



Provisioning patterns in the cooperatively breeding acorn woodpecker: does feeding behaviour serve as a signal?



Walter D. Koenig^{a, b, *}, Eric L. Walters^c

^a Cornell Lab of Ornithology, Ithaca, NY, U.S.A.

^b Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, U.S.A.

^c Department of Biological Sciences, Old Dominion University, Norfolk, VA, U.S.A.

ARTICLE INFO

Article history:

Received 19 February 2016

Initial acceptance 7 April 2016

Final acceptance 10 May 2016

MS number A16-00144

Keywords:

cooperative breeding

pay-to-stay

provisioning behaviour

signalling

social prestige

Acorn woodpeckers, *Melanerpes formicivorus*, are cooperative breeders in which social groups consist of both nonbreeding helpers at the nest (offspring from prior reproductive attempts) and cobreeders of one or both sexes (usually siblings or a parent and his/her offspring). Regardless of composition, groups generally have one nest at a time at which all individuals participate in provisioning offspring. We tested the hypothesis that provisioning behaviour serves a signalling function used to gain social advantages within groups by enhancing dominance or social prestige, or by reducing the likelihood of being expelled from the group ('pay-to-stay'). We found that birds adjusted their provisioning behaviour based on the activities of other group members by clumping their visits and by alternating their visits with other group members, thus synchronizing and coordinating provisioning within groups. Despite this evidence that acorn woodpeckers respond to the provisioning behaviour of other group members, analyses of feeding rates and patterns of overlap revealed no support for the hypothesis that provisioning functions as a signal to other group members in any of three ways: breeder males signalling to breeder females to increase their probability of mating; helpers signalling to other helpers to enhance their dominance or social prestige; or helpers signalling to breeders to reduce the probability that they will be considered 'lazy' and be evicted from the group. Our results add to previous studies that have thus far failed to support a signalling function for provisioning behaviour in avian cooperative breeders.

© 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Provisioning of nestlings is a key behaviour of altricial birds, consuming a large fraction of the time and energy budgets of provisioners and having a correspondingly critical effect on parental fitness (Sæther, 1994). It is consequently unsurprising that provisioners pay close attention to the needs of nestlings, as evidenced by both their response to nestling begging signals (Kilner & Johnstone, 1997; Leonard & Horn, 2001) and their response to changes in the feeding rate of other caregivers (Harrison, Barta, Cuthill, & Székely, 2009; Hinde & Kilner, 2007; Johnstone & Hinde, 2006). The latter is particularly important and complex in cooperative breeders, where nestlings are fed by multiple individuals whose fitness benefits and thus optimal patterns of investment in the brood often differ considerably (Hatchwell, 1999; Koenig & Walters, 2012; Raihani, Nelson-Flower, Moyes, Brown-ing, & Ridley, 2010).

Despite apparently focusing on different aspects of nesting, however, the response of caregivers to both nestling begging signals and feeding behaviour of other caregivers often comes down to the question of how provisioners respond to nestling need, the difference being that the former addresses this issue directly while the latter addresses it indirectly. That is, the results of studies investigating changes in feeding behaviour when provisioning activities of caregivers are altered are typically interpreted as being due to concomitant changes in nestling need. When an individual reduces its feeding rate, it results in increased nestling need and compensatory feeding by other group members; conversely, increases in feeding rate by an individual lead to decreased nestling need and 'load lightening' or reduced provisioning by other group members (Canestrari, Marcos, & Baglione, 2007; Hatchwell, 1999; Koenig & Walters, 2012; Meade, Nam, Beckerman, & Hatchwell, 2010). In contrast, there have been relatively fewer studies investigating how or whether caregivers respond to the feeding behaviour of other provisioners independent of their effect on nestling need (Liebl, Browning, & Russell, 2016).

* Correspondence and present address: W. Koenig, Hastings Reservation, 38601 E. Carmel Valley Rd, Carmel Valley, CA 93924, U.S.A.

E-mail address: wdk4@cornell.edu (W. D. Koenig).

Why, however, should caregivers be influenced by other provisioners? Two possibilities proposed in the context of group living include the ‘social prestige’ hypothesis (Zahavi, 1977, 1990, 1995), which proposes that individuals are able to enhance their dominance or social standing within the group by means of their provisioning behaviour, and the ‘pay-to-stay’ hypothesis, which proposes that increased provisioning by subordinates reduces the likelihood of dominant birds expelling them from the group (Gaston, 1978; Kokko, Johnstone, & Wright, 2002; Wright & McDonald, 2016).

Here we test these two hypotheses, focusing on provisioning behaviour in the cooperatively breeding acorn woodpecker, *Melanerpes formicivorus*, a species with both a complex polygynandrous mating system and nonbreeding helpers at the nest (Koenig, Walters, & Haydock, 2016). The general question we address is: do birds alter their behaviour in response to other group members when provisioning nestlings, and if so, is it in a way that indicates they are either attempting to gain some social advantage or otherwise exhibiting their behaviour to other group members so as to decrease the likelihood of dominant birds expelling them from the group? Both these possibilities assume that provisioning behaviour serves a signalling function, which has been supported in at least one social species (the sociable weaver, *Philetairus socius*; Doutrelant & Covas, 2007), although not in others (McDonald, Kazem, Clarke, & Wright, 2008; Nomano et al., 2013, 2015; Wright & McDonald, 2016).

We first looked for evidence that birds adjusted their provisioning behaviour based on nest visits by other group members. To do so, we considered several dimensions of such adjustment (Fig. 1). Nonrandomness in provisioning behaviour along at least one of the three dimensions would indicate that birds are responding to the provisioning behaviour of other individuals in the group, a finding that is necessary in order to demonstrate that provisioning may be used by birds to enhance their social prestige or reduce their probability of being evicted from the group.

Sensitivity to the provisioning behaviour of other group members is not, however, sufficient to demonstrate that such behaviour is being used to enhance social prestige. To unambiguously test whether provisioning serves a signalling function, we conducted two additional sets of analyses. First, we compared the feeding rates of birds as a function of whether they were or were not potentially in competition with other birds of the same sex and status in the group. The prediction of these tests is that if birds are trying to increase their status or prestige by advertising their quality with their provisioning behaviour, they should feed more frequently when they are in groups containing other birds of the same sex and status than when they are not.

Second, we quantified the extent that provisioning visits by different individuals overlapped in time more than expected by chance. There are at least three reasons why such behaviour might be advantageous. First, helpers might be attempting to advertise

(A) Runs more common than expected (time sharing)

		Clumping pattern			
		1. Individuals and groups		3. Neither individuals nor groups	
Bird 1					
Bird 2					
Bird 3					
Group					
Synchronized?		Yes			No
Coordinated?		Yes			Yes

(B) Runs random

		Clumping pattern		
		1. Individuals and groups	2. Groups but not individuals	3. Neither individuals nor groups
Bird 1				
Bird 2				
Bird 3				
Group				
Synchronized?		Yes	Yes	No
Coordinated?		No	No	No

(C) Runs less common than expected (alternate feeding)

		Clumping pattern		
		1. Individuals and groups	2. Groups but not individuals	3. Neither individuals nor groups
Bird 1				
Bird 2				
Bird 3				
Group				
Synchronized?		Yes	Yes	No
Coordinated?		Yes	Yes	Yes

Figure 1. A visualization of the potential patterns of clumping and runs of uninterrupted feeding visits by individuals including whether the pattern is considered to exhibit synchronization or coordination among individuals. Numbers and letters refer to rows and columns, respectively, in Table 1. In each case, time moves horizontally and a vertical line represents a feeding visit by one of three individuals or all group members combined.

their provisioning to breeders so as to reduce the probability that the latter will expel them from the group; this is the 'pay-to-stay' hypothesis. Second, breeder males might be advertising their quality to breeder females, in this case by increasing their effort as perceived by breeder females, thereby potentially increasing the probability of siring young in subsequent breeding attempts. Third, helpers might be advertising their quality to other same-sex helpers, thus increasing their dominance and potentially gaining advantages later when they potentially become cobreeders. All three of these possibilities assume a social prestige function for provisioning behaviour in which birds are advertising their quality or propensity to cooperate for some future reproductive advantage.

The 'pay-to-stay' hypothesis has been tested previously in the cooperatively breeding bell miner, *Manorina melanophrys*, where experimental removal of breeders failed to alter the provisioning behaviour of helpers, thus failing to support the hypothesis that feeding behaviour by helpers serves as a signal to gain social advantage within groups (McDonald et al., 2008). In the acorn woodpecker, helpers that fed more were indeed likely to remain helpers longer and were more likely to inherit their natal territory than broodmates that fed less, predictions consistent with pay-to-stay (Koenig & Walters, 2011). This result, however, appeared to be a consequence of differences in dispersal behaviour rather than prior feeding history.

Several other attempts have failed to identify pay-to-stay in cooperative breeders (Hatchwell, 2016; McDonald et al., 2008; Mitchell, 2003; Santema & Clutton-Brock, 2012), but there is strong evidence for this mechanism playing a role in driving helping behaviour in the cooperatively breeding cichlid fish, *Neolamprologus pulcher* (Taborsky, 2016) and experimental evidence that has been interpreted as supporting this mechanism in the superb fairy-wren, *Malurus cyaneus* (Mulder & Langmore, 1993). Thus, additional examination of this hypothesis is clearly warranted.

METHODS

Study Site and Field Methodology

We studied a marked population of acorn woodpeckers at Hastings Reservation, central coastal California, U.S.A., between 1973 and 2015, during which time the population was continuously monitored (Koenig & Mumme, 1987). Analyses of feeding rates that did not require more detailed data on the timing of individual feeding visits were based on nest watches conducted between 1979 and 2015. Tests that required information on the timing of visits, including analyses of overlap, clumping and feeding intervals, were based on nest watches conducted during 1990–1998, 2001–2002 and 2004–2015, inclusive. For all watches, observers sat in blinds located away from active nests and recorded the identities of all birds engaged in feeding visits with the aid of a spotting scope (Koenig & Walters, 2012).

Watches varied in length, but were typically 3 h long. During each feeding visit, bird identity, time at which the bird arrived at the nest, time it entered the nest and time it left the nest were recorded and later transcribed into a computer file. A small percentage (1.4%) of feeding visits were made by birds that were not identified; these were included in the analyses when individual identity was not relevant to the analysis. The total data set for analyses involving the timing of feeding visits included 1713 watches lasting 4932 h at 555 different nests of 88 different social groups of birds and included a total of 56 345 feeding visits. A total of 269 breeder males, 221 breeder females, 298 helper males and 212 helper females were used in the analyses. For the analysis of

feeding rates, we included data from a total of 3405 nest watches lasting 9993 h at 1056 different nests.

The mean \pm SD feeding interval for individual birds was 12.6 ± 15.7 min ($N = 49\,403$ intervals), ranging from 11.1 ± 14.0 min for breeder females to 14.5 ± 18.6 min for helper males. For all four categories of birds, the distribution of feeding intervals followed an exponential decay function, with between 36.4% and 44.6% of feeding visit intervals being <5 min (Fig. 2).

Detecting and Interpreting Patterns of Provisioning Behaviour

Provisioning behaviour within groups is potentially adjustable along at least three dimensions: clumping of visits by groups of birds, clumping of visits by individual birds and the incidence of 'runs' of uninterrupted visits by the same bird. A visualization of the three dimensions is provided in Fig. 1 and summarized in Table 1.

We refer to runs of uninterrupted visits more common than expected (Table 1, column A) as 'time sharing,' since birds are temporally separating sets of feeding bouts. Runs less common than expected (Table 1, column C) are referred to as 'alternate feeding,' since in this case birds alternate their feeding visits with those of other birds in the group (Bebbington & Hatchwell, 2016; Johnstone et al., 2014). In either case, birds are coordinating their visits with other group members; this is not the case if the lengths of runs are random (Table 1, column B). Feeding visits may be clumped (multiple visits may occur within limited periods of time; Table 1, rows 1 and 2); if so, we refer to this as feeding bouts that are synchronized. It is also possible that feeding bouts by groups but not individuals are clumped (Table 1, row 2; this possibility does not exist if there is time sharing), but we consider the converse (individuals but not group visits are clumped) unlikely, and do not consider it further. Potential fitness benefits of synchronized and coordinated feeding visits include lower predation and thus increased survivorship due to reduced activity around the nest, as has been reported in the cooperatively breeding pied babbler, *Turdoides bicolor*, and long-tailed tit, *Aegithalos caudatus* (Bebbington & Hatchwell, 2016; Raihani et al., 2010), and reduced parental conflict over care, as proposed for great tits, *Parus major* (Johnstone et al., 2014).

To test for clumping of visits, we considered individuals and all group members combined; individuals were subdivided into one of four categories (breeder males, breeder females, helper males and helper females) based on their origin and prior history (Koenig, Mumme, & Pitelka, 1984). For each category of bird, we identified visits occurring at least 5 min after any prior provisioning visit of birds in the same category. We then counted visits by the individual or the group as a whole occurring within the next 5 min interval. For comparison with each such event, we randomly chose a time during the watch and counted feeding visits by the bird(s) in the target category during the subsequent 5 min. We then calculated the number of visits (0 to 3+) as the percentage greater or less than expected for each category of bird and tested the differences with chi-square tests. Clumping of visits was demonstrated by fewer values in the '0' and '1' categories and more in the '2' and '3+' visits within 5 min intervals. The 5 min criterion used in these analyses was based on the distribution of feeding visit intervals plotted in Fig. 2, but is none the less arbitrary. Parallel analyses using 10 min intervals did not alter the results, however.

To test for uninterrupted runs of visits by the same individual, we first determined the observed frequency of runs that were 1, 2, 3 or 4+ visits in length for individuals within each watch for each of the four categories of birds (breeder males, breeder females, helper males and helper females). The expected frequency was then determined for each watch by counting the total number of visits during the watch by the target bird and all other birds,

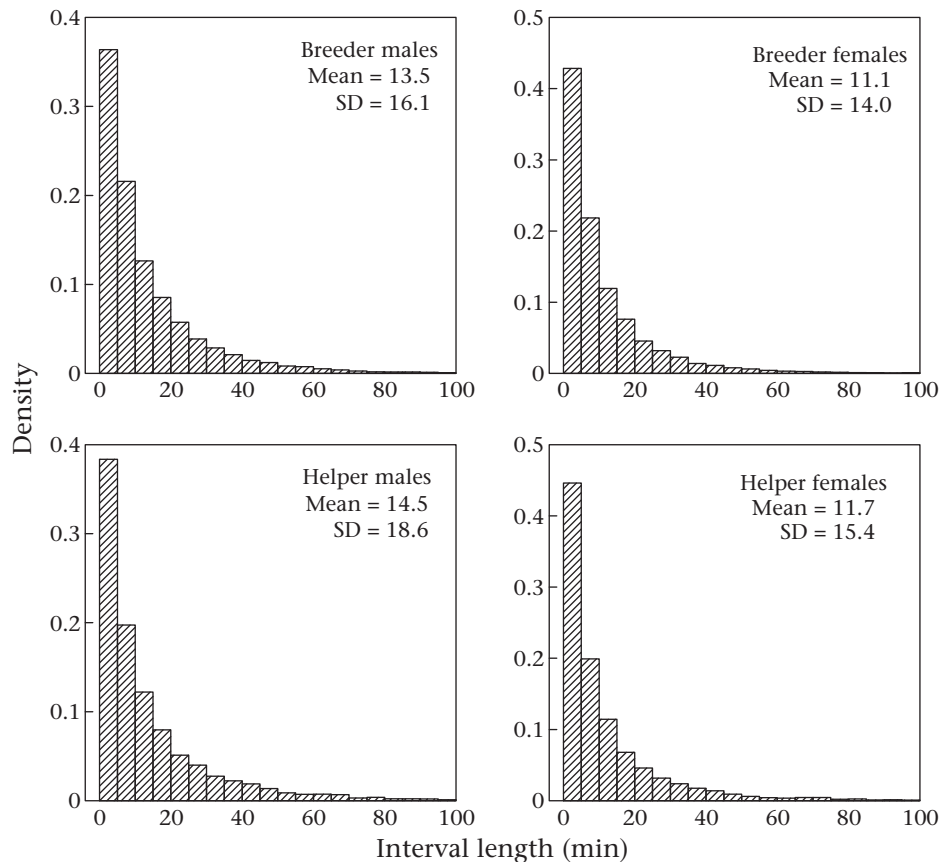


Figure 2. Distribution of feeding intervals for the four categories of birds. Values are binned into 5 min intervals, with the Y axis being the proportion of feeding intervals by individual birds that occurred within that time interval.

Table 1

Potential outcomes of the analyses and their interpretation

Clumping pattern	(A) Runs of uninterrupted visits more common than expected (time sharing)	(B) Runs random	(C) Runs of uninterrupted visits less common than expected (alternate feeding)
(1) Visits are clumped in time for both individuals and groups	Feeding bouts synchronized and coordinated	Feeding bouts synchronized but not coordinated	Feeding bouts synchronized and coordinated
(2) Visits are clumped in time for groups but not individuals	NA—	Feeding bouts synchronized but not coordinated	Feeding bouts synchronized and coordinated
(3) Visits are not clumped in time for either individuals or groups	Feeding bouts coordinated but not synchronized	Feeding bouts neither synchronized nor coordinated	Feeding bouts coordinated but not synchronized

NA: this combination was considered an incompatible outcome.

randomizing their order, and counting the runs for the target bird that emerged. Randomizations were performed 100 times and the observed number of runs was then compared to the expected frequency as determined by the mean number of runs of each length counted in the randomization trials. Differences were tested with chi-square tests.

All cases except the scenario in which runs are random and there is no clumping of feeding bouts by either individuals or groups (Table 1, cell B3) are consistent with the hypothesis that birds are responding to the provisioning behaviour of other individuals in the group and thus that provisioning may serve a signalling function. As mentioned earlier, however, these patterns do not prove that birds are signalling one another. For example, provisioning patterns involving greater clumping than expected, particularly at the level of groups (Table 1, rows 1 and 2), could emerge as a consequence of birds foraging together at the same

temporally variable food patches, or from other advantages of staying together and moving as a group, rather than because they are sensitive to each other's provisioning activities. Patterns that do not involve clumping of visits and that are more evenly distributed in time than expected by chance (Table 1, cells A3 and C3) are consistent with cooperation among caregivers resulting in optimizing interfeeding intervals and efficient feeding of young, since prior work has found that high feeding rates can reduce the mean retention time of digesta in nestling guts and reduce digestive efficiency (Budden & Wright, 2007; Karasov & Wright, 2002; Lepczyk, Caviades-Vidal, & Karasov, 1998). Such an outcome also potentially emerges from the scenario in which there is no clumping and run length is random (Table 1, cell B3), although in this case it is an emergent property of individual behaviour and not because birds are altering their behaviour in response to the provisioning behaviour of others in the group.

Adjustment of Feeding Rate and Overlap

We tested the hypothesis that birds adjusted their feeding rates so as to advertise their quality by means of linear mixed-effects models in which we included the number of birds in the target category in the group as an independent explanatory factor along with variables identified previously as being important to feeding rates in this population: number of nestlings in the nest at the time of the watch (brood size), number of young surviving to banding age, nestling age (both linear and quadratic terms), total group size, time of day the watch began (Pacific Standard Time), and maximum temperature on the day of the watch based on data from the Hastings Reservation weather station (Koenig & Walters, 2012). The three-way nested factor of 'bird ID' within 'nest' within 'territory' was included as a random factor.

We performed analyses testing two hypotheses: first, that breeder males increase their feeding rates in the presence of cobreeder males so as to advertise their quality to females, and second, that helpers increase their feeding rate in the presence of other helpers of the same sex in order to enhance their social prestige within same-sex coalitions. Reproductive skew between cobreeder males within nests is high, with the most successful male siring three times as many young as the next most successful male, thus setting the stage for more socially dominant cobreeder males to gain a considerable reproductive advantage (Haydock & Koenig, 2002). In contrast, joint-nesting females share maternity within nests equally (Haydock & Koenig, 2003) and thus we did not perform parallel tests with breeder females since we have no evidence that females are able to gain a reproductive advantage over their cobreeders as a result of increased social dominance.

We performed two sets of analyses for each of the two hypotheses using mixed-effects models (procedure 'lme' in library 'nlme'; Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2013). The first set controlled for group composition by including the number of birds in each of the four sex and status categories as explanatory factors; only results for the target category are reported. The second set restricted analyses to groups with a specific composition for birds other than those of the target category. For breeder males, we restricted analysis to groups with a single breeder female and no helpers; for helpers, we restricted analysis to groups with a single breeder of both sexes and no helpers of the opposite sex.

For analysis of overlaps, we first determined all cases in which a bird visiting the nest overlapped (within 5 s) with a bird already in or at the nest. Once an incidence of overlap was included, all birds involved in that event were excluded from further consideration, thus reducing pseudoreplication. (When two birds were recorded as being at the nest at the same time, the first bird recorded was assumed to be the bird in the nest and the second was assumed to be the bird arriving at the nest.) Because the analysis of overlaps required precise timing, we restricted tests to nests observed from 2007 onwards, years in which we transcribed nest watches using a computer program written specifically for this purpose. This limited analysis to 578 watches at 260 nests lasting a total of 1758 h, and yielded a total of 5111 overlap events.

To generate expected values, we then chose, for each overlap event, a bird of one of the four sex/status categories to be the 'expected' overlapping individual based on the proportion of visits made during the watch by the four categories of birds, excluding the bird already in the nest. For each category of bird, we then summed the observed number of overlaps by birds of each category over all watches and determined the expected number of overlaps for birds of each category based on the mean of 100 randomization trials. Differences were tested with chi-square tests and plotted as the percentage of overlap events observed for each sex/status category combination that was more or less than expected by chance.

Statistical analyses were conducted in R 3.0.3 (R Core Team, 2014).

Ethical Note

Birds originating within the study area were colour-banded as nestlings; immigrants were colour-banded by capturing birds at night in their roost cavities. In both cases, birds were returned to their territories as quickly as possible (usually within 1 h) or at dawn in order to minimize disturbance. Observations were made from blinds using spotting scopes so as to not alter natural patterns of provisioning behaviour. Procedures were approved by the Animal Care and Use Committees of the University of California, Berkeley (protocol R010–0412), Cornell University (protocol 2008–0185) and Old Dominion University (protocol 12–001).

RESULTS

All categories of birds, and all birds combined, clumped their feeding visits, in most cases significantly (Fig. 3). Generally this involved three or more visits within 5 min periods, the only exception being helper females, which most frequently fed only twice within 5 min periods. Visits were also clumped when considering all visits regardless of bird identity (Fig. 3, 'all birds').

In contrast, all categories of birds exhibited fewer uninterrupted runs of two or more visits in a row than expected by chance (Fig. 4). Thus, birds most closely exhibited the pattern shown in cell C1 in Table 1: visits were clumped in time for both individuals and groups whereas runs of uninterrupted visits were less common than expected by chance due to alternate feeding. Visit bouts were both synchronized and coordinated among group members.

These results are consistent with the hypothesis that birds are sensitive to the provisioning behaviour of other individuals in the group and adjust their feeding behaviour accordingly. We tested whether such behaviour was potentially directed towards other individuals of a particular sex or status, thereby serving a signalling function, in two ways. First, focusing on absolute feeding rates, we found that birds in all three categories fed less, not more, when other individuals of the same sex/status were present, although the differences were significant for breeder males and only for helper females in groups with a standardized composition (Table 2).

Second, we tested whether feeding was potentially directed towards other individuals by quantifying patterns of overlap at the nest (Fig. 5). When either a breeder male or a breeder female was at or in the nest, the only category of bird that overlapped more frequently than expected was other breeder females. There was no tendency for helpers of either sex to overlap with breeders at the nest more frequently than expected by chance. When helper males were at or in the nest, there was but a marginally significant difference in the tendency for birds of different categories to overlap with them, primarily due to a relatively high incidence of helper female, rather than helper male, overlap. Differences in overlap by different categories of birds when helper females were at or in the nest were not significant.

DISCUSSION

Our analyses indicated that acorn woodpeckers both synchronize and coordinate their feeding visits with other group members significantly more than expected by chance. Such a pattern is consistent with the hypothesis that provisioning is a signal used by at least some birds in the group to advertise either their quality or their propensity to provision to other group members, as predicted by the social prestige and pay-to-stay hypotheses. Analyses of feeding rates by breeder males and overlap between birds during

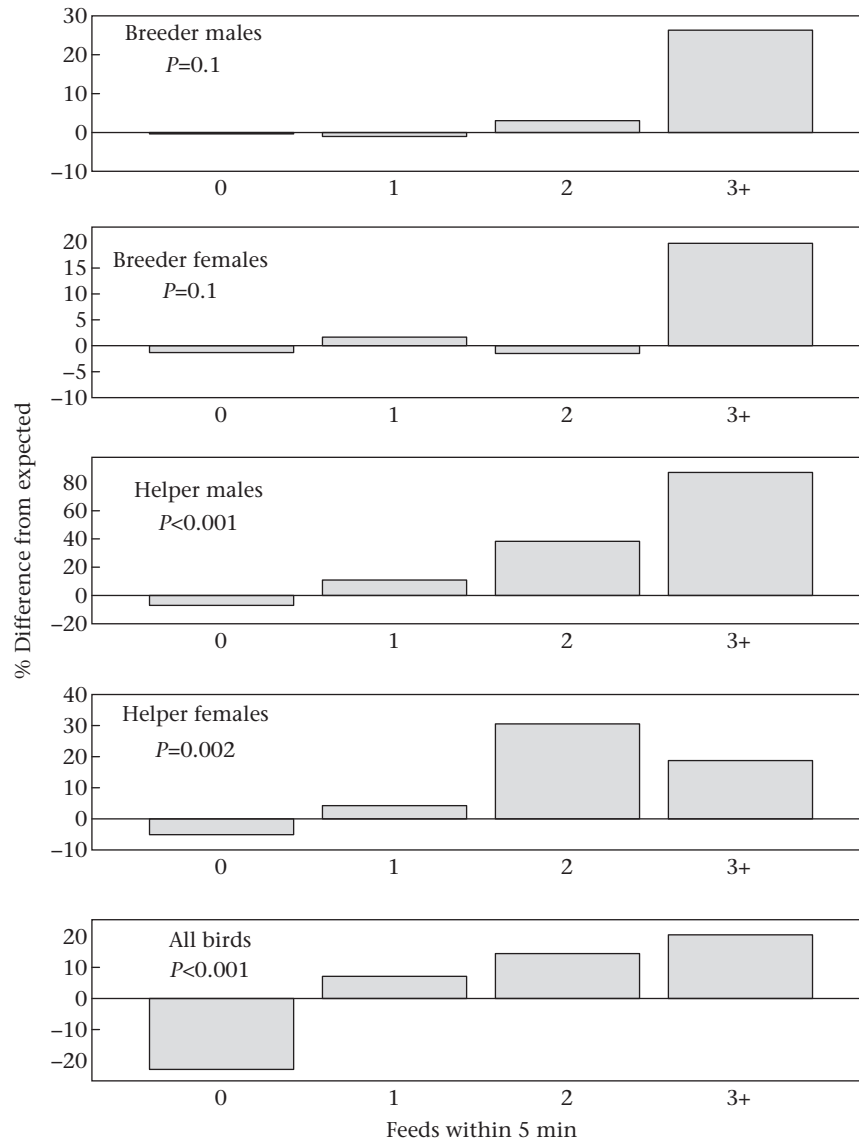


Figure 3. Clumping of feeding visits (number of feeding visits within 5 min of a feeding visit occurring at least 5 min after any other visit) by individual birds (breeder males, breeder females, helper males and helper females) and by all birds combined within groups. Plotted is the percentage difference from that expected by chance based on visits occurring at random during the watch (see text). Differences are tested with chi-square tests with $df = 3$; P values are listed. χ^2 values (category; N visits): 6.3 (breeder males; 14 375), 6.2 (breeder females; 12 433), 44.2 (helper males; 5159), 15.1 (helper females; 3867) and 202.7 (all birds combined; 17 816).

provisioning visits, however, failed to support either of these hypotheses. Three potential signalling functions were investigated.

Breeder Males Signalling Breeder Females (Social Prestige)

Two ways that provisioning behaviour might be used by breeder males to signal their quality to breeder females is by increasing their actual feeding rate and by increasing their perceived feeding rate by overlapping more frequently with breeder females when the latter are at or in the nest. Controlling for other factors, including composition of other sex/status categories, breeder males provisioned nestlings significantly less, not more, frequently when they were in competition with other cobreeders for the attention of breeder females (Table 2). In terms of overlap, the incidence of breeder males overlapping with breeder females when the latter were at or in the nest was not statistically different from chance (Fig. 5). We are aware of no prior tests of this hypothesis, which is only applicable to the small

proportion of cooperatively breeding species, such as the acorn woodpecker, in which cobreeding occurs regularly.

Helpers are Signalling to Other Helpers of the Same Sex (Social Prestige)

Helpers often form same-sex sibling coalitions that disperse together and eventually cobreed. Thus, helpers that signal their quality by provisioning more frequently or by overlapping more with other helpers of the same sex could potentially enhance their status or social prestige in a way that provides them with an advantage later in life by signalling their quality to same-sex siblings. Our analyses, however, indicated that helpers did not feed more frequently when living in groups with other helpers of the same sex. Similarly, in terms of overlap, helpers exhibited little tendency to overlap their provisioning with other helpers of the same sex more than expected by chance. Although not specifically tested, no evidence for synchronous provisioning visits by helpers

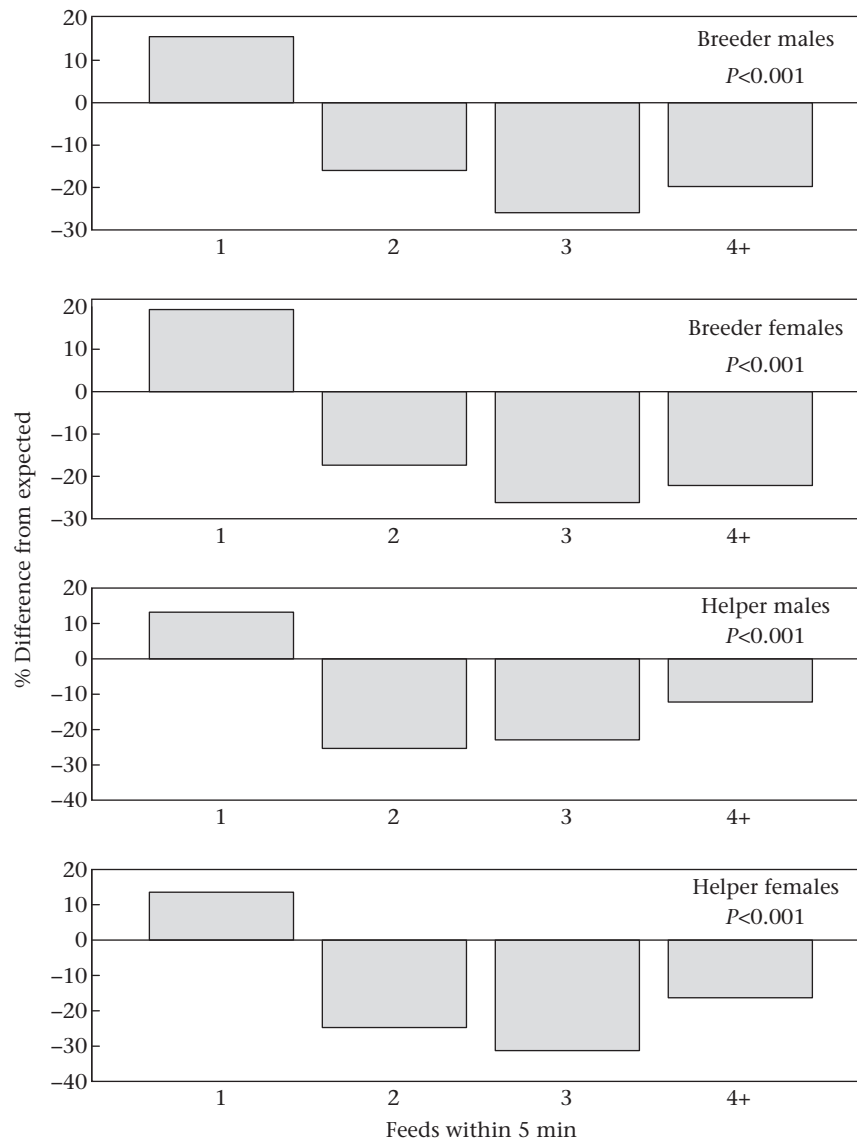


Figure 4. Runs of uninterrupted feeding visits by individual birds (breeder males, breeder females, helper males and helper females). Plotted is the percentage difference from that expected by chance based on randomization tests (see text). Differences are tested with chi-square tests with $df = 3$; P values are listed. χ^2 values (category; N visits): 178.7 (breeder males; 17246), 214.6 (breeder females; 15704), 59.0 (helper males; 5549) and 48.9 (helper females; 4158).

was reported in the chestnut-crowned babbler, *Pomatostomus ruficeps* (Nomano et al., 2015).

Helpers are Signalling to Breeders (Pay-to-Stay)

If provisioning by helpers is acting as a pay-to-stay mechanism, then helpers would be expected to overlap more frequently with breeders so as to ensure that the latter do not perceive them as being 'lazy' and evict them from the group. Our results indicated that helper males did not overlap more frequently than expected with either breeder males or breeder females, and that there was no significant difference overall in overlap by helper females across the four sex/status categories. Similarly, negative results testing this hypothesis were found for bell miners in an experimental study in which helpers failed to alter their provisioning behaviour when breeders (the presumptive audience) were temporarily removed (McDonald et al., 2008), and in a study of chestnut-crowned babblers, in which unrelated helpers were unresponsive, and exhibited no evidence

of advertising their provisioning behaviour, to dominant males (Nomano et al., 2015).

Provisioning Behaviour as a Signal

Our results fail to support the hypothesis that provisioning functions as a signal to other group members in any of the ways that we considered plausible, despite the emergence of detectable patterns in the feeding bouts of both individual birds and groups as a whole indicating that birds are sensitive to the provisioning activities of others in the group. Birds tended to clump their feeding visits, a finding that suggests either that birds are foraging in some coordinated manner or that they are paying attention to the provisioning activities of other birds so as to synchronize their feeding visits. This pattern runs counter to the hypothesis that birds are attempting to feed young in an efficient manner that is likely to maximize digestive efficiency (Karasov & Wright, 2002; Lepczyk, Caviedes-Vidal, & Karasov, 1998). Concomitantly, runs of uninterrupted visits were less common

Table 2

Results of mixed-effects models testing whether breeder males, helper males or helper females adjust their feeding rate depending on whether they are in the group (and thus competing) with other birds of the same category

Variable	Effect size (mean±SE)	df	t	P
Analyses including all four sex/status categories				
Breeder males	-0.36±0.05	926	-6.83	<0.001
Helper males	-0.02±0.04	2463	-0.49	0.62
Helper females	-0.08±0.09	376	-0.87	0.38
Analyses of groups with a standardized composition				
Breeder males	-0.50±0.11	153	-4.47	<0.001
Helper males	-0.15±0.12	34	-1.24	0.22
Helper females	-0.87±0.34	11	-2.53	0.03

Analyses controlled for group composition by including the number of birds in other sex/status categories as explanatory factors (top half) or by limiting analysis to groups with a standardized composition. The latter were: one breeder female and no helpers (for breeder males); one breeder of both sexes and no helpers of the opposite sex (for helper males and helper females). Although not listed, each of the six models included the number of young in the nest, the number of young banded, maximum temperature on the day of the watch, time of day and age of the nestlings (both linear and quadratic terms) as explanatory factors along with the number of breeder males or number of helpers of the listed sex. All analyses included the nested random factor 'bird ID' within 'nest' within 'group'.

than expected, suggesting that birds alternate their feeding visits, a pattern that has been detected in the socially monogamous great tit where it was proposed to be a mechanism of negotiation between parents reducing parental conflict over offspring care (Johnstone et al., 2014), and was found to be associated with increased reproductive success in the cooperatively breeding long-tailed tit, possibly due to reduced activity around the nest (Bebbington & Hatchwell, 2016).

None the less, neither synchronization nor alternation resulted in one category of birds overlapping significantly more at the nest than expected with another category of birds in any of the ways we predicted if provisioning were a signal that enhanced fitness. Similarly, neither breeder males nor helpers fed more frequently when in groups with other birds of the same sex/status category. Thus, although birds are apparently sensitive to what other group members are doing when they provision at nests, they do so indiscriminately, contrary to the predictions of either the social prestige or pay-to-stay hypothesis, both of which are predicated on the idea that provisioning is an opportunity for birds to advertise their quality or helpfulness to specific group members (Wright & McDonald, 2016).

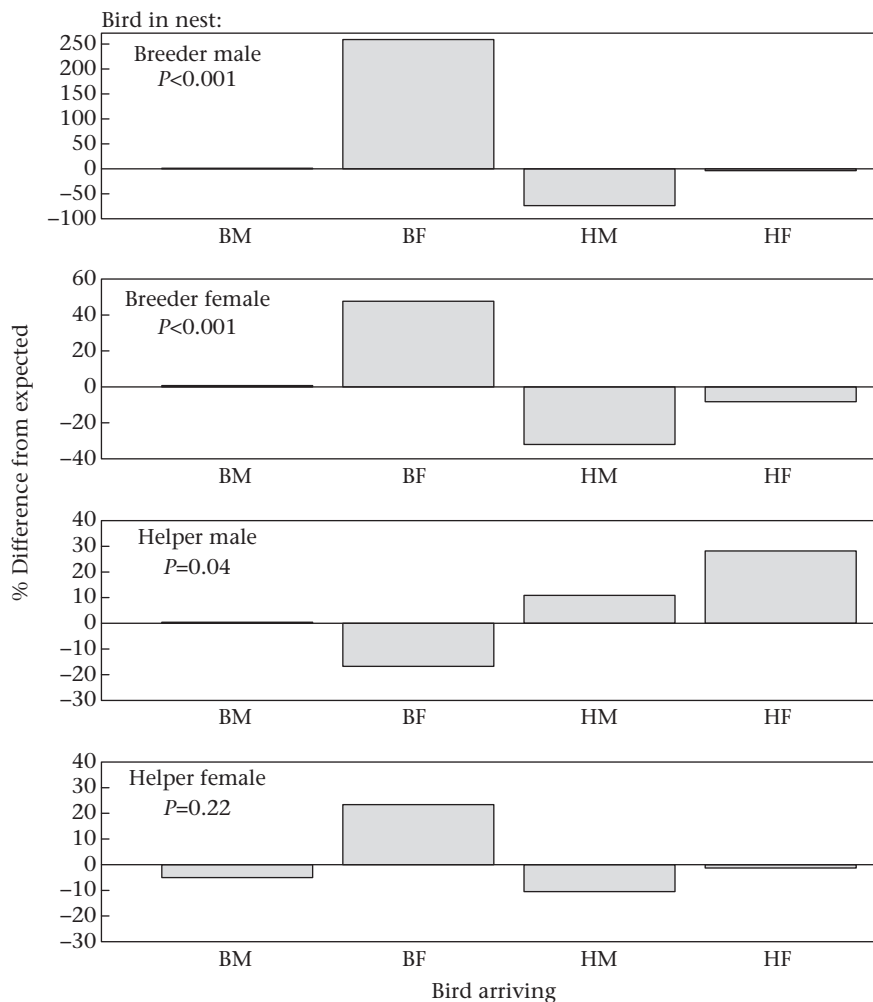


Figure 5. Overlap in visits during provisioning visits by individual birds of the four sex/status categories. Plotted is the percentage difference from that expected by chance for the proportion of times birds of the given category (BM = breeder males; BF = breeder females; HM = helper males; HF = helper females) arrived at the nest and overlapped with a bird already at or in the nest of the category listed. The expected values are generated from randomization trials based on the number of visits by birds in each category during watches (see text). Differences are tested with chi-square tests with $df = 3$; P values are listed. χ^2 values (category; N overlap events): 743.7 (breeder males; 2154), 40.5 (breeder females; 1594), 8.4 (helper males; 709) and 4.3 (helper females; 595). Note that the Y-axis scales are not the same across the four graphs.

These results add to previous studies that have failed to support the hypothesis that provisioning behaviour functions as a signal in cooperative breeders, including the bell miner (McDonald et al., 2008; Wright, 1997; Wright & McDonald, 2016), and several investigations of ‘false-feeding’ behaviour (Canestrari, Marcos, & Baglione, 2004; Clutton-Brock, Russell, Sharpe, & Jordan, 2005; McDonald et al., 2007; Wright, 1997), which was proposed as a deceptive strategy employed by helpers to enhance their social prestige at minimal cost in white-winged choughs, *Corcorax melanorhamphos* (Boland, Heinsohn, & Cockburn, 1997). The only exception to this generalization is the cooperatively breeding fish *N. pulcher*, in which pay-to-stay has been carefully examined both empirically and experimentally and shown to be key to helping behaviour (Taborsky, 2016). It is worth noting, however, that *Neolamprologus* differs from the cooperative breeding birds discussed here in that ‘helpers’ are generally aspiring breeders rather than related offspring (Koenig, Dickinson, & Emlen, 2016).

As mentioned above, there are other potential benefits to birds altering their behaviour in response to the provisioning of others and adjusting their own behaviour accordingly beyond the obvious adjustments that take place in feeding rates due to the loss, or addition, or provisioning by other group members (Liebl et al., 2016). These include reducing predation risk by reducing the number of temporally separate nest visits (Bebbington & Hatchwell, 2016; Raihani et al., 2010) and reduced parental conflict over nestling care (Johnstone et al., 2014). Thus the coordinated provisioning behaviour found here may serve one of these other selective functions. It is even possible that provisioning behaviour acts as a signal to conspecifics in some way other than those considered here. In our case, however, acorn woodpeckers neither display nor regularly vocalize during feeding visits, and thus what such a covert signal might consist of is not obvious. Although one of the activities of many species that is easiest to observe and quantify, provisioning behaviour appears to be used as a signal that is acted upon by few, if any, cooperatively breeding birds.

Acknowledgments

We thank the many assistants who conducted the nest watches included in this study, students from Old Dominion University Learn and Earn Advantage Program for digitizing historical nest watches, Annie Sabo for organizing the data, and particularly Doug Schaefer, who wrote the Excel program used to computerize the nest watch data. We gratefully acknowledge the Museum of Vertebrate Zoology (UC Berkeley) and Hastings Reservation for logistical support, the National Science Foundation for financial support (most recently through grants IOS-1455881 and IOS-1455900), and the referees for their comments.

References

- Bebbington, K., & Hatchwell, B. J. (2016). Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology*, 27, 652–659.
- Boland, C. R. J., Heinsohn, R., & Cockburn, A. (1997). Deception by helpers in cooperatively breeding white-winged choughs and its experimental manipulation. *Behavioral Ecology and Sociobiology*, 41, 251–256.
- Budden, A. E., & Wright, J. (2007). Effects of feeding frequency on nestling begging and digestion. *Ibis*, 150, 234–241.
- Canestrari, D., Marcos, J. M., & Baglione, V. (2004). False feeding at the nests of carrion crows *Corvus corone corone*. *Behavioral Ecology and Sociobiology*, 55, 477–483.
- Canestrari, D., Marcos, J. M., & Baglione, V. (2007). Costs of chick provisioning in cooperatively breeding crows: An experimental study. *Animal Behaviour*, 73, 349–357.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., & Jordan, N. R. (2005). ‘False feeding’ and aggression in meerkat societies. *Animal Behaviour*, 69, 1273–1284.
- Doutrelant, C., & Covas, R. (2007). Helping has signalling characteristics in a cooperatively breeding bird. *Animal Behaviour*, 74, 739–747.
- Gaston, A. J. (1978). The evolution of group territorial behavior and cooperative breeding. *American Naturalist*, 112, 1091–1100.
- Harrison, F., Barta, Z., Cuthill, I., & Székely, T. (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. (2016). Long-tailed tits: Ecological causes and fitness consequences of redirected helping. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution, and behavior* (pp. 39–57). Cambridge, U.K.: Cambridge University Press.
- Haydock, J., & Koenig, W. D. (2002). Reproductive skew in the polygynandrous acorn woodpecker. *Proceedings of the National Academy of Sciences (U.S.A.)*, 99, 7178–7183.
- Haydock, J., & Koenig, W. D. (2003). Patterns of reproductive skew in the polygynandrous acorn woodpecker. *American Naturalist*, 162, 277–289.
- Hinde, C. A., & Kilner, R. M. (2007). Negotiations within the family over the supply of parental care. *Proceedings of the Royal Society B: Biological Sciences*, 274, 53–60.
- Johnstone, R. A., & Hinde, C. A. (2006). Negotiation over offspring care—how should parents respond to each other’s efforts? *Behavioral Ecology*, 17, 818–827.
- Johnstone, R. A., Manica, A., Fayet, A. L., Stoddard, M. C., Rodriguez-Gironés, M. A., & Hinde, C. A. (2014). Reciprocity and conditional cooperation between great tit parents. *Behavioral Ecology*, 25, 216–222.
- Karasov, W. H., & Wright, J. (2002). Nestling digestive physiology and begging. In J. Wright, & M. L. Leonard (Eds.), *The evolution of begging: Competition, cooperation and communication* (pp. 199–219). New York: Kluwer Academic Press.
- Kilner, R. M., & Johnstone, R. A. (1997). Begging the question: Are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution*, 12, 11–15.
- Koenig, W. D., Dickinson, J. L., & Emlen, S. T. (2016). Synthesis: Cooperative breeding in the twenty-first century. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution, and behavior* (pp. 353–374). Cambridge, U.K.: Cambridge University Press.
- Koenig, W. D., & Mumme, R. L. (1987). *Population ecology of the cooperatively breeding acorn woodpecker*. Princeton, NJ: Princeton University Press.
- Koenig, W. D., Mumme, R. L., & Pitelka, F. A. (1984). The breeding system of the acorn woodpecker in central coastal California. *Zeitschrift für Tierpsychologie*, 65, 289–308.
- 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. *Animal Behaviour*, 82, 437–444.
- Koenig, W. D., & Walters, E. L. (2012). Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker. *Behavioral Ecology*, 23, 181–190.
- Koenig, W. D., Walters, E. L., & Haydock, J. (2016). Acorn woodpeckers: Helping at the nest, polygyny, and dependence on a variable acorn crop. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution and behavior* (pp. 217–236). Cambridge, U.K.: Cambridge University Press.
- Kokko, H., Johnstone, R. A., & Wright, J. (2002). The evolution of parental and alloparental effort in cooperatively breeding groups: When should helpers pay to stay? *Behavioral Ecology*, 13, 291–300.
- Leonard, M. L., & Horn, A. G. (2001). Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). *Behavioral Ecology and Sociobiology*, 49, 170–175.
- Lepczyk, C. A., Caviades-Vidal, E., & Karasov, W. H. (1998). Digestive responses during food restriction and realimentation in nestling house sparrows (*Passer domesticus*). *Physiological Zoology*, 71, 561–573.
- Liebl, A. L., Browning, L. E., & Russell, A. F. (2016). Manipulating carer number versus brood size: Complementary but not equivalent ways of quantifying carer effects on offspring. *Behavioral Ecology*. <http://dx.doi.org/10.1093/beheco/aww038>.
- McDonald, P. G., Kazem, A. J. N., Clarke, M. F., & Wright, J. (2008). Helping as a signal: Does removal of potential audiences alter helper behavior in the bell miner? *Behavioral Ecology*, 19, 1047–1055.
- 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? *Behavioral Ecology and Sociobiology*, 61, 1623–1635.
- Meade, J., Nam, K.-B., Beckerman, A. P., & Hatchwell, B. J. (2010). Consequences of ‘load-lightening’ for future indirect fitness gains by helpers in a cooperatively breeding bird. *Journal of Animal Ecology*, 79, 529–537.
- Mitchell, J. S. (2003). Social correlates of reproductive success in false clown anemonefish: Subordinate group members do not pay-to-stay. *Evolutionary Ecology Research*, 5, 89–104.
- Mulder, R. A., & Langmore, N. E. (1993). Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour*, 45, 830–833.
- Nomano, F. Y., Browning, L. E., Rollins, L. A., Nakagawa, S., Griffith, S. C., & Russell, A. F. (2013). Feeding nestlings does not function as a signal of social prestige in cooperatively breeding chestnut-crowned babbler. *Animal Behaviour*, 86, 277–289.
- Nomano, F. Y., Browning, L. E., Savage, J. L., Rollins, L. A., Griffith, S. C., & Russell, A. F. (2015). Unrelated helpers neither signal contributions nor suffer retribution in chestnut-crowned babbler. *Behavioral Ecology*, 26, 986–995.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2013). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-113. <http://CRAN.R-project.org/package=nlme>.

- R Core Team. (2014). *R: A language and environment for statistical computing* (Version 3.0.3). Vienna, Austria: R Foundation for Statistical Computing <http://www.R-project.org/>.
- Raihani, N. J., Nelson-Flower, M. J., Moyes, K., Browning, L. E., & Ridley, A. R. (2010). Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. *Journal of Animal Ecology*, 79, 44–52.
- Sæther, B.-E. (1994). Food provisioning in relation to reproductive strategy in altricial birds: A comparison of two hypotheses. *Evolution*, 48, 1397–1406.
- Santema, P., & Clutton-Brock, T. (2012). Dominant female meerkats do not use aggression to elevate work rates of helpers in response to increased brood demand. *Animal Behaviour*, 83, 827–832.
- Taborsky, M. (2016). Cichlid fishes: A model for the integrative study of social behavior. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution, and behavior* (pp. 272–293). Cambridge, U.K.: Cambridge University Press.
- Wright, J. (1997). Helping-at-the-nest in Arabian babblers: Signalling social status or sensible investment in chicks? *Animal Behaviour*, 54, 1439–1448.
- Wright, J., & McDonald, P. G. (2016). Bell miners: Kin-selected helping decisions. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution, and behavior* (pp. 165–180). Cambridge, U.K.: Cambridge University Press.
- Zahavi, A. (1977). Reliability in communication systems and the evolution of altruism. In B. Stonehouse, & C. M. Perrins (Eds.), *Evolutionary ecology* (pp. 253–259). London: Macmillan.
- Zahavi, A. (1990). Arabian babblers: The quest for social status in a cooperative breeder. In P. B. Stacey, & W. D. Koenig (Eds.), *Cooperative breeding in birds: Long term studies of ecology and behavior* (pp. 103–130). Cambridge, U.K.: Cambridge University Press.
- Zahavi, A. (1995). Altruism as a handicap—the limitations of kin selection and reciprocity. *Journal of Avian Biology*, 26, 1–3.