexual Conflict Over Parental Care Resolved: A Meta-Analysis." *Journal of Evolutionary Biology* 22: 1800–1812.

Hatchwell, B. J. 1999. "Investment Strategies of Breeders in Avian Cooperative Breeding Systems." *American Naturalist* 154: 205–219.

Hatchwell, B. J., and A. F. Russell. 1996. "Provisioning Rules in Cooperatively Breeding Long-Tailed Tits *Aegithalos caudatus*: An Experimental Study." *Proceedings of the Royal Society B* 263: 83–88.

Haydock, J., W. D. Koenig, and M. T. Stanback. 2001. "Shared Parentage and Incest Avoidance in the Cooperatively Breeding Acorn Woodpecker." *Molecular Ecology* 10: 1515–1525.

Heinsohn, R. G. 2004. "Parental Care, Load-Lightening, and Costs." In *Ecology and Evolution of Cooperative Breeding in Birds*, edited by W. D. Koenig and J. L. Dickinson, 67–80. Cambridge University Press.

Hinde, C. A. 2006. "Negotiation Over Offspring Care?—A Positive Response to Partner-Provisioning Rate in Great Tits." *Behavioral Ecology* 17: 6–12.

Hinde, C. A., and R. M. Kilner. 2007. "Negotiations Within the Family Over the Supply of Parental Care." *Proceedings of the Royal Society B* 274: 53–60.

Johnstone, R. A. 2011. "Load Lightening and Negotiation Over Offspring Care in Cooperative Breeders." *Behavioral Ecology* 22: 436–444.

Johnstone, R. A., and C. A. Hinde. 2006. "Negotiation Over Offspring Care—How Should Parents Respond to Each Others Efforts?" *Behavioral Ecology* 17: 818–827.

Kingma, S. A., M. L. Hall, E. Arriero, and A. Peters. 2010. "Multiple Benefits of Cooperative Breeding in Purple-Crowned Fairy-Wrens: A Consequence of Fidelity?" *Journal of Animal Ecology* 79: 757–768.

Koenig, W. D., J. Haydock, and M. T. Stanback. 1998. "Reproductive Roles in the Cooperatively Breeding Acorn Woodpecker: Incest Avoidance Versus Reproductive Competition." *American Naturalist* 151: 243–255.

Koenig, W. D., and R. L. Mumme. 1987. *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton University Press.

Koenig, W. D., and E. L. Walters. 2012a. "Brooding, Provisioning, and Compensatory Care in the Cooperatively Breeding Acorn Woodpecker." *Behavioral Ecology* 23: 181–190.

Koenig, W. D., and E. L. Walters. 2012b. "An Experimental Study of Chick Provisioning in the Cooperatively Breeding Acorn Woodpecker." *Ethology* 118: 566–574.

Koenig, W. D., E. L. Walters, P. B. Stacey, M. T. Stanback, and R. L. Mumme. 2020. "Acorn Woodpecker (*Melanerpes formicivorus*), Version 1.0." In *Birds of the World*, edited by P. G. Rodewald and B. K. Keeney. Cornell Lab of Ornithology.

Kushnick, G. 2012. "Helper Effects on Breeder Allocations to Direct Care." *American Journal of Human Biology* 24: 545–550.

Liebl, A. L., F. Y. Nomano, L. E. Browning, and A. F. Russell. 2016. "Experimental Evidence for Fully Additive Care Among Male Carers in the Cooperatively Breeding Chestnut-Crowned Babbler." *Animal Behaviour* 115: 47–53.

MacRoberts, M. H., and B. R. MacRoberts. 1976. "Social Organization and Behavior of the Acorn Woodpecker in Central Coastal California." *Ornithological Monographs* 21: 1–115.

Meade, J., K.-B. Nam, A. P. Beckerman, and B. J. Hatchwell. 2010. "Consequences of 'Load-Lightening' for Future Indirect Fitness Gains by Helpers in a Cooperatively Breeding Bird." *Journal of Animal Ecology* 79: 529–537.

Meade, J., K.-B. Nam, J.-W. Lee, and B. J. Hatchwell. 2011. "An Experimental Test of the Information Model for Negatiation of Biparental Care." *PLoS One* 6, no. 5: e19684.

Nomano, F. Y., J. L. Savage, L. E. Browning, S. C. Griffith, and A. F. Russell. 2019. "Breeding Phenology and Meteorological Conditions Affect Carer Provisioning Rates and Group-Level Coordination in Cooperative Chestnut-Crowned Babblers." *Frontiers in Ecology and Evolution* 7: 423.

Pinheiro, J., and D. Bates. 2025. "nlme: Linear and Nonlinear Mixed Effects Models." https://CRAN.R-project.org/package=nlme.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Valencia, J., C. De La Cruz, J. Carranza, and C. Mateos. 2006. "Parents Increase Their Parental Effort When Aided by Helpers in a Cooperatively Breeding Bird." *Animal Behaviour* 71: 1021–1028.

van Boheemen, L. A., M. Hammers, S. A. Kingma, et al. 2019. "Compensatory and Additive Helper Effects in the Cooperatively Breeding Seychelles Warbler (*Acrocephalus sechellensis*)." *Ecology and Evolution* 9: 2986–2995.

Weathers, W. W., W. D. Koenig, and M. T. Stanback. 1990. "Breeding Energetics and Thermal Ecology of the Acorn Woodpecker in Central Coastal California." *Condor* 92: 341–359.

Wright, J. 1998. "Helpers-At-The-Nest Have the Same Provisioning Rule as Parents: Experimental Evidence From Play-Backs of Chick Begging." *Behavioral Ecology and Sociobiology* 42: 423–429.

Wright, J., and N. J. Dingemanse. 1999. "Parents and Helpers Compensate for Experimental Changes in the Provisioning Effort of Others in the Arabian Babbler." *Animal Behaviour* 58: 345–350.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Results of mixed-effects models of the total and per bird provisioning rate at nests. *Nest ID* within *group ID* included as a random effect. df = 2619; $N = 1225$ nests. The quadratic group size term was not statistically significant in the total provisioning rate model and was not included. Plots of total and per bird provisioning rates on group size for nests containing 3 young are illustrated in Figure 2b. SE, standard error. **Table S2:** Effect size (±SE) of linear mixed-effects models (procedure *lme*) testing the provisioning effort of a focal individual of a given sex/status category on group composition (the number of birds in the group of each sex/status category). Each sample is the provisioning rate of a bird during a 3-h watch. In all models, *bird ID* within *nest ID* within *territory* was included as a random factor and the N birds of each sex/status category were scaled to render the estimate values comparable. "Age" = age of nestlings. Sample size: 4587 watches at 1375 nests. Results vis-à-vis group composition are plotted in Figure 2. **Table S3:** Effect size (±SE) of linear mixed-effects models (procedure *lme*) testing the provisioning effort of a focal individual of a given sex/status category on the observed provisioning rates of each sex/status category of birds (excluding that of the focal individual). Only includes watches made when nestlings were 18–25 days old. Each sample is the provisioning behavior of a bird during a 3-h watch. In all models, *bird ID* within *nest ID* within *territory* was included as a random factor and the provisioning rates of each sex/status category were scaled to render the estimate values comparable. "Age" = age of nestlings. Results vis-à-vis group composition are plotted in Figure 3.