**ORIGINAL ARTICLE** 



# Active facilitation of helper dispersal by parents and siblings in the cooperatively breeding acorn woodpecker

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# Abstract

Offspring that delay dispersal in cooperatively breeding species have been hypothesized to gain direct fitness benefits via parental facilitation—being passively tolerated on their natal territory by their parents—thereby enjoying enhanced survival and increased probability of acquiring a breeding position in the population. Here we describe active facilitation in the acorn woodpecker (*Melanerpes formicivorus*) by parents and siblings assisting the dispersal of helpers in their social group. Helpers in this species compete for reproductive opportunities in "power struggles" that take place when all breeders of one sex die or disappear, creating a reproductive vacancy. Individuals compete at power struggles in coalitions of relatives, in which larger coalitions are more likely to be victorious. Based on observations of banded birds, we found that an estimated 26% of individuals competing as part of a winning coalition at a power struggle returned to their home territory at its conclusion, suggesting that they were facilitating the dispersal of kin (generally parents or siblings) that stayed to become breeders on the new territory. In at least one group, sibling facilitation was reciprocated; that is, a bird that was helped at a power struggle by a sibling joined that same sibling as part of a coalition at a subsequent power struggle. Dispersal facilitation is a novel means by which parents can nepotistically enhance the direct fitness of offspring and siblings can enhance each other's inclusive fitness in this highly social species.

# Significance statement

Parental facilitation—being passively tolerated on the natal territory—may provide significant direct fitness benefits to helpers in cooperatively breeding species. We describe active facilitation of helper dispersal in the acorn woodpecker, where helpers compete in coalitions for reproductive opportunities at "power struggles" following the death or disappearance of all breeders of one sex. About one-fourth of individuals—including both parents and siblings—competing at power struggles were apparently facilitators who assisted related helpers by participating in the power struggle but then returned to their home territory rather than stay to breed on the new territory. In at least one group, dispersal facilitation was reciprocated; that is, a bird that was helped at a power struggle by a relative later joined that same relative as part of a coalition at a subsequent power struggle. Active dispersal facilitation by parents and siblings is an important, previously unrecognized, form of nepotistic behavior in this highly social species.

Keywords Acorn woodpecker · cooperative breeding · dispersal facilitation · parental facilitation. reciprocity

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# Introduction

Cooperative breeders are species in which individuals beyond a pair assist in the production of young at a single brood or litter (Koenig and Dickinson 2016). One of the most common forms of cooperative breeding is "helping at the nest" in which individuals, typically offspring of the breeders in the group, delay their own reproduction and help provision younger siblings rather than breed independently (Cockburn 1998; Riehl 2013). This has led to a vibrant literature focusing on the potential ways that helping behavior may benefit the fitness of both the breeders in the group and the helpers themselves (Dickinson and Hatchwell 2004). As for the latter, helpers can gain significant indirect fitness benefits by feeding nestlings, protecting young from predators, and otherwise contributing to successful reproduction by related breeders (Brown 1980; Mumme 1992; Cusick et al. 2018).

Delayed dispersal by helpers can, however, yield fitness benefits in at least two additional ways. First, helpers may enhance survivorship of their parents by being vigilant and reducing the risk of their parents being depredated. Second, by having continued access to resources on their natal territory, the probability that helpers will disperse successfully and become a breeder on a high-quality territory may be enhanced. When this latter mechanism involves the offspring's parents it is referred to as "parental facilitation" (Brown 1987; Ekman et al. 2000; Chiarati et al. 2011) and is "passive" in that parents are assumed merely to be tolerating the presence of the helpers on their territory. In species with helpers, such parental facilitation can be considered a form of delayed reciprocity, since parents assist offspring that provided help previously at the parent's nest. Prior research in the Siberian jay (Perisoreus infaustus) and Seychelles warbler (Acrocephalus sechellensis) has shown that offspring with access to parental resources have higher survivorship and are more likely to acquire breeding positions, suggesting that parental facilitation can be a powerful means of increasing offspring fitness (Ekman et al. 2004; Eikenaar et al. 2007). Our understanding of the role of parental facilitation in cooperative breeding systems is, however, limited.

Here we document two forms of active facilitation parental and sibling—in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*). This species lives in permanently territorial groups of up to 15 (rarely more) individuals including a polygynandrous core of between one to eight cobreeding males, one to three joint-nesting females, and a variable number of nonbreeding helpers of both sexes from prior nests (Koenig et al. 2016, 2020). Cobreeding males are closely related to each other as are joint-nesting females; in both cases they are generally siblings (often something in between "full" and "half" siblings) or, more rarely, parents (or a parent's sibling) and their offspring. There is no extra-group mating (Dickinson et al. 1995), and thus helpers are related to the cobreeders of both sexes in their group.

Reproductive vacancies in acorn woodpecker groups occur following the death or disappearance of all the breeders of one sex (either all cobreeding males or all joint-nesting females). Vacancies provide opportunities for helpers to attain breeding status, either by dispersing to fill a vacancy of the same sex in another group (Koenig et al. 2000), or by inheriting breeding status within their natal territory after the opposite-sex breeders in their home group disappear, creating a reproductive vacancy that is filled by a coalition of immigrant birds unrelated to the residents (Koenig et al. 1998). Helpers of the same sex as the vacancy typically leave the group after the vacancy is filled; whether they do so voluntarily or are evicted by the new breeders is unknown.

Individuals attempting to fill a vacancy outside their natal group compete against birds from other groups that converge on the territory and fight in coalitions. These contests to fill reproductive vacancies, known as power struggles (Koenig 1981), can involve dozens of birds from up to several kilometers away, last for days or weeks, and are, importantly, typically won by the largest competing coalition of birds. Birds in the winning coalition become, at least potentially, the new cobreeders in the group (Hannon et al. 1985). Participants in power struggles also sometimes include breeders from other territories that are attempting to secondarily disperse (Koenig et al. 2016) and "trade up" to a breeding situation of superior quality.

Although power struggles are, in a few cases, motivated by other reasons such as an attempt to evict the resident group and take over control of a desirable territory (Koenig 1981), most fit the above description and are precipitated by a reproductive vacancy. However, participants in such power struggles do not always appear to be candidates for filling the reproductive vacancy even when one exists, and not all birds that fight as part of a winning coalition remain in the new group (Hannon et al. 1985; Barve et al. 2020b). If a bird returns to its natal territory rather than remaining on the new territory after its coalition has won a power struggle, what is the bird's motivation for attending the power struggle? Here we propose that such individuals are facilitating the dispersal of their relatives that do remain (or would have remained) on the new territory. They do this by increasing the coalition's size and thus its probability of winning the power struggle. Our method consists of identifying the benefit each bird present at a series of power struggles apparently stood to gain by its participation.

#### Methods

#### **General methods**

This work was part of a long-term study of acorn woodpecker social behavior at Hastings Natural History Reservation in central coastal California, USA ( $36^{\circ} 23'$  N,  $121^{\circ} 33'$  W), where > 6,000 birds have been color-banded and their life histories recorded since 1972 (MacRoberts and Mac-Roberts 1976; Koenig and Mumme 1987). The Reservation consists of a mix of plant communities (Griffin 1974); those inhabited extensively by acorn woodpeckers include foothill woodland, oak savanna, and riparian woodland (Koenig and Mumme 1987). Group composition was monitored by means of censuses made at approximately bimonthly intervals. Most birds were banded either as nestlings or as adults when feeding young or roosting in cavities at night (Stanback and Koenig 1994).

Power struggles were detected by raucous calls and displays of both intruding and resident individuals. Once a power struggle was encountered, we conducted one or more behavioral watches daily, usually lasting up to 3 h, observing birds through spotting scopes from blinds located in view of the group's granary. Watches were conducted until activity returned to normal, usually after several days but sometimes over a longer period. The data reported here are based on 11 power struggles monitored carefully between August 2013 and August 2017 to ascertain the identity of competing individuals and the coalitions of which they were a part out of an estimated 60 breeder turnovers taking place during this period. In total, 58 watches totaling approximately 102 h of observation were made at the 11 power struggles that were carefully observed. To supplement these observations, we include data from power struggles reported previously by Koenig (1981) and Hannon et al. (1985).

To interpret the apparent motivation for power struggles, we determined the composition of groups prior to their start and at their conclusion. It was not unusual, however, for a power struggle to take place intermittently, sometimes over a period of days or weeks, before resolution was achieved. In such cases, we considered the multiple outbreaks of fighting a single power struggle event. Unbanded birds, which inevitably make up a sizeable proportion of birds at power struggles, were not included in the analyses except in a few cases when they were involved in its resolution. It was not possible to record data blind because our study involved focal animals in the field.

### Categorizing birds at power struggles

When, as is usually the case, a power struggle is precipitated by a reproductive vacancy, we refer to the sex of the vacancy as "sex A." Birds observed at power struggles are referred to as "attendees." We partitioned attendees into four categories:

*1. Residents.* Current members of the group where the power struggle took place were considered "residents." For a power struggle of sex A, residents typically included cobreeders of sex B and any helpers of either sex that were still present in the group at the time of the power struggle. Note, however, that when several helpers of sex A are present in a group, they are sometimes able to rebuff attempts to fill the vacancy (Koenig et al. 1999).

2. *Contenders*. For a typical power struggle where the vacancy was of sex A, "contenders" were generally

helpers of sex A from other groups whose motivation was presumably to achieve breeder status in the group where the power struggle took place. Contenders often competed in coalitions, usually of siblings but sometimes including breeders from their home group. If the vacancy was precipitated by the disappearance of both sexes, contenders could be helpers of either sex. If no reproductive vacancy existed initially, motivation for the power struggle was apparently to evict some or all the resident birds.

3. Facilitators. Birds assisting contenders by fighting as part of their coalition were considered "facilitators." When a coalition won a power struggle, facilitators were identified as relatives that returned to their home group after the conclusion of the power struggle rather than remain in the (new) group. If the coalition did not win the power struggle, facilitators were birds that were related to contenders but judged to have been unlikely to remain in the new group had their coalition won the power struggle either because they were of the wrong sex as the vacancy or because they had previously attained breeder status and there was no evidence that they might have been interested in secondary dispersal. We identified two classes of facilitators. The first was related breeders of either sex from the same group as one or more contenders. Such birds were apparently assisting their offspring and returned to their home territory at the conclusion of the power struggle. We considered these cases of parental facilitation. The second class of facilitators was helpers, usually but not always of sex A, that were part of a coalition fighting for the vacancy, but then, after winning the power struggle, returned to their natal group rather than staying to become a cobreeder with their siblings at the new group. These were considered cases of sibling facilitation. Facilitators are believed to gain indirect fitness benefits by increasing the chances of related contenders (their offspring or siblings) winning a power struggle and thereby enhancing the contenders' reproductive success over what would have been achievable as part of a smaller coalition not including the facilitators.

4. Others. Not all attendees fit into one of the above categories. Some individuals took advantage of the chaos of the power struggle to steal stored acorns from the granary, structures central to acorn wood-pecker territories where acorns are stored in the autumn for later consumption. Other individuals, from groups adjacent to the power struggle, may have been defending their own territory from birds participating in the power struggle. We refer to birds observed at power struggles that we could not identify as residents, contenders, or facilitators as "oth-

ers," as their motivation was apparently unrelated to dispersal of themselves or their relatives.

A recurring problem in our efforts to categorize individuals involved attendees that were breeders in their home group but apparently did not have any known potential helpers of the appropriate sex participating in the power struggle. Our classification of such individuals was based, as much as possible, on their individual history. If a breeder remained in the new group following the conclusion of the power struggle or if the breeder continued to exhibit behavior suggesting an interest in switching groups (such as being observed intruding at other groups or attending other power struggles), we considered it a contender attempting to disperse secondarily from its current group. If the breeder did neither of these, we placed the individual in the "other" category. Details concerning individual cases are summarized in the "Notes" column of Table 3.

# Results

Table 1 summarizes the power struggles monitored for this study. Combined with non-experimentally induced power struggles reported by Koenig (1981) and Hannon et al. (1985), nearly half (46.9%) were motivated by female vacancies, while nearly one-third (31.3%) involved male vacancies (Table 2). Three (9.4%) involved vacancies of both sexes or took place on a vacant territory. Four (12.5%) occurred on a territory where there was no reproductive vacancy and resulted in either no change in group composition or eviction and replacement by the invading group; such cases apparently involved groups attempting to improve their situation

Table 1 Summary of power struggles (PS) monitored for this study

PS	Dates	Group	Original cause	Result	Comments
1	11–12 Aug 2013	CAVI	♀ vacancy combined with temporary capture of 2 of the 3 ♂♂	♀ vacancy filled by a ♀ from PLQE; ♂♂ evicted and replaced by a coalition of $3 ♂♂$ from BLMP	♀ had been gone for some time, but the PS started following 2 of the ♂♂ being captured and held temporarily for process- ing; the ♂♂ were subsequently driven out by a large coalition from group BLMP (one of which had previously moved to MISH)
2	30 Mar & 2 May 2014	JAIM	♀ vacancy	Filled by a $\circleon$ from KNOL	Preplaced in March; fighting resumed into May but did not lead to further change in group composition
3	7 Mar 2014	ROBH	$\bigcirc$ vacancy	Filled by a coalition of 2 ♀♀ from CAVI	
4	25 Mar & 2 May 2014	PLQE	♂ vacancy	Entire group evicted and replaced	Territory taken over by UPBA group and forced into an adja- cent territory
5	18-25 Mar 2014	KNOL	$\bigcirc$ vacancy	Filled by a coalition of 3 ♀♀ from PLQE	
6	14–15 May 2014	LHAY	♂ vacancy	$\stackrel{\bigcirc}{_{\sim}}$ breeder evicted, replaced by coalition of 2 $\stackrel{\bigcirc}{_{\sim}}\stackrel{\bigcirc}{_{\sim}}$	With new $QQ$ , the 2 helper $dd$ in the group inherited and became breeders
7	8 Apr 2015	UPBA	Vacant territory	New group	Colonized by a coalition of $2 \Im \Im$ from PLQE and a $\Im$ from CABI
8	2–4 Apr 2016	A1	$\bigcirc$ vacancy	Filled by a coalition of 3 ♀♀ from KOUT	
9	3–4 Apr 2016	RE10	Vacant territory	New group	Colonized by a $\Im$ from BINO and a coalition of 2 NOBA $\Im \Im$
10	Mar–Aug 2017	PLQE	$\bigcirc$ vacancy	Eventually filled by a coalition of $4 \bigcirc \bigcirc$ from JAIM	PS continued intermittently for months
11	5–6 Aug 2017	1800	No initial vacancy	් replaced by a coalition of 2 NOBA ්්	Started with $\bigcirc \bigcirc$ fighting but after several days the breeder $\bigcirc$ disappeared

Table 2Summary of theapparent causes of powerstruggles monitored for thisstudy and reported by Koenig(1981) and Hannon et al.(1985); excluded are powerstruggles of unknown origin andthose initiated by experimentalremovals

Apparent cause	This study	Koenig (1981)	Hannon et al. (1985)	Total
♀ vacancy	5 (45.5%)	7 (46.7%)	3 (50.0%)	15 (46.9%)
3 vacancy	2 (18.2%)	5 (33.3%)	3 (50.0%)	10 (31.3%)
Vacancy of both sexes	1 (9.1%) <sup>a</sup>	_	_	1 (3.1%)
Vacant territory	2 (18.2%)	_	_	2 (6.3%)
No initial vacancy	1 (9.1%)	3 (20.0%) <sup>b</sup>	_	4 (12.5%)
N power struggles	11	15	6	32

<sup>a</sup>Includes PS1 (Table 1), where there was a female vacancy but the power struggle started following the capture of two of the three males for unrelated reasons

<sup>b</sup>In two of these three cases there was no change in group composition, while in the third the entire group was expelled

by usurping a territory of superior quality. Thus, most power struggles—87.5% of the total sample—were motivated by the potential for invading birds to attain a breeding position by filling a reproductive vacancy attributable to the death or disappearance of the breeders in the group where the power struggle took place.

In total, we identified 36 males and 81 females attending power struggles from groups other than the one at which the power struggle took place. Table 3 provides background information on these individuals, including the rationale for their categorization. The size of coalitions is not stated explicitly in Table 3 but can be deduced by adding up the number of birds listed as being at the power struggle from the same group along with, when relevant, relatives present at the power struggle that had dispersed previously to another group (as stated in the "Notes" column).

Some of the complexities of sibling facilitation, along with a case of apparent reciprocity, are illustrated by the histories of seven helper (H) female siblings from group PLQE at three power struggles (PS), all of which they won (Fig. 1). All five extant helpers participated in PS1 (Fig. 1a, top) at group CAVI in August 2013. After winning that power struggle,  $\bigcirc$  5151 and  $\bigcirc$  5390 remained at group CAVI (where they attained breeder status), while the other three returned to group PLQE, remaining as helpers (Fig. 1a, bottom). The next spring, H<sup>Q</sup> 5079 and her two sisters that had previously remained at group CAVI ( $\bigcirc$ 5151 and  $\bigcirc$ 5390) fought as a coalition in PS3 at group ROBH (Fig. 1b, top), after which 25390 remained at group ROBH as a breeder while 25079returned to group PLQE (as a helper) and B<sup>Q</sup> 5151 returned to group CAVI. Later the same month, four of these sisters, again including 25151, were joined by two younger sisters hatched the prior spring (H $\stackrel{\bigcirc}{_{+}}$ 5482 and H $\stackrel{\bigcirc}{_{+}}$ 5486) in PS5 at group KNOL (Fig. 1c, top). After winning PS5, ♀5007 and 25079 remained as breeders (along with a third bird, presumably a younger sibling fledged from a missed nest who was thus unbanded and not illustrated in Fig. 1). Meanwhile, the other sisters returned to group PLQE or, in the case of B $\bigcirc$ 5151, previously joined by  $\bigcirc$ 5007 and  $\bigcirc$ 5079 at PS1, to group CAVI (Fig. 1c, bottom).

This example illustrates that siblings competing in coalitions at power struggles can include relatives that had previously dispersed and achieved breeding status elsewhere. Such cases can thus involve reciprocity, as illustrated by  $\bigcirc$ 5151, who was joined by her sisters  $\bigcirc$ 5007,  $\bigcirc$ 5079, and  $\bigcirc$ 5390 in moving to group CAVI (PS1) but later joined  $\bigcirc$ 5079 and  $\bigcirc$ 5390 to win PS3 (after which  $\bigcirc$ 5390 moved to group ROBH) and with  $\bigcirc$ 5007 and  $\bigcirc$ 5079 (along with  $\bigcirc$ 5389 and the two younger sisters) to win PS5, thereby facilitating  $\bigcirc$ 5007 and  $\bigcirc$ 5079's move to group KNOL.

In total, 38.9% of males and 72.8% of females identified at the power struggles were believed to be contenders attempting to disperse to and become a breeder on the territory where the power struggle occurred (Table 4). Thirty birds (41.7% of males; 18.5% of females) were judged to be facilitators, of which slightly over one-fourth (26.7%) were parental facilitators and the other 73.3% sibling facilitators. The remaining 12.0% of birds ("others") were apparently at the power struggle for some reason other than potentially dispersing themselves or facilitating the dispersal of relatives.

## Discussion

#### **Dispersal facilitation**

Most power struggles were initiated by a reproductive vacancy and a large fraction of the participating birds were helpers from other groups that would benefit by moving to, and achieving breeding status in, the territory where the power struggle took place (referred to as the "new" territory). These contenders were identified from groups up to 1.86 kms away and from as many as 15 different social groups (Table 3, PS10). Of particular interest are the 41.7% of males and 18.5% of females that returned to their home territory after winning the power struggle (or that we believe

Table 3 Banded acorn woodpeckers observed at the power struggles monitored for this study and their apparent motivation for attendance

PS	Group	Residents	Contenders	Facilitators	Others	Notes
1	CAVI	B♂3165x B♂3284x H♂5094x H♂5378x	B♂4621 (BLMP) H♂4933 (BLMP) H♂4935 (BLMP) H♂5278 (SHIL) H♀5151 (PLQE) H♀5325 (CABI) H♀5390 (PLQE)	H $^{3}$ 5376s (BLMP) <sup>1</sup> H $^{3}$ 5377s (BLMP) <sup>1</sup> H $^{5}$ 5007s (PLQE) <sup>1</sup> H $^{5}$ 5007s (PLQE) <sup>1</sup> H $^{5}$ 5389s (PLQE) <sup>1</sup>	B♀4938 (JAIM) <sup>2</sup>	<sup>1</sup> These were all siblings of the birds that displaced the residents but returned home rather than remain at CAVI at the conclusion of the PS. <sup>2</sup> B♀4938 was observed at CAVI taking acorns from the granary to her home group JAIM, which was adjacent to CAVI.
2	JAIM	B∂4890	H $\bigcirc$ 5103 (KNOL) B $\bigcirc$ 4854 (UPBA) <sup>3</sup> H $\bigcirc$ 4470 (SHIL) H $\bigcirc$ 5091 (SHW) H $\bigcirc$ 5430 (PIPE)			<sup>3</sup> B♀4854 was involved in PSs at JAIM (PS2) and at PLQE (PS4), territories very close to each other where PSs occurred nearly simultaneously. Her involvement at PS2 may have been secondary to the one at PLQE (where she ultimately moved), but she was apparently prospecting to leave UPBA and thus categorized as a <i>contender</i> .
3	ROBH	B♂4884 B♂5220 H♂5583inh H♂5585inh	B⊊5390 (CAVI) <sup>4</sup>	H♀5079s (PLQE) <sup>4</sup> B♀5151s (CAVI) <sup>4</sup>		${}^{4}$ B $\bigcirc$ 5390 stayed at CAVI following PS1 but moved here after being facilitated by two of her sisters, H $\bigcirc$ 5079 (still at group PLQE) and B $\bigcirc$ 5151, her sister who had moved with her to group CAVI following PS1.
4	PLQE	$H^{3}5152x$ $H^{3}5153x$ $B \bigcirc 4629x$ $H^{2}5151x$ $H \bigcirc 5389x$ $H \bigcirc 5482x$ $H \bigcirc 5486x$	<b>B</b> $^{\circ}$ <b>5006 (UPBA)</b> H $^{\circ}$ <b>5</b> 303 (DIPS) H $^{\circ}$ <b>5</b> 474 (DIPS) H $^{\circ}$ <b>5</b> 474 (PLAN) <b>B</b> $^{\circ}$ <b>4854 (PLAN)</b> <b>B</b> $^{\circ}$ <b>4854 (UPBA)</b> <b>B</b> $^{\circ}$ <b>5014 (UPBA)</b> H $^{\circ}$ <b>5</b> 317 (CHIM) H $^{\circ}$ <b>5</b> 370 (SHIL)		B♂4890 (JAIM) <sup>5</sup> B⊊5103 (JAIM) <sup>5</sup>	<sup>5</sup> B♂4890 had been a successful breeder at JAIM for over 2 years, while B♀5103 had recently moved to JAIM (PS2) and remained there until 2017. Thus neither bird was likely to be prospecting, nor did they have offspring whose dispersal they might have been facilitating. Also, JAIM is adjacent to PLQE, making it likely they were defending their own territory or drawn into the PS for some other reason.
5	KNOL	B♂3399 B♂3753 B♂5059	H♀5007 (PLQE) H♀5079 (PLQE) ♀NOBA (PLQE)	B♀5151s (CAVI) <sup>6</sup> H♀5389s (PLQE) H♀5482s (PLQE) H♀5486s (PLQE)	ి5204 (HORS) <sup>7</sup>	<sup>6</sup> B♀5151 had previously moved to CAVI but was born at PLQE and a sister of the 3 PLQE ♀♀ that remained (including the ♀NOBA, who was presumably from a missed nest). <sup>7</sup> ♂5204 had not been seen since leaving his home group early in 2013. As a ♂ at what was an unambiguous ♀PS with no known relatives whose dispersal he might have been facilitating, we classified him as <i>other</i> .
6	LHAY	H♂4928inh H♂5251inh B♀4570x B♀4590x	H♀ <b>5476 (DIPS)</b> H♀5247 (BLM2) H♀5140 (HORS)	B♂5250s (BRWN) <sup>8</sup> H♂5202s (HORS) H♂5207s (HORS) H♂5416s (HORS)		<sup>8</sup> B♂5250 had previously moved to BRWN but was born at LHAY and was thus a sibling of the two helper ♂residents, H♂4928 and H♂5251. He therefore was presumably helping them defend the territory against intruders and was considered a <i>sibling</i> <i>facilitator</i> . He later switched territories and returned home to LHAY, joining H♂5251 (now B♂5251) as a cobreeder.
7	UPBA		H♂5562 (PLQE) H♂5698 (PLQE) H♀4904 (CABI)	B♂5006p (PLQE) <sup>9</sup> B♂5153p (PLQE) <sup>9</sup> H♂5700s (PLQE) <sup>9</sup> H♂5701s (PLQE) <sup>9</sup> B♀4854p (PLQE) <sup>9</sup>		<sup>9</sup> These birds returned to PLQE following the PS, and thus were all considered <i>facilitators</i> of the 2 helpers that remained.
8	A1	B♂4561 H♂5750inh	H $\bigcirc$ 5309 (KOUT) H $\bigcirc$ 5642 (KOUT) H $\bigcirc$ 5740 (KOUT) B $\bigcirc$ 5155 (LAMB) <sup>10</sup> H $\bigcirc$ 5349 (BKOK) H $\bigcirc$ 5383 (LA2) H $\bigcirc$ 5465 (LA2)	H⊋5741s (KOUT)	B♂4568 (UA2) <sup>11</sup> H♂5265 (UA2) <sup>11</sup> H♂5658 (BINO) <sup>11</sup>	<sup>10</sup> B♀5155 had previously inherited breeder status at LAMB in late 2015. However, the group did not appear to have bred in 2016 and thus B♀5155 is considered a <i>contender</i> potentially prospecting for a new group. <sup>11</sup> These 3 males from nearby groups had no known ♀♀ relatives participating in this ♀PS, and may have been defending their own territories. We thus classified them as <i>athers</i>

Ta	able 3 (continued)						
PS	Group	Residents	Contenders	Facilitators	Others	Notes	
9	RE10		H♂5658 (BINO) H∂5739 (KOUT) <sup>13</sup> 2 NOBA ♀♀ (UNK)	B♂4051p (BINO) <sup>12</sup> H⊋5825s (KOUT) <sup>13</sup>		<sup>12</sup> B <sup>3</sup> √4051 fought at this PS as a <i>parental facilitator</i> of H <sup>3</sup> √5658, his son from 2015. <sup>13</sup> H <sup>3</sup> √5739 and H <sup>2</sup> 5825 were siblings that both participated in the PS. Since RE10 had been vacant, either, but not both, could have remained and bred had they won (which they did not). We therefore classified one of them (H <sup>3</sup> √5739, who was older) as a <i>contender</i> and H <sup>2</sup> √5825 as a <i>sibling facilitator</i> .	
10	PLQE	B♂5006 B♂5152 B♂5153 H♂5878 H⊋5876x	B ${}^{\circ}$ 5103 (JAIM) H ${}^{\circ}$ 5944 (JAIM) H ${}^{\circ}$ 5946 (JAIM) B ${}^{\circ}$ 4713 (BUCK) <sup>14</sup> H ${}^{\circ}$ 5192 (PIPE) H ${}^{\circ}$ 5498 (CECN) H ${}^{\circ}$ 5715 (KNOL) B ${}^{\circ}$ 5734 (HORS) <sup>15</sup> H ${}^{\circ}$ 5771 (1500) H ${}^{\circ}$ 5912 (LOLF) B ${}^{\circ}$ 6001 (CAB) <sup>16</sup> H ${}^{\circ}$ 5972 (MACR) H ${}^{\circ}$ 5938 (Y) H ${}^{\circ}$ 5938 (Y) H ${}^{\circ}$ 5953 (UPBA) H ${}^{\circ}$ 5955 (CHIM) H ${}^{\circ}$ 5955 (CHIM) H ${}^{\circ}$ 5977 (ROBH) ${}^{\circ}$ 6005 (UNK)	H36002s (CHIM) <sup>17</sup> H35891s (JAIM) B35698p (UPBA) <sup>18</sup> H35952s (UPBA) <sup>18</sup> B24904p (UPBA) <sup>18</sup>	H∂5880 (CAVI) <sup>19</sup> H∂5881 (CAVI) <sup>19</sup> B♀4629 (CAVI) <sup>19</sup> B♀4493 (FNCH) <sup>20</sup> B♀4968 (RE03) <sup>21</sup> B♀509 (AMAD) <sup>21</sup> B♀5659 (MIKE) <sup>22</sup>	<ul> <li><sup>14</sup>Although B Q4713 had been a breeder at BUCK since 2013, she apparently left the group after the long-time breeder ∂disappeared in early 2016. Thus, we considered her a <i>contender</i> interested in switching territories.</li> <li><sup>15</sup>B Q5734 bred at HORS in 2015 and 2016, but the group failed to initiate a nest either year. By 2017 she was foraying, presumably in search of a new breeding opportunity, and thus we considered her a <i>contender</i> both here and at PS11.</li> <li><sup>16</sup>At the time of this PS, CABI had no breeder ∂. Thus, although B Q6001 was apparently the breeder Q at CABI, we assumed she was prospecting for a new territory and considered her a <i>contender</i> along with her daughter HQ5970.</li> <li><sup>17</sup>The origin of H∂6002 (banded at CHIM early in 2017) was unclear, but he was thought to be from a missed nest, and thus a sibling of HQ5954 and HQ5955. We thus classified him as a <i>sibling facilitator</i>.</li> <li><sup>18</sup>Both B∂5698 and BQ4904 bred at UPBA in 2017 and 2018 and were thus assumed to be <i>parental facilitators</i> of HQ5950, their daughter from 2016. Since this was a Q vacancy, we classified H<sup>3</sup>5952 as a <i>sibling facilitator</i> of his sister, HQ5950.</li> <li><sup>19</sup>These three birds were from the adjacent CAVI territory that did not contain any helper Q poserved at the PS. Further, BQ4629 bred successfully at CAVI in both 2015 and 2016 and was still breeding there as of 2022. We thus classified them as <i>other</i>.</li> <li><sup>20</sup>BQ4493 was a long-time breeder at her home group (FNCH) and was considered unlikely to be prospecting for a new territory. Group FNCH, however, contained one helper Q, who was not seen at the PS. We thus considered her <i>other</i>, but it is possible that the helper Q was missed and that BQ4493 was a <i>parental facilitator</i>.</li> <li><sup>21</sup>Females BQ496, and BQ5209 were long-time breeders at their home groups and were judged unlikely to be interested in switching territories. Neither of their home groups contained a helper Q who might have competed at the PS, and thus we considered</li></ul>	

#### Table 3 (continued)

PS	Group	Residents	Contenders	Facilitators	Others	Notes
11	1800	B♂4589x B♀4261	δ6069 (UNK)           δNOBA (UNK)           H\$\25636 (1500)           H\$\25771 (1500)           H\$\25774 (1500)           B\$\25774 (1600)           H\$\25763 (1600)           H\$\25855 (1600)           H\$\25712 (SHIL)           H\$\25990 (SHIL)	B♀4672p (1500) <sup>23</sup> B♀5813p (SOSP) <sup>23</sup>		<sup>15</sup> See PS10. <sup>23</sup> These 2 ♀♀ were breeders in their home groups in 2016 and 2017 and were likely present at this PS as <i>parental facilitators</i> of their daughters (H♀5636, H♀5771, and H♀5774 from group 1500 and H♀5866 from group SOSP, respectively).

Birds winning the power struggle and remaining in the territory are boldface. *B* breeder; *H* helper; 4-letter code in parentheses is the group from which the bird originated; PS numbers refer to power struggles in Table 1; "x" indicates a bird leaving or being evicted from the group; "s" indicates a sibling facilitator; "p" a parental facilitator; "inh" indicates a bird that inherited the territory following the power struggle; *NOBA* unbanded bird; *UNK* unknown group



**Fig. 1** Histories of seven helper female siblings from group PLQE at three power struggles in 2013 and 2014, all of which they won. The seven sisters are illustrated at the top along with the year they were born. The three power struggles go left to right starting with PS1 (see Table 1) at group CAVI (**a**), followed by PS3 at group ROBH (**b**), and ending with PS5 at group KNOL (**c**). The top panels illustrate the birds participating in the power struggle, the groups in which

they were living, and (in boldface) the group where the power struggle took place. The bottom panels illustrate the groups where each bird stayed at the conclusion of the power struggle (separated by the dashed lines), either remaining in the group where the power struggle took place or returning to their prior group. Also provided is the approximate distance between the main groups involved. Further details are provided in the text

 Table 4
 Summary of attendees at power struggles (excluding residents)

Category	Males	Females	Total	
Contenders	14 (38.9%)	59 (72.8%)	73 (62.4%)	
Parental facilitators	4 (11.1%)	4 (4.9%)	8 (6.8%)	
Sibling facilitators	11 (30.6%)	11 (13.6%)	22 (18.8%)	
Others	7 (19.4%)	7 (8.6%)	14 (12.0%)	
N birds	36	81	117	

would have had they won the power struggle) and thus whose participation apparently facilitated the dispersal of relatives by fighting as part of, and thus increasing the competitiveness of, their coalition. Although the reasons for why these birds did not remain on the new territory are unknown and likely diverse, the result is altruistic in that it potentially enhanced the fitness of relatives that stayed in the new group at a cost of time and energy to themselves. These individuals included breeders helping their offspring (parental facilitation), and offspring helping their siblings (sibling facilitation). A case of facilitation of dispersal by presumed female siblings was reported previously by Hannon et al. (1985).

Both sibling and parental facilitation were common. Of the 11 power struggles investigated here, parental facilitation was identified at 4 (36.4%) and sibling facilitation at 8 (72.7%). Given the many unbanded birds typically present at power struggles, these values likely underestimate the frequency of facilitation. Facilitation increases coalition size, rendering them more likely to win power struggles (Hannon et al. 1985). What, however, is the benefit to facilitators, and why do they not remain at the new territory?

Although larger coalitions of birds are more likely to win power struggles, inclusive fitness of cobreeders declines with coalition size, dramatically so for larger coalitions; the only apparent exception being that of joint-nesting female duos (Koenig et al. 2023a). Thus, although apparently altruistic, birds that facilitate the dispersal of relatives may achieve greater fitness by assisting relatives to disperse and then returning home than they would by remaining in the new group as part of a large breeding coalition. In at least some cases, facilitation may be reciprocated, as illustrated by the sisters at group PLQE (Fig. 1).

Unknown is the basis on which birds in a coalition decide whether to remain in the new territory or not. One possibility is that such facilitators are subordinate to the birds that stay to become breeders, a hypothesis consistent with the evidence that larger, and presumably older, individuals within broods are more successful at gaining reproductive opportunities (Koenig et al. 2011a). Contrary to the prediction that older helpers in a coalition are more likely to remain in the new group following a power struggle, however, the birds remaining in PS1 ( $\bigcirc$ 5151 and  $\bigcirc$ 5390) were two of the youngest birds in the coalition.

A difficulty with identifying parental facilitators is excluding the possibility that breeders attending a power struggle are trying to improve their own current position by dispersing secondarily. Although we can never be certain about the intent of such individuals, we attempted to identify them based on what we knew about their prior history. At one end of the spectrum was  $\bigcirc$  5734 (PS10 and PS11). Although this bird was the breeder female at HORS in 2015 and 2016, the group apparently failed to initiate a nest either year. Prior to the 2017 breeding season,  $\bigcirc$  5734 was observed foraying and participating in power struggles at several territories. We therefore judged that she was likely prospecting for a superior breeding position and was a contender at these power struggles. Alternatively, 34051 attended PS9 with his son (H $^{5}$ 5658) from the prior year. After they won the power struggle, 35658 remained as the new breeder while 34051 returned home to group BINO. In this case, 34051's participation facilitated the successful dispersal of his son who, as a singleton, would have been unlikely to win the power struggle otherwise.

# **Facilitation and reciprocity**

Offspring acorn woodpeckers almost always help at the nest, a behavior that enhances reproductive success under most environmental conditions (Koenig et al. 2011b). Thus, when breeders assist helper dispersal by increasing the size of their coalition at a power struggle, they are reciprocating the help they received while breeding. The opposite of "pay-to-stay" (Kokko et al. 2002; Bergmüller and Taborsky 2005), helpers can be considered being repaid for their prior assistance. Sibling facilitation of offspring dispersal can also involve reciprocity. Birds that acquired a breeding position previously with the assistance of siblings may temporarily rejoin those same siblings to help compete as a coalition for a subsequent vacancy. By facilitating the dispersal of kin, such birds are increasing the presence of relatives on the landscape, which could potentially provide opportunities for refuge (secondary dispersal) should a bird later lose its granary or be evicted from its territory.

Parental facilitation as envisioned by Brown (1987) encompassed three behaviors: (1) increased survival of offspring as a consequence of not being evicted from their home territory; (2) increased chance of achieving breeding status associated with using the home territory as a base from which to foray and search for reproductive vacancies; and (3) an increased possibility of inheriting and achieving breeding status on their home territory. All are potentially applicable to acorn woodpeckers (Barve et al. 2020a; Koenig et al. 2023b). Such behaviors are passive, only involving parents tolerating the presence of offspring. In contrast, the behaviors we describe here involve facilitators actively participating in coalitions that fight to fill a reproductive vacancy at a group to which their offspring or siblings will potentially disperse and subsequently breed. We are aware of no comparable nepotistic behavior previously described in a cooperative breeder.

# Participants in power struggles

Based on an automated radio-telemetry system, Barve et al. (2020b) reported on the birds detected at three putative female power struggles. Of the birds detected, those that were considered candidates for potentially filling the vacancy (female helpers) were referred to as "warriors." Breeder females and any males from other groups were referred to as "spectators," since they either already had breeding status elsewhere or were presumed to be of the wrong sex to potentially fill the vacancy that initiated the power struggle. Birds identified as spectators spent an average of 52 min day<sup>-1</sup> at power struggles and were hypothesized to be gathering social information-that is, gaining information about the group and other birds present at the power struggle. This hypothesis is consistent with the extensive knowledge that acorn woodpeckers apparently have about the social status of other individuals in the population (Pardo et al. 2018, 2020a, b).

Our analyses here, based on behavioral observations, clarifies the motivation of many of the participants at power struggles that are apparently not candidates to fill an initiating reproductive vacancy. Of 44 birds attending power struggles that were neither residents nor contenders, 30 (68.2%) were classified as either parental or sibling facilitators. The motivation of the remaining 14 (31.8%) nonresidents and noncontenders was apparently for a reason other than facilitating dispersal of kin. Some of these latter birds were possibly attracted to the activity from a nearby group or were apparently trying to "steal' stored acorns. Others, however, may have been "spectators" attempting to gather information, either of the territory where the power struggle was taking place or of other attendees at the power struggle. If so, the information being acquired, and how such information might eventually benefit them, remains to be determined.

#### **Facilitation and fitness**

Quantifying the benefit of joining a coalition to enhance its competitiveness at a power struggle is difficult. Ideally, it would be necessary to know the success rate of differentsized coalitions, a value that is likely to differ depending on the season, population density, quality of the territory, and other factors, including the fitness consequences of breeding in coalitions—which itself has proved challenging to determine (Mumme et al. 1988; Barve et al. 2021; Koenig et al. 2023a). Estimating the success rate of coalitions is likely to remain out of reach until it is possible to track the fate of birds emigrating out of the study area. Although current tracking technology has yielded insight on the foray behavior of acorn woodpeckers (Barve et al. 2020a), much remains to be done before it will be possible to resolve the dispersal-mortality confound of finite study areas such as ours (Koenig et al. 1996).

Power struggles are chaotic affairs involving a great deal of fighting and physical contact. It is not unusual for birds to fall to the ground, locked leg-to-leg in combat (Koenig 1981). We have observed occasional injuries, and birds participating in power struggles are clearly vulnerable to predation. Moreover, given that power struggles can start within minutes of a vacancy arising (Hannon et al. 1985), parental facilitators fighting elsewhere risk losing their own territory when leaving it undefended. There are thus significant costs to participating in power struggles. Facilitators apparently gain more than they risk by increasing the chances of close relatives gaining a reproductive opportunity, particularly if the relative has no other samesex siblings and is thus unlikely to win a power struggle on its own. It is also possible, however, that facilitators do not fight as vigorously or spend as much time fighting as contenders that eventually gain a reproductive opportunity after winning a power struggle. We currently do not have data to examine this possibility.

To estimate inclusive fitness of social behaviors like breeding in coalitions, one needs to compare fitness when breeding singly (Koenig et al. 2023a). The difficulties in determining the costs and benefits of facilitation, however, render its inclusive fitness consequences unclear. Nonetheless, parental and sibling facilitation of dispersal provide yet another example of the importance of kin selection to the evolution of social behavior (Hamilton 1964a, b).

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Author contributions NDGH and ELW conceived the study; NDGH collected the observational data at the power struggles; all authors helped collect background data used to interpret results. WDK wrote the initial draft of the paper based in part on NDGH's PhD thesis; all authors reviewed and edited subsequent drafts.

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Data availability All data are available in the Tables.

#### Declarations

**Ethics approval** All applicable international, national, and institutional guidelines for the use of animals were followed. This study was conducted under the auspices of the Animal Care and Use Committees of Old Dominion University (protocols 12–001 and 15–001), the University of California, Berkeley (protocol R010-0412), and Cornell University (protocol 2008–0185).

**Competing interests** The authors certify that they have no financial or non-financial competing interests.

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