



Articles

Age-related provisioning behaviour in the cooperatively breeding acorn woodpecker: testing the skills and the pay-to-stay hypotheses

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Helpers in cooperatively breeding acorn woodpeckers, *Melanerpes formicivorus*, gain indirect fitness benefits by provisioning related offspring, but may also gain direct fitness benefits by any of several mechanisms. We tested the ‘skills’ hypothesis, which proposes that provisioning behaviour provides helpers with experience that allows them to be more successful when they breed later in life, and the ‘pay-to-stay’ hypothesis, which proposes that provisioning behaviour by helpers is rewarded by dominant breeders, allowing helpers to remain in their natal group longer, thus reaping nepotistic benefits. We found that young helpers provisioned at relatively low rates, which in most cases increased with age, a necessary requirement of the skills hypothesis. Analyses of birds with known feeding histories, however, revealed that helper males that fed young at higher rates had no greater reproductive success later in life than less helpful helper males, contrary to the skills hypothesis. In accord with pay-to-stay, males that fed more as second-year helpers remained in their natal group as helpers significantly longer and were more likely to inherit than were male broodmates that fed less. An analysis controlling for the time that birds remained in their natal groups, however, failed to indicate that prior feeding history played a significant role in these differences, which are more likely to be a consequence of differences in dispersal behaviour. In acorn woodpeckers, as in other species of cooperative breeders in which helpers are close relatives, the primary benefits of provisioning behaviour are indirect via kin selection rather than direct via either the acquisition of skills or payment of rent.

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Helpers in cooperative breeders typically, although not invariably, gain indirect fitness benefits by helping to feed related but nondescendant offspring (Dickinson & Hatchwell 2004). More controversial are the potential direct fitness benefits helpers gain by helping (Clutton-Brock 2002). These include the possibility that the fitness benefits of helping are reciprocated, either directly by helpers being aided in the future by the nestlings they currently feed (Ligon & Ligon 1978), or indirectly by the offspring they feed, increasing the overall success of the group (‘group augmentation’; Brown 1987; Kokko et al. 2001); that helpers gain social status or prestige that increases their future access to mates (Zahavi 1995); that by helping, individuals acquire experience enabling them to be more successful when they eventually attain breeding status (the ‘skills’ or ‘experience’ hypothesis; Selander 1964); or that individuals must help in order to be allowed access to communal resources (the ‘pay-to-stay’ hypothesis; Mulder & Langmore 1993).

Consider the skills hypothesis. Although obliquely suggested by at least one early author (Bryant 1928), this hypothesis was first clearly delineated in the context of cooperative breeding by Selander (1964, page 206), who suggested the possibility that ‘...by serving as a helper, the young bird would gain experience in parental activities which could enhance reproductive success later in life’. As expressed by Selander, this definition of the skills hypothesis encompasses two parts: first, that young individuals are relatively incompetent and must learn the skills needed for successful reproduction, and second, that the necessary skills are acquired specifically via the process of helping behaviour. In the context of the evolution of cooperative breeding, learning through helping assumes that individuals gain greater skills, or at least equal skills at lower cost, by acting as helpers as opposed to engaging in alternative behaviours, including attempted independent reproduction, thus contributing to why helpers delay breeding and help rather than attempt to breed on their own. As such, the skills hypothesis is more exclusive than the ‘skill hypothesis’ modelled by Brown (1987, pp. 65–70), who, following up on earlier ideas of the importance of learning to delayed reproduction (Lack 1954; Ashmole 1963), focused on how delayed dispersal might be facilitated by the need to acquire skills (the first part of the definition),

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but not on how the acquisition of such skills might be facilitated by helping behaviour per se (the second part of the definition).

Testing the skills hypothesis has proved difficult because of possible confounds between experience and other characters, including age, individual quality and territory quality. For example, Khan & Walters (1997) found no significant difference in success between 2-year-old novice breeding red-cockaded woodpeckers, *Picoides borealis*, that helped as yearlings and same-aged birds that had not helped. This comparison avoids a confound with age but not necessarily with quality, since the birds also differed in whether they were philopatric in their first year, which may in turn be related to individual quality if better birds are more likely to disperse (Dickinson & Hatchwell 2004). A similar confound may have influenced the unexpected result of the much higher success for female Seychelles warblers, *Acrocephalus sechellensis*, that had helped as yearlings than among inexperienced delayers, due primarily to better placement of nests and more effective incubation (Komdeur 1996). This is the only study thus far to provide evidence for the importance of the skills hypothesis in a cooperative breeder. By contrast, no evidence for the skills hypothesis was found when comparing novice breeders that had previously delayed dispersal but had or had not helped in white-fronted bee-eaters, *Merops bullockoides* (Emlen & Wrege 1988), while in western bluebirds, *Sialia mexicana*, former helpers that remained on the study area to breed suffered worse fledging success than birds that had not been known to act as helpers (Dickinson et al. 1996).

The pay-to-stay hypothesis has proved equally problematical. First proposed by Gaston (1978) as the 'payment effect', the premise is that a portion of the assistance provided by helpers can be regarded as payment for the right to remain in the group if helpers are in a situation where it is to their immediate benefit to stay, but not to the immediate benefit of the breeders. Theoretical considerations of this hypothesis by researchers have subsequently investigated the conditions under which such payment might be expected (Kokko et al. 2002; Hamilton & Taborsky 2005), while experiments in superb fairy-wrens, *Malurus cyaneus* (Mulder & Langmore 1993), and the cooperatively breeding cichlid fish *Neolamprologus pulcher* (Balshine-Earn et al. 1998; Bergmüller & Taborsky 2005; Bergmüller et al. 2005; Brintjes & Taborsky 2008) have provided some empirical support. At least two tests of this hypothesis in bell miners, *Manorina melanophrys* (McDonald et al. 2008), and in clown anemonefish, *Amphiprion ocellaris* (Mitchell 2003), however, have failed to find evidence for this phenomenon, and a recent review of cooperative breeding in *Neolamprologus pulcher* questioned the role of pay-to-stay in the evolution or maintenance of helping behaviour in this species, despite evidence of this from earlier studies (Wong & Balshine 2011).

Here we examine the relationship between provisioning behaviour by helpers and their subsequent fate as a test of the skills and pay-to-stay hypotheses in the cooperatively breeding acorn woodpecker, *Melanerpes formicivorus*, a species in which both helping-at-the-nest and cooperative polygynandry is common (Koenig et al. 1995). Cobreeders of the same sex, both male and female, are generally either siblings or parents and offspring, and are thus closely related. There is virtually no extragroup parentage, and helpers are almost always offspring of the breeding individuals (Dickinson et al. 1995; Haydock et al. 2001). Furthermore, although there are differences related to both sex and ecological conditions (Koenig et al., in press), helpers enhance both the survivorship and reproductive success of the breeders. Consequently, birds gain significant indirect fitness benefits as helpers, although not enough to compensate for their failure to breed independently. Thus, the questions we address here are whether helpers gain experience as a consequence of their helping behaviour that allows them to be more successful at raising young when they attain breeder status,

as proposed by the skills hypothesis, and whether there is evidence that by provisioning, helpers remain in their natal group longer in a way that benefits them later on in life, as proposed by the pay-to-stay hypothesis.

METHODS

We studied a colour-marked population at Hastings Reservation, central coastal California, between 1973 and 2010, during which time the population was continuously monitored (Koenig & Mumme 1987). The analyses performed here are based in part on nest watches conducted between 1979 and 2010, during which observers sat in blinds located a discrete distance from active nests and, with the aid of spotting scopes, recorded the identities of all birds engaged in feeding visits during what was typically a 3 h period. During each feeding visit the identity of bird, length of time the bird spent in the nest potentially brooding, and whether the bird removed a faecal sac or not, were recorded on tape and later transcribed and summarized. The total data set encompassed 3585 nest watches at 968 nests of 85 social groups for a total of 10 506 h of observation conducted throughout the breeding season and throughout the 30–34 day nestling period. Included in these observations were data on the provisioning behaviour of 1622 breeder males, 1160 breeder females, 909 helper males and 595 helper females. Territory quality, assessed each year, was a binary index based on the size of the storage facilities, which are key resources for groups in which acorns are stored each autumn (low: <1000 storage holes; high: >1000 storage holes).

For the acorn crop itself, a critical resource affecting both reproduction and survivorship of the birds (Koenig & Mumme 1987; Koenig et al., in press), analyses were restricted to the 30 years between 1981 and 2010, during which time we assessed mean crop size the prior autumn each year by counting a sample of acorns on 250 trees originally tagged in 1980 and distributed among all five major oak species (*Quercus* spp.) present in the study area. The mean acorn crop was estimated by the mean of the ln-transformed number of acorns counted in 30 s ($x \ln 30 = \ln(N \text{ acorns counted} + 1)$) across all trees surveyed (Koenig et al. 1994a, b). In all cases we used the prior autumn's acorn crop (year $x-1$) as a potential factor influencing feeding rates in year x .

Testing the Skills Hypothesis

The first part of the skills hypothesis requires that young individuals be relatively incompetent at raising offspring. To test this, we examined age-related feeding rates of helpers. Previous analyses (Koenig et al., in press) have found that prior breeding experience significantly enhances reproductive success, a finding consistent with young, inexperienced birds being relatively poor parents. Here we focus on the feeding behaviour of helpers vis-à-vis age. Two sets of analyses were conducted, the first including all watches and the second including only watches during which a bird was observed feeding. The latter thus excluded periods during which birds were involved in other activities, primarily foraging in search of breeding opportunities outside their natal territory, an activity that precludes helping-at-the-nest (Mumme & de Queiroz 1985). These analyses re-examine the conclusion of Mumme et al. (1990) that first-year birds are as competent at caring for nestlings as older birds of the same sex and status, and that to the extent that young acorn woodpeckers provision less than older birds, this decreased provisioning pattern is due to the greater amount of time the younger individuals invest in outside activities.

We first performed linear mixed-effects models fitted by restricted maximum likelihood methods separately for helper males and helper females to determine whether age significantly

influenced feeding rates. In all analyses, the dependent variable was the feeding rate per hour, where the length of each watch was the total length minus the amount of time until the first visit to the nest to feed, the latter being subtracted to control for disturbance associated with setting up for a watch. Age of helpers was divided into three categories (2Y = second year, i.e. the year after hatching; 3Y = third year; 4Y+ = fourth year and older). Independent variables, other than bird age, were the number of nestlings in the nest at the time of the watch (brood size), age of nestlings (in days since hatching), total group size, time of day the watch began (Pacific Standard Time), maximum temperature for the day of the watch (measured at Hastings Reservation headquarters), Julian date, the mean (ln-transformed) acorn crop from the prior autumn, and the number of nestlings banded (generally done when nestlings were 21 days old). This last term was included along with current brood size because brood reduction, particularly early in the nestling period, is common (Stanback 1994), and thus the number of young in the nest during a watch frequently differed (24% of watches) from the number of young banded. Quadratic terms for nestling age, Julian date and the mean acorn crop were also included, as were two interaction terms ('nestling age \times brood size' and 'nestling age \times time of day'). 'Nest identity' was nested within 'group' as a random factor to control for nonindependence of groups and nests. To visualize differences in feeding rates as a function of helper age, we plotted mean feeding rates for helpers by age category along with the percentage of watches during which helpers were observed feeding. All statistical procedures were conducted in R v.2.11.1 (R Development Core Team 2010).

As a more controlled test for age effects, we extracted cases in which the feeding rates of individual birds that were helpers for 2 or more years could be compared. Differences in group composition, brood size and other variables known to influence feeding rates were dealt with by calculating the expected feeding rate for each bird during each watch using the 'predict' function in R based on the observed values of the independent variables listed above, excluding helper age. We then subtracted the expected from the observed feeding rate to yield a feeding rate index (FR_{index}) that was positive when birds fed more than expected, negative when they fed less than expected, and independent of group size, brood size and nestling age (the correlation between the FR_{index} and each of these three variables was <0.01).

Using all watches and those watches for which we excluded individuals that did not feed, we then calculated mean feeding rates

(using the FR_{index}) for each individual for all nests of their group for which we had data and compared the overall contributions individual helpers made at nests at which they helped during 2 successive years (or, in a few cases, skipping a year) using paired Wilcoxon signed-ranks tests. Comparisons were made between the feeding rates of 2Y versus 3Y helpers, 2Y versus 3Y+ (3Y and older) helpers, and 3Y+ versus 4Y+ helpers. Individuals were included only the first time they occurred in any one analysis.

The second, more restrictive part of the skills hypothesis postulates that by helping, young individuals gain experience that allows them to be more successful when they become breeders later in life. To test this hypothesis, we performed general linear models (when the response variable was binary) or mixed-effects models (when the response variable was continuous) in which the fate or success of helpers was the dependent variable and the independent variables were the territory quality of their natal group, the mean acorn crop of the prior autumn and the bird's mean FR_{index} in its first year as a helper (2Y). 'Group' was included as a random factor in the mixed-effects models.

As discussed above, a difficulty in testing the skills hypothesis lies in trying to ensure that individuals are comparable in age and quality such that any differences detected are due to experience rather than some confounding factor. To address this problem, we compared same-sex broodmates in terms of how much they provisioned as 2Y helpers, based on the mean FR_{index} of birds present during nests attempted that year. Analyses were made using data from all nest watches (regardless of whether a particular individual fed) and from those restricted to watches during which an individual was observed to feed. When more than two same-sex broodmates were available, we compared the bird that fed the most with the bird that fed the least. Then, using only birds that were no longer present in the study area as of July 2010 (either because they had died or dispersed elsewhere), we compared the subsequent fate of these matched pairs of birds, in all cases comparing the bird that fed more as a 2Y helper (the α broodmate) with the bird that fed less (the β broodmate), either by paired Wilcoxon signed-ranks or binomial tests. The prediction of the skills hypothesis is that α individuals would acquire more experience as a consequence of their greater provisioning behaviour and would therefore be more successful later in life, defined in terms of becoming a breeder at a younger age or fledging more young the first year upon becoming a breeder, compared to β individuals. We examined only first breeding attempts (both controlling and not controlling for age)

Table 1

Effect sizes (\pm SE) and significance of factors influencing the feeding rate of helper male and helper female acorn woodpeckers based on mixed-effects models including all watches (left) and only watches during which an individual fed (right)

Variable	All watches				Watches during which an individual fed			
	Helper males		Helper females		Helper males		Helper females	
	Model parameters	<i>t</i>						
Bird age	0.308 \pm 0.083	3.70***	0.338 \pm 0.143	2.36*	0.103 \pm 0.100	1.03	0.257 \pm 0.178	1.44
Group size	-0.097 \pm 0.037	-2.64**	-0.153 \pm 0.056	-2.76**	-0.068 \pm 0.039	-1.77	-0.111 \pm 0.059	-1.88
Brood size	0.167 \pm 0.081	2.07*	-0.011 \pm 0.127	-0.09	0.172 \pm 0.096	1.79	0.181 \pm 0.171	1.06
Nestling age	0.102 \pm 0.029	3.57***	0.095 \pm 0.047	2.01*	0.117 \pm 0.034	3.47***	0.154 \pm 0.061	2.52*
(Nestling age) ²	-0.130 \pm 0.047 ($\times 10^{-2}$)	2.79**	0.023 \pm 0.100 ($\times 10^{-2}$)	0.23	-0.148 \pm 0.052 ($\times 10^{-2}$)	2.86**	-0.095 \pm 0.128 ($\times 10^{-2}$)	-0.74
<i>N</i> young banded	0.012 \pm 0.072	0.16	0.055 \pm 0.117	0.47	0.046 \pm 0.078	0.59	0.181 \pm 0.171	1.06
Maximum temperature	-0.012 \pm 0.008	-1.52	-0.010 \pm 0.012	-0.77	-0.011 \pm 0.010	-1.10	-0.003 \pm 0.016	-0.20
Date	-0.060 \pm 0.017	-3.50***	-0.002 \pm 0.026	-0.07	-0.068 \pm 0.019	-3.59***	-0.030 \pm 0.030	-0.99
(Date) ²	0.018 \pm 0.005 ($\times 10^{-2}$)	3.51***	0.009 \pm 0.075 ($\times 10^{-3}$)	0.12	0.020 \pm 0.006 ($\times 10^{-2}$)	3.61***	0.089 \pm 0.087 ($\times 10^{-3}$)	1.03
Time of day	0.020 \pm 0.030 ($\times 10^{-2}$)	0.66	0.049 \pm 0.046 ($\times 10^{-2}$)	1.06	0.019 \pm 0.036 ($\times 10^{-2}$)	0.53	0.024 \pm 0.062 ($\times 10^{-2}$)	0.38
Mean acorn crop	0.737 \pm 0.528	1.40	1.731 \pm 0.870	1.99*	0.836 \pm 0.550	1.52	1.517 \pm 0.961	1.58
(Mean acorn crop) ²	-0.228 \pm 0.143	-1.60	-0.525 \pm 0.233	-2.26*	-0.249 \pm 0.149	-1.67	-0.476 \pm 0.256	-1.86
Nestling age \times brood size	0.011 \pm 0.004	2.59**	0.018 \pm 0.006	2.78**	0.007 \pm 0.005	1.39	0.014 \pm 0.008	1.73
Nestling age \times time of day	-0.025 \pm 0.017 ($\times 10^{-3}$)	-1.46	-0.061 \pm 0.027 ($\times 10^{-3}$)	-2.23*	-0.017 \pm 0.021 ($\times 10^{-3}$)	-0.79	-0.075 \pm 0.035 ($\times 10^{-3}$)	-2.15*

Sample sizes: all watches: *N* watches = 3186 (males), *N* = 1955 (females); only watches during which an individual fed: *N* = 2281 (males), *N* = 1324 (females). **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

since a bird's subsequent success is likely to be dependent on the experience it may have gained through breeding and, thus, subsequent attempts are not relevant to the skills hypothesis as it potentially applies to helping behaviour.

Although this latter procedure controls for age and most maternal effects, it does not control for differences in individual quality. In acorn woodpeckers, two metrics known to correlate with dominance within broods, and thus at least potentially with both quality and subsequent success, are relative wing length and relative body mass prior to fledging (Stanback 1994). Thus, we tested for differences between α and β chicks in these two variables measured when broodmates were banded at 21 days old. A statistical association between subsequent success and either relative wing length or relative body mass would suggest that differences between α and β broodmates may have been due to differences in quality rather than experience.

Testing Pay-to-Stay

The first demographic prediction of pay-to-stay is that there should be a positive correlation between provisioning by helpers and the length of time they remain in their natal group; that is, more helpful helpers should stay in their natal group longer than less helpful helpers. By remaining in their natal group as helpers longer, the most likely benefit birds could potentially gain is a higher probability of inheriting and becoming a breeder. This possibility was tested in the analyses described above. There is a potential confound, however, in that birds that remain as helpers longer may be more likely to inherit their natal territory not because of their provisioning behaviour, but rather as a consequence of 'being there' longer and thus being more likely to be present when the breeders of the opposite sex die and it becomes possible for them to inherit (Koenig et al. 1998). To investigate this possibility, we calculated the age-specific probabilities of inheriting among all offspring regardless of their provisioning history as well as for α and β broodmates separately. We tested for age-specific changes in the overall probability of inheriting using proportions test for a trend (Dalgaard 2008). Differences between α and β birds were tested by logistic regressions using 'age' and 'status' (α or β) as explanatory factors and the joint significance of the factors determined using χ^2 deviance tests (Dalgaard 2008).

RESULTS

Do Feeding Rates Increase with Age?

Based on the mixed-effects models of feeding rates for helper males and helper females, 'age' significantly affected feeding rates of both sexes when all watches were included, but not when analyses were restricted to watches when an individual fed (Table 1). Other variables that significantly influenced feeding rates in one or more of the analyses included group size, brood size, nestling age, date, the acorn crop, and the two interaction terms ('nestling age \times brood size' and 'nestling age \times time of day'). Plotting mean values, the main difference was clearly in the feeding rates of 2Y compared to older helpers (Fig. 1a), a difference that was reduced and no longer significant (Fig. 1b) in the models (Table 1) when controlling for the higher proportion of watches at which 2Y helpers failed to participate (Fig. 1c).

A stronger test for age effects was made via paired comparisons of standardized feeding rates (the FR_{index}) of birds during successive years. Results indicated that relative feeding rates increased significantly between 2Y and older birds in all analyses except that including all watches for females, but that there was no increase in feeding rates with age after a bird's third year (Table 2; note that for

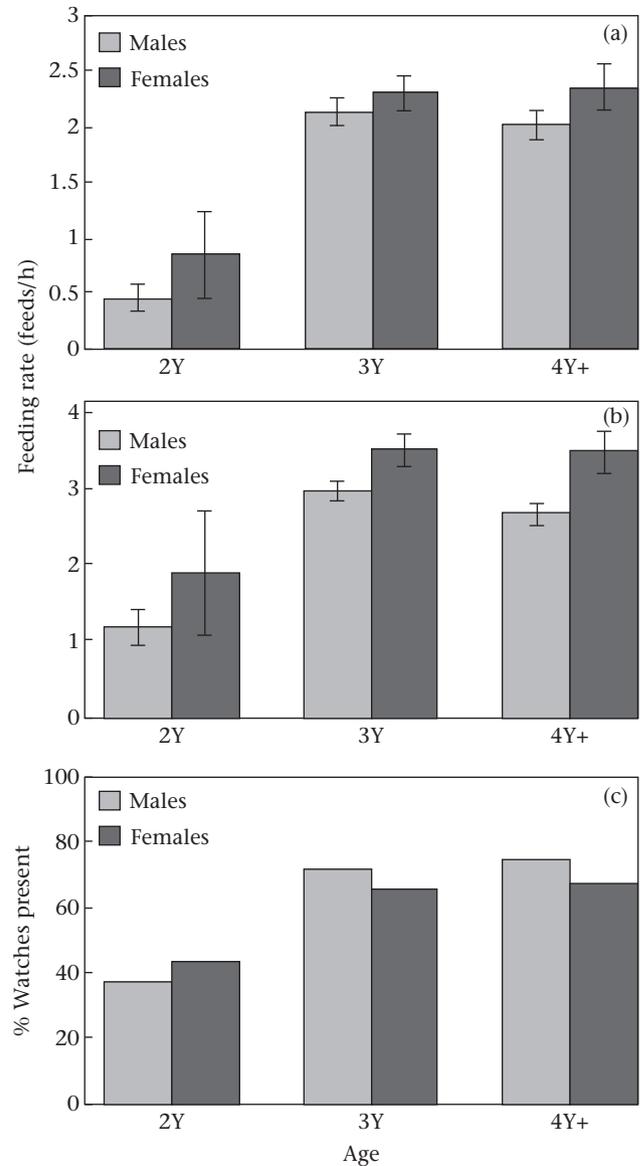


Figure 1. Mean \pm 95% confidence interval (CI) feeding rate of acorn woodpecker helpers for all watches. 2Y = second-year birds; 3Y = third-year birds; 4Y+ = birds in their fourth year and older. (b) Mean \pm 95% CI feeding rate of helpers only for watches during which an individual was observed feeding. (c) Percentage of watches during which helpers fed as a function of age.

males, there were marginally significant differences between 3Y+ and 4Y+ birds, but the differences were in the direction of older birds feeding less).

Is Success Related to Prior Feeding History?

First, we examined whether the fate or success of birds was related to their provisioning rates as 2Y helpers. Models included a measure of natal territory quality and the mean acorn crop from the prior autumn as a measure of resource abundance. Results (Table 3) revealed no significant effects for females or for either sex using only watches when helpers fed (latter results not shown). For males in analyses including all watches, however, birds that fed more as 2Y birds and during good acorn years remained as helpers longer. None of the explanatory factors significantly affected the number of young fledged in the groups of birds known to have become breeders during the first year they bred.

Table 2

Comparison of the feeding rates (mean \pm SE difference between the observed feeding rate and the feeding rate predicted from the mixed-effects models) of individual acorn woodpeckers in sequential years depending on age

Sex and age	All watches				Watches during which an individual fed			
	Year 1	Year 2	N	P	Year 1	Year 2	N	P
Males								
2Y \rightarrow 3Y	-0.90 \pm 0.26	0.80 \pm 0.48	14	0.004	-0.67 \pm 0.30	1.30 \pm 0.44	13	0.002
2Y \rightarrow 3Y+	-0.75 \pm 0.22	0.65 \pm 0.39	21	0.002	-0.45 \pm 0.25	1.20 \pm 0.38	19	0.001
3Y+ \rightarrow 4Y+	0.29 \pm 0.15	-0.03 \pm 0.13	149	0.04	0.69 \pm 0.15	0.36 \pm 0.13	144	0.04
Females								
2Y \rightarrow 3Y	-1.96 \pm 0.24	-0.71 \pm 0.67	7	0.22	-2.32 \pm 0.41	0.66 \pm 1.12	6	0.018
2Y \rightarrow 3Y+	-1.80 \pm 0.23	-0.40 \pm 0.54	10	0.053	-2.40 \pm 0.36	0.91 \pm 0.98	7	0.011
3Y+ \rightarrow 4Y+	0.08 \pm 0.20	0.48 \pm 0.21	86	0.19	0.70 \pm 0.23	0.78 \pm 0.20	85	0.73

Values are for birds of that sex/status category controlling for brood size, age of nestlings, group size, time of day, date of watch and maximum temperature that day. Thus, negative values indicate that birds fed less than predicted, while positive values indicate that they fed more than predicted. *P* values based on paired Wilcoxon signed-ranks tests; thus, a significant value means that 'year 2' was significantly different from 'year 1'. Significant ($P < 0.05$) results are in boldface.

There were 48 male and 24 female pairs of broodmates for which we had data as nestlings, 2Y helpers, and information as to their subsequent fate. Based on these data, we again detected no significant differences in the fate of females vis-à-vis their feeding performance as 2Y helpers. In contrast, α males that fed more as 2Y helpers again remained as helpers longer on their natal territory and in addition were more likely to inherit their natal territory and be present in the study area significantly longer than β broodmates that fed less (Table 4). There were no significant differences between α and β birds in their mean age at first breeding, the mean group size of the group in which they first bred, or the number of young fledged by their group during their first breeding season; the latter was true for males even when we restricted the analysis to cases in which both birds bred at the same age. We also detected no significant differences in terms of either wing chord or body mass at banding.

Is Inheritance Related to Prior Feeding History?

The findings that males stayed as helpers longer (both analyses) and were more likely to inherit and become breeders in their natal group (paired comparisons only) are consistent with two key predictions of the pay-to-stay hypothesis: first, that more helpful helpers should be allowed to remain as helpers longer; and second, that by doing so, they gain fitness benefits, specifically an increased possibility of inheriting the natal territory. This latter finding, however, could be the result of birds being present in their natal group longer rather than their helping behaviour per se. To examine this possibility, we looked at the age-specific probability of inheritance.

Using all data, the age-specific probability of inheriting during the subsequent year increased with age, significantly so for males (Fig. 2). Thus, older males were more likely to inherit than younger

males, as predicted by pay-to-stay. To test whether this was related to provisioning rates, we compared the age-specific probability of male broodmates used in the paired analyses inheriting their natal territory in a logistic regression in which 'N years helping' (1 versus 2+) and 'status' (α or β) were the explanatory factors. Results indicated that neither factor was significant (Fig. 2b). However, α s were in both cases more likely to inherit than β s, so as an alternative test, we used only paired male broodmates with known feeding histories taken from the prior analyses in which both individuals helped for the same number of years. Out of 22 such pairs of broodmates, an equal number of α and β birds (2, or 9%) inherited. Thus, comparison of age-specific inheritance by α and β birds failed to support the hypothesis that the increase in inheritance was related to prior provisioning rates.

DISCUSSION

At the heart of the conundrum of cooperative breeding is the question of what fitness benefits helpers gain by provisioning offspring that are not their own. In acorn woodpeckers, as in a majority of other cooperatively breeding species, helpers both enhance the reproductive success of groups where they are present and are typically closely related to the nestlings they help rear, thus fulfilling the two requirements for indirect fitness benefits (kin selection). Nevertheless, helpers may gain from any of several direct fitness benefits as well. Here we test two of these benefits. First is the skills hypothesis, which proposes that, by provisioning, offspring helpers gain experience that allows them to become more successful as breeders later in life. Second is the pay-to-stay hypothesis, which hypothesizes that dominant breeders allow helpers to stay as a consequence of their provisioning of offspring. Although both hypotheses were articulated over 30 years ago

Table 3

Importance (*z* values of the effect size with *P* values in parentheses) of feeding rates as a 2Y helper to an individual acorn woodpecker's subsequent fate and success, controlling for territory quality and the size of the acorn crop

Character	Males				Females			
	Feeding rate as 2Y helper	Territory quality	Mean acorn crop	N	Feeding rate as 2Y helper	Territory quality	Mean acorn crop	N
Inherited	0.24 (0.80)	-0.40 (0.69)	0.20 (0.85)	291	0.54 (0.59)	-0.44 (0.66)	0.07 (0.94)	218
Became a breeder	1.12 (0.26)	-0.96 (0.34)	-1.19 (0.24)	291	0.57 (0.57)	-1.03 (0.31)	-1.39 (0.17)	218
Mean N years as a helper	2.08 (0.04)	1.55 (0.12)	2.32 (0.02)	285	0.70 (0.49)	1.07 (0.29)	-1.24 (0.22)	212
Life span/time in study area (years)	1.57 (0.12)	1.81 (0.07)	0.08 (0.94)	292	0.98 (0.33)	-0.15 (0.88)	-1.86 (0.06)	219
Mean age at 1st breeding	1.36 (0.18)	-0.32 (0.75)	1.08 (0.28)	107	0.66 (0.51)	0.74 (0.47)	-0.26 (0.79)	61
Mean group size when first bred	-0.60 (0.55)	1.29 (0.20)	-0.36 (0.72)	122	0.68 (0.50)	1.29 (0.21)	0.19 (0.85)	80
Young fledged during 1st breeding season	-0.31 (0.76)	1.27 (0.21)	0.45 (0.65)	122	-0.57 (0.57)	0.26 (0.79)	-1.13 (0.26)	80

Includes only birds that died or were no longer present in the study area. Comparisons are by general linear models with a binomial error term (probability of inheriting and probability of becoming a breeder) and mixed-effects models with 'group' as a random effect (all others). Significant ($P < 0.05$) results are in boldface. Negative *z* values indicate a negative effect. Results include all watches; there were no significant effects restricting analyses to only watches during which a bird fed (results not shown).

Table 4
Relationship of feeding rates as 2Y helpers to the subsequent fate and success of acorn woodpeckers in paired comparisons of same-sex broodmates in which one broodmate fed more (the α) and the other fed less (the β)

Character	Males				Females					
	α (fed more)	β (fed less)	N	P	α (fed more)	β (fed less)	N	P		
								All	Fed only	
% Inheriting	16.7	6.3	48	0.039	0.09	8.33	0.00	24	0.25	0.25
% Known to have become a breeder	43.8	39.6	48	0.31	0.69	45.8	37.5	24	0.39	0.39
Mean N years as a helper	2.21±0.22	1.71±0.12	48	0.03	0.047	1.71±0.20	1.43±0.18	23	0.37	0.28
Life span/time in study area (years)	4.16±0.40	3.31±0.38	48	0.08	0.025	2.74±0.30	2.70±0.38	24	0.63	0.33
Mean age at 1st breeding	3.00±0.25	2.62±0.26	10	0.85	0.35	3.22±0.47	2.43±0.32	3	1.00	1.00
Mean group size when first bred	4.49±0.45	4.00±0.44	20	1.00	0.87	4.36±0.78	4.40±1.02	6	0.17	1.00
Young fledged during 1st breeding season	2.31±0.35	2.66±0.38	20	0.62	0.48	2.43±0.70	1.90±0.82	6	0.35	1.00
Young fledged during 1st breeding season (ages of $\alpha=\beta$)	2.73±0.35	3.18±0.38	11	0.37	0.37	3.33±0.70	3.33±0.82	3	—	—
Mean wing chord at banding (mm)	69.8±2.2	72.0±2.0	68	0.16	0.32	71.7±3.0	69.1±3.3	32	0.22	0.29
Mean body mass at banding (g)	79.4±1.2	79.5±1.7	68	0.69	0.71	75.8±1.6	75.0±1.6	32	0.63	0.07

Includes only birds that had died or were no longer present in the study area. Comparisons are by binomial tests (percentage inheriting and known to have become a breeder) and paired Wilcoxon signed-ranks tests (all others). Values are presented using data for all watches, but P values are given for tests using all watches and only watches during which a bird fed. Significant ($P < 0.05$) results are in boldface.

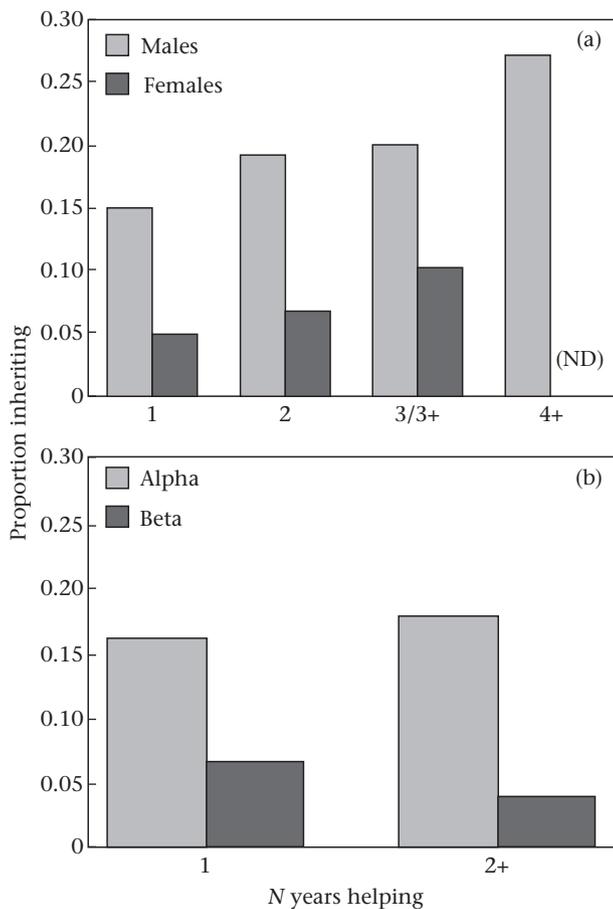


Figure 2. (a) Age-specific probability of acorn woodpecker helpers inheriting their natal territory. For males, birds that helped 4 or more years (4Y+) are combined; for females; birds that helped 3 or more years (3Y+) are combined ('ND' = data not plotted; values combined in the prior category). Sample sizes for the age categories are: males: 323, 126, 60 and 37; females: 294, 104 and 60. Differences tested using proportions test for a trend (Dalgaard 2008); males: $\chi^2_1 = 4.12$, $P = 0.042$; females: $\chi^2_1 = 2.58$, $P = 0.11$. (b) Proportion of males inheriting their natal territory as a function of whether they helped 1 year or 2+ years. Plotted are values for α males and β males from paired broodmates with known feeding histories. Sample sizes (helped 1 year, helped 2+ years): α (25, 28); β (30, 26). Neither N years helping nor status was significant in a logistic regression (deviance test, years helped: $\chi^2_1 = 0.3$, $P = 0.56$; status: $\chi^2_1 = 1.55$, $P = 0.21$).

(Selander 1964; Gaston 1978), few tests of either have been conducted, and many of those that have been performed are potentially confounded by age and/or quality.

Our results, based on a long-term study of marked individuals, indicate that, overall, both helper males and helper females increase their feeding rates with age, primarily between their second (2Y) and third (3Y) years. Although these differences were due primarily to the relatively low proportion of watches during which helpers participated when they were younger, paired comparisons of individuals indicated that males increased their relative feeding rates from when they were 2Y helpers, whether all watches or only watches at which they participated were included, and females did so when watches at which they participated were included. Thus, in most cases helpers fulfil this first requirement of the skills hypothesis.

More difficult is demonstrating that, by provisioning, helpers gain experience that benefits them later in life. We tested this using both linear models of all helpers for which we had data and comparing matched pairs of same-sex broodmates based on their feeding performance as 2Y helpers. These latter tests were not confounded by age or maternal effects since birds were born in the same year, reared together in the same group, and had the opportunity to feed at the same nests as 2Y helpers. Based on both sets of tests, we found no significant differences related to early provisioning rates among helper females, a finding that is not surprising given that a high proportion of females disperse out of the study and, thus, relatively few inherit their natal territory or otherwise remain in the study as breeders (Koenig et al. 2000). For males, the most cogent result was that birds provisioning more as 2Y helpers remained as helpers longer than birds provisioning less. Remaining longer in their natal group as a helper, α broodmates that fed more as 2Y birds were more likely to inherit (16.7% versus 6.3%) and become a breeder (43.8% versus 39.6%) in the population and, on average, survived (or were present) in the study area nearly a year longer (4.16 versus 3.31 years) than β broodmates that fed less. We found no evidence from either set of analyses, however, that more helpful helpers were more successful during their first breeding attempt when they did breed, even when matched by age, thus failing to support this critical prediction of the skills hypothesis. We also found no relationship between feeding status as a 2Y bird and size at banding, thus indicating that individual quality, as indicated by either size or dominance, was unlikely to have confounded these results.

Thus, contrary to the skills hypothesis, we found no evidence that the experience birds gain as 2Y helpers translates into greater success when birds become breeders, at least insofar as feeding behaviour provides an index of that experience. We are, however,

left with the question of whether the increased probability of inheritance gained by more helpful α birds was a consequence of their increased provisioning behaviour. Such a relationship would provide strong support for the pay-to-stay hypothesis, since it would be consistent with the idea that more helpful helpers are allowed to remain in the group longer and thereby are more likely to reap benefits of nepotism by eventually inheriting and breeding in their natal territory (Ekman et al. 2004).

Overall, the probability of inheriting the natal territory increased with age, significantly so for males. However, the age-specific probability of inheritance was not significantly different between α and β males, suggesting that whatever the cause of the increased inheritance by older birds, it was unrelated to their prior feeding history. Thus, our results failed to support the hypothesis that helpers in acorn woodpeckers gain significant direct fitness benefits either as a consequence of the skills they acquire through helping behaviour, or by being allowed to remain longer in their natal group by dominant breeders. It is always possible that larger sample sizes might result in more statistically significant differences, but given that our analyses are based on considerable data and few of our critical tests verge on significance, we consider it likely that any real fitness differences associated with feeding rates in this species are probably small at best.

The pay-to-stay hypothesis is predicated on the assumption that helpers are potentially evicted from groups if they do not provision at a rate expected by the breeders. No evidence for such behaviour exists in our population, where helpers appear to maintain access to group resources, particularly the granary where acorns are stored over the winter, despite the fact that they frequently do not participate in provisioning of young and may even leave their natal group entirely only to return months or years later, presumably after having attempted independent breeding off the study site. Whether experimental evidence in superb fairy-wrens (Mulder & Langmore 1993) or cooperatively breeding cichlid fishes (Balshine-Earn et al. 1998; Bergmüller & Taborsky 2005; Bergmüller et al. 2005) provides good support for this hypothesis is debatable, as discussed in the latter case by Wong & Balshine (2011). In the case of acorn woodpeckers, an alternative explanation for our finding that more helpful helpers remain in their natal group longer relies on the trade-off that helpers face between provisioning and engaging in other activities, in particular, foraging in search of reproductive opportunities (Mumme & de Queiroz 1985; Mumme et al. 1990; Walters et al. 1992). Specifically, helpers that feed less are likely to have more time to search for reproductive opportunities and consequently will be able to potentially find and disperse to such positions sooner than helpers that spend more time feeding offspring and less time searching for outside breeding opportunities. These latter birds are likely to be less successful at finding reproductive vacancies and thus remain as helpers longer, a side-effect of which is that they are more likely to inherit their natal territory and become a breeder within the confines of the study area (but not necessarily overall, since many helpers that disappear most likely find breeding opportunities outside the study area; Koenig et al. 1996, 2000). In other words, rather than postulating a direct link between provisioning behaviour and inheritance, as does pay-to-stay, we propose that differences in inheritance are an indirect result of the amount of time that helpers spend searching for outside breeding positions.

Both hypotheses predict that more helpful helpers will remain longer as helpers. However, in order to confirm pay-to-stay, it would be necessary to demonstrate that unhelpful helpers are more likely to be evicted by breeders. Such expulsion of helpers has not been observed in our population.

In acorn woodpeckers, as in most cooperatively breeding species, helpers are related to the young they feed and the fitness benefits

they receive by feeding, as opposed to merely by delaying dispersal, are primarily indirect via kin selection. Whether such species ever gain significant direct fitness benefits as a consequence of their provisioning behaviour remains to be demonstrated. Clearly, however, indirect fitness benefits cannot be a significant evolutionary force in species in which helpers are typically unrelated to the breeders (Clutton-Brock 2002; Hamilton & Taborsky 2005; Snowdon & Cronin 2007; McDonald et al. 2009). It is in such species, which make up a relatively small fraction of cooperative breeders, that fitness benefits such as the development of skills necessary for breeding and paying-to-stay are most likely to be found.

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