Animal Behaviour 119 (2016) 125–134

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 19 February 2016
Initial acceptance 7 April 2016
Final acceptance 10 May 2016
Available online 26 July 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.

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, Browning, & 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).

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http://dx.doi.org/10.1016/j.anbehav.2016.06.002
0003-3472/

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	II II IIII	I I I I
Bird 2	IIII III II	I I I
Bird 3	III IIII III	I I I I
Group	IIIIIIIII IIIIIIIII IIIIIIIII	I I I I I II I I I
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	II I II II	I I I	I I I I
Bird 2	I II III	I I I	I I I I I
Bird 3	III I II	I I I	I I I I
Group	IIIII IIIII	III III III	I I I II I I I I II I I
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	I I I I I I	I I I	I I I I
Bird 2	I II I II	I I I	I I I
Bird 3	I II I II	I I I	I I I I
Group	IIIIIII IIIIIII	III III III	I I I I I I I I I I I
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.