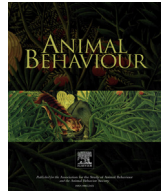




Contents lists available at ScienceDirect

## Animal Behaviour

journal homepage: [www.elsevier.com/locate/anbehav](http://www.elsevier.com/locate/anbehav)

## Territory inheritance and the evolution of cooperative breeding in the acorn woodpecker

Walter D. Koenig<sup>a,\*</sup> , Joseph Haydock<sup>b</sup>, Hannah L. Dugdale<sup>c,d</sup> , Eric L. Walters<sup>e</sup> <sup>a</sup> Hastings Natural History Reservation, University of California Berkeley, Carmel Valley, CA, U.S.A.<sup>b</sup> Department of Biology, Gonzaga University, Spokane, WA, U.S.A.<sup>c</sup> Faculty of Biological Sciences, School of Biology, University of Leeds, Leeds, U.K.<sup>d</sup> Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands<sup>e</sup> Department of Biological Sciences, Old Dominion University, Norfolk, VA, U.S.A.

## ARTICLE INFO

## Article history:

Received 23 April 2023

Initial acceptance 7 June 2023

Final acceptance 18 July 2023

Available online xxx

MS. number: A23-00204R

## Keywords:

acorn woodpecker

cooperative breeding

dispersal

fitness

lifetime reproductive success

*Melanerpes formicivorus*

territory inheritance

There are two main hypotheses for why offspring in cooperatively breeding taxa delay dispersal and remain on their natal territory rather than disperse. First, ecological constraints may force offspring to remain on their natal territory until a reproductive opportunity presents itself in an otherwise saturated habitat. Alternatively, delaying dispersal and helping kin may increase an offspring's inclusive fitness. One means by which offspring might enhance their direct fitness by delaying dispersal is by inheriting breeding status on their natal territory. Such territory inheritance regularly occurs in acorn woodpeckers, *Melanerpes formicivorus*, a species whose social groups consist of a cooperatively polygynandrous breeding core along with nonbreeding helpers of both sexes that are offspring from prior breeding efforts. Here we examine the life-history differences and the fitness consequences of birds attaining breeder status by either inheriting their natal territory or dispersing to a new territory. Despite significant differences in life history, including the mean territory quality on which individuals bred and mean co-breeder coalition size of breeders, we found no statistical differences in either direct or kin-selected (indirect) fitness benefits for breeders that inherited and dispersed. The incidence of birds engaging in both strategies, inheriting their natal territory and later dispersing, or dispersing but later returning to inherit their natal territory, further reduces the potential direct fitness benefits of inheritance relative to dispersal, since neither precludes the other. Territory inheritance is an important, alternative means of achieving breeding status in this population. However, ecological constraints to dispersal and kin-selected fitness benefits as a helper likely play larger roles driving the acorn woodpecker's extraordinary social system.

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The debate over whether ecological constraints or benefits of remaining on the natal territory ('benefits of philopatry') are the selective drivers of delayed dispersal and helping behaviour in cooperative breeders (species in which more than one pair of individuals assist in raising young; Koenig & Dickinson, 2016) dates back over 40 years (Emlen, 1982; Koenig et al., 1992; Stacey & Ligon, 1987). Although controversy continues, in many cases both constraints and benefits of philopatry appear to be involved, their relative importance varying depending upon environmental conditions (Rubenstein, 2011; Shen et al., 2017).

The fitness benefits that offspring may gain by delaying dispersal and helping to raise nondescendent young are many. These include increased survivorship attributable to living on a familiar territory (the 'safe haven' and 'parental facilitation' hypotheses; Brown & Brown, 1984; Kokko & Ekman, 2002), acquisition of experience (the 'skills' hypothesis; Heinsohn, 1991; Skutch, 1961), enhanced survivorship or potential to breed stemming from larger group size (the 'group augmentation' hypothesis; Brown, 1987; Kokko et al., 2001) or enhanced social prestige (Bergmüller et al., 2007) and the increased potential for acquiring breeding status by taking over or acquiring part of their natal territory ('territorial budding'; Komdeur & Edelaar, 2001; Woolfenden & Fitzpatrick, 1984) or inheritance of a high-quality territory (Clutton-Brock, 2002; Kokko et al., 2001; Lindström, 1986; Stacey & Ligon, 1991; Wiley & Rabenold, 1984). Testing these alternatives is

\* Corresponding author.

E-mail address: [wdkoenig@berkeley.edu](mailto:wdkoenig@berkeley.edu) (W. D. Koenig).<https://doi.org/10.1016/j.anbehav.2023.08.021>0003-3472/© 2023 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

often challenging, as ecological and social factors can have complex effects and may interact with each other. The cost of provisioning by helpers, for example, may counteract benefits to helper survivorship via increased group size and enhanced skills (Reyer, 1984).

Here, based on long-term work on the cooperatively breeding acorn woodpecker, *Melanerpes formicivorus*, we examine one of these potential benefits of delayed dispersal, that of territory inheritance, contrasting its fitness consequences with dispersal, the alternative route to achieving a breeding position in this population. This permanently territorial population combines helping behaviour by both male and female offspring with cooperative polygynandry in which up to eight co-breeding males share one to three co-breeding (or joint-nesting) females (Koenig et al., 2020; Koenig, Walters, et al., 2016). Co-breeding males are close relatives, usually brothers or a father and his sons. Similarly, co-breeding females are usually sisters or a mother and her daughter. Extra-group parentage is at best rare (Dickinson et al., 1995), and helpers are always offspring of the breeders. Thus, all birds within a group are close relatives, except for the breeder males to the breeder females (Koenig & Pitelka, 1979).

After delaying dispersal and remaining as a helper for one or more years, many offspring find a breeding opportunity elsewhere and leave their natal group, a process that in some cases involves 'budding' off a part of their natal territory (Komdeur & Edelaar, 2001; Woolfenden & Fitzpatrick, 1984). If, however, all the breeders of one sex or the other die or leave the group, this creates a reproductive vacancy, which is filled by an unrelated individual or a coalition from elsewhere in the population. Helpers of the sex opposite that of the reproductive vacancy can then inherit and become co-breeders with previous same-sex breeders, generally their parent or other close relatives (Koenig et al., 1998). Typically, birds that inherit are still helpers on their natal territory when a vacancy is filled by a bird (or coalition) of the sex opposite to that of the inheriting helper. In some cases, however, a helper may have dispersed prior to a reproductive vacancy arising on its natal territory and later return home to inherit with its same-sex kin. Thus, territory inheritance is not necessarily dependent on delayed dispersal (Koenig, Walters et al., 2016). Conversely, birds may inherit breeder status on their natal territory but later disperse to become a breeder on another territory. The frequency of these cases is discussed below.

Helpers living on their natal territory devote considerable time and energy to forays in search of reproductive vacancies. When a vacancy is detected, related helpers often join together into coalitions to fight in competitions, called 'power struggles', that determine which birds ultimately fill the vacancy, with some or all of the winning coalition members subsequently assuming breeder status in the new group (Barve, Lahey, et al., 2020; Hannon et al., 1985; Koenig, 1981). As in most field studies, dispersal outside the study area is difficult to distinguish from mortality, and dispersal distance is often unknown or skewed because of observation bias (Koenig et al., 1996).

In this paper, we first update earlier summaries of the frequency of dispersal and territory inheritance (Koenig et al., 2000). Second, we quantify life-history differences between birds that achieved breeding status by (1) inheriting their natal territory from birds that dispersed, (2) filling a reproductive vacancy elsewhere and (3) doing both (i.e. they either inherited but later dispersed or dispersed but later returned to inherit their natal territory). Third, we compare the lifetime direct and indirect fitness of birds inheriting their natal territory versus those achieving breeding status by dispersing, and between birds that inherited their natal territory versus birds that both inherited and dispersed. Our goal was to determine whether the fitness benefit of territory inheritance plays a key role in driving this species' extraordinary social system.

## METHODS

### *Study System and Field Methods*

We studied acorn woodpeckers at Hastings Natural History Reservation in central coastal California (36°23' N, 121°33' W) between 1972 and 2021 (Koenig et al., 2020; Koenig & Mumme, 1987). We considered a bird to be a breeder when the birds of the opposite sex in its group were unrelated to it, as occurs when a bird disperses to another group or following the replacement of the breeders of the opposite sex. Because of reproductive skew, particularly among co-breeding males, achieving breeding status does not, however, necessarily imply that a bird genetically sires offspring in a particular nesting attempt, within a breeding season, or even over a period of several years (Haydock & Koenig, 2002, 2003). Thus, whether a bird was categorized as a breeder or not was based on social organization, whereas reproductive success was based on parentage analysis (Hoogland et al., 2019).

Birds were captured using nets or in their roost or nest cavities (Stanback & Koenig, 1994). Captured birds were uniquely colour-banded and bled for parentage analysis. On average, 94.6% ( $N = 31$  years) of the birds in the population were banded at any one time at the start of the spring breeding season for the years used in the analyses performed here (1986–2016). Group composition was monitored at approximately bimonthly intervals using blinds and spotting scopes. Nests were monitored and young banded when approximately 21 days old, 10–12 days before fledging (Weathers et al., 1990).

### *Life-history Comparisons*

We only considered birds born and achieving breeding status within the study area. Birds were divided into two main groups: 'inheritors' were birds born within the study area that inherited and achieved breeding status on their natal territory, while 'dispersers' were birds born in the study area that dispersed (at least once) and achieved breeding status outside their natal territory. We also distinguished inheritors that later dispersed and became breeders elsewhere within the study area from dispersers that later returned to inherit and become breeders on their natal territory. Sample sizes for these two latter categories were small, however, and differences between them were nonsignificant (Appendix Table A1). Thus, birds that both inherited and dispersed were combined (category 'both') in subsequent analyses, regardless of the order in which they occurred.

Two potentially important differences between inheritors and dispersers are the birds' initial familiarity with the site on which they attempted to breed and their familiarity with neighbouring individuals. Inheritors, having grown up on the site, are familiar with the area and with the birds living in the vicinity; indeed, they typically co-breed with at least some of the (same-sex) birds that raised them. In contrast, familiarity with a new breeding site for most dispersers likely declines with distance, at least initially. Prior analyses found the mean ( $\pm$ SD) distance of dispersers in the population to be  $0.22 \pm 0.48$  km for males and  $0.53 \pm 0.52$  km for females (Koenig et al., 2000); the maximum distance between groups in the study area was 4.3 km, and the maximum distance any bird was known to disperse within the study area was 3.4 km. Pardo et al. (2018) found that birds were able to recognize associations between individuals of other groups up to a mean ( $\pm$ SD) distance of  $430 \pm 256$  m. Assuming that birds dispersing within this distance (mean  $\pm 2SD = -1$  km) are therefore likely to have some familiarity with their neighbours, we compared dispersers that moved less than 1 km (short-distance dispersers) with the relatively few birds detected that moved farther than 1 km (long-distance dispersers).

The differences between the two categories were modest and generally not statistically different (Appendix Table A2), and thus all dispersers were combined in subsequent analyses.

Life-history variables examined included how many years a bird was a helper, mean cohort size of same-sex helpers while the bird was a helper, age at which the bird first genetically sired (males) or produced (females) (collectively referred to as 'produced') an offspring, how many years the bird was a social breeder (i.e. unrelated to the breeders of the opposite sex) within its group (irrespective of whether it produced any offspring), mean territory quality and mean size of the same-sex co-breeder coalition of which the bird was a part, both of which were averaged over the years the bird was a social breeder. As a proxy for territory quality, we used the size of a group's granary, the tree or other structure in which the birds cache acorns (Koenig et al., 2020). Territories were divided into three categories, low-quality (<1000 storage holes), medium-quality (1000–2500 holes) and high-quality (>2500 holes).

Because many of the response variables in our analyses were non-normally distributed, we used chi-square tests and, to compare categories, nonparametric Wilcoxon signed-rank tests. Because we generally compared inheritors to dispersers and inheritors to birds that both dispersed and inherited, we conservatively set the  $\alpha$  level for statistical significance at  $P \leq 0.025$ . All analyses were performed using R 4.2.0 (R Core Team, 2022).

#### Genetic Analyses

Young parented by individual breeders were determined by genetic parentage analyses using blood samples taken when birds were banded. Blood was stored in Longmire's solution (Longmire et al., 1988) at  $-20^\circ\text{C}$  until DNA extraction and analysis. Microsatellite loci (8–18) were developed based on standard protocols (Armour et al., 1994; Gibbs et al., 1997; Jones et al., 2002).

Overall, paternity was assigned with at least 95% confidence for 85.0% of 3460 offspring sampled during the study. Further details regarding parentage assignment are presented in the Appendix.

#### Quantifying Fitness

We determined two nonoverlapping indices of fitness for 424 birds (268 males, 156 females): the lifetime number of fledged offspring produced by the focal individual (direct fitness) and the lifetime number of fledged offspring produced by co-breeders of the focal individual (i.e. other same-sex breeders within the same social group; indirect fitness). Nestlings banded on or about day 21 were assumed to have fledged successfully. Individuals included in the analyses were all those born in the population between 1986 and 2006 that achieved breeder status within the population at some point in their lives. We only included birds born in the population through 2006 to minimize including birds that were still alive beyond 2016, the last year for which we had parentage data.

We determined direct and indirect fitness for each year a bird had breeding status within the population (Koenig et al., 1998). We did not include the indirect fitness birds gained as helpers prior to attaining breeder status in our comparisons of inheritors versus dispersers to avoid confounding the fitness effects of helping with the fitness consequences of the route by which a bird became a breeder. Fitness values were weighted by estimated genetic relatedness,  $r$ . For direct fitness,  $r$  is the relatedness between parents and offspring ( $r_{po} = 0.5$ ). For indirect fitness,  $r$  is the relatedness between the focal individual and the offspring of his or her co-breeders ( $r_{co} \times r_{po}$ ). Individuals within a co-breeding coalition are generally siblings or 'parents' of their co-breeders, where the 'parent' may or may not be the genetic parent but is itself a close

relative of the genetic parent (Koenig et al., 1998; Koenig & Pitelka, 1979). Thus, co-breeders vary in relatedness ( $r_{co}$ ) from 0.25 (half-siblings) to 0.5 (full siblings or parents and their genetic offspring). Coefficients of relatedness between co-breeders were estimated using pedigrees going back two generations whenever possible, and, when pedigrees were unknown, were estimated as the overall mean  $r_{co}$  values (0.40 between co-breeder males and 0.43 between co-breeder females). Details are provided in the Appendix. The relatedness of 46.9% ( $N = 894$ ) of co-breeding male pairs and 31.9% ( $N = 339$ ) of co-breeding female pairs were estimated from pedigrees.

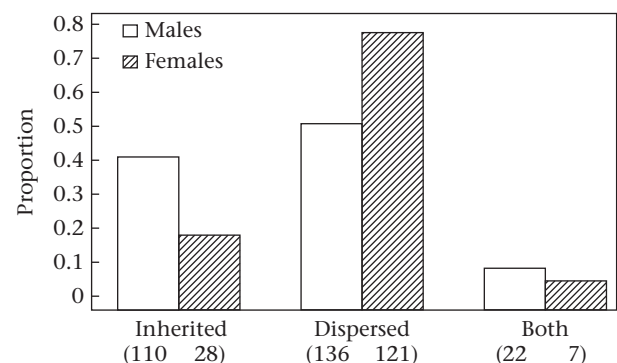
Because fitness values were generally non-normal, we used Wilcoxon signed-rank tests to compare inheritors to dispersers and inheritors to birds that both inherited and dispersed. However, to control for two variables that have important effects on fitness, territory quality and the coalition size of co-breeders (Koenig et al., 2023), we conducted linear models in which, in addition to whether the bird dispersed or inherited, we included mean territory quality during years the bird was a breeder and the mean number of co-breeders with which the focal bird bred during its years as a breeder. Both linear and quadratic effects of the number of co-breeders were included in the models, but the quadratic term was dropped when  $P > 0.05$  to aid interpretation of the first-order effect. Because fitness differences between categories were unchanged when controlling for these variables, the uncontrolled values were plotted for illustrative purposes.

#### Ethical Note

Birds involved in this study were wild animals. Permission to mark and bleed birds (up to 90  $\mu\text{l}$  was taken from the brachial vein) was approved by the Institutional Animal Care and Use Committees of the University of California, Berkeley (protocol R010-0412), Cornell University (protocol 2008-0185) and Old Dominion University (protocol 12-001). Birds were handled and banded under California Scientific Collecting Permit SC-007368 and Federal Bird Banding Permits 21508 and 23803.

## RESULTS

Compared to females, males that attained breeding status in the population were significantly more likely to inherit their natal territory rather than disperse within the study area (110 of 268 (41%) of males versus 28 of 156 (18%) of females were inheritors;  $\chi^2_1 = 26.3$ ,  $P < 0.001$ ; Fig. 1). These categories were not mutually



**Figure 1.** Proportion of acorn woodpecker breeders that inherited their natal territory ('inherited'), dispersed from their natal territory to another territory within the study area ('dispersed') and both inherited their natal territory and dispersed to another territory within the study area ('both'). Sample sizes (males, females) are listed under their respective categories.

exclusive, and a small proportion of birds (8% of males, 4% of females) both inherited their natal territory and dispersed to a different territory during their lives. Of these, about half (13 of 22 (59%) males, 4 of 7 (57%) females) dispersed but later returned to inherit their natal territory (Appendix Table A1).

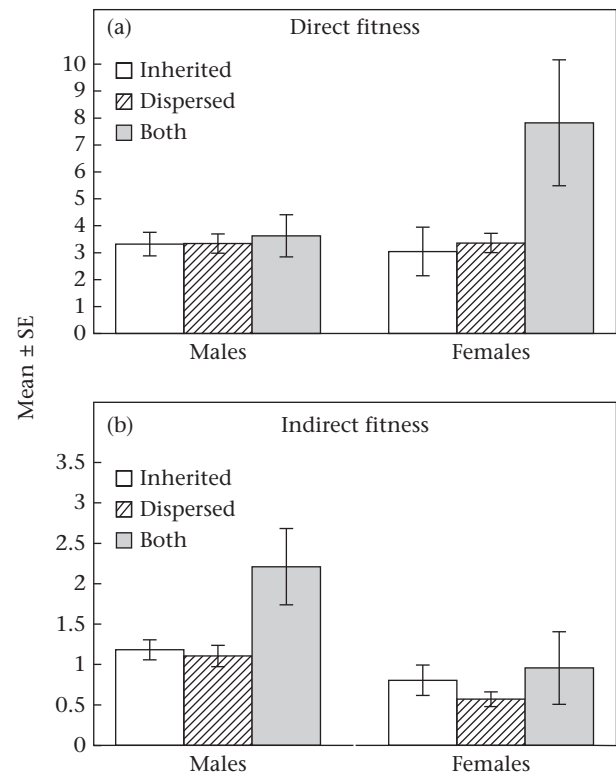
Comparing male inheritors to male dispersers, inheritors were part of smaller same-sex helper cohorts and were older when they first produced an offspring (Table 1). Male inheritors also bred on higher-quality territories and joined a larger co-breeder coalition, on average, than male dispersers. Female inheritors also had the advantage of breeding on higher-quality territories. There were no differences between female inheritors and females that both inherited and dispersed, while males that both inherited and dispersed bred for significantly more years on lower-quality territories, on average, than males that inherited their natal territory but did not subsequently disperse.

There were no differences in fitness (either direct or indirect) between inheritors and dispersers, or between inheritors and birds that both inherited and dispersed (Table 1, Fig. 2). There were also no statistical differences in fitness between categories in models controlling for the (in many cases) significant effects of breeding territory quality and mean coalition size (Appendix Tables A3–A4).

## DISCUSSION

Much of the controversy concerning the evolutionary basis of cooperative breeding has focused on the fitness costs and benefits of delayed dispersal. Why do helpers, typically offspring with limited breeding opportunities in their natal group because of incest avoidance (Koenig & Haydock, 2004; Koenig & Pitelka, 1979; Riehl, 2013), delay dispersal and help raise younger siblings rather than disperse and attempt to breed independently once they achieve independence? The territory inheritance hypothesis posits that there are inclusive fitness benefits, both to the parents and to their offspring, of the latter remaining in their natal group, benefits attributable to the potential for offspring inheriting and eventually breeding on their (usually high-quality) natal territory (Balshine-Earn et al., 1998; Brown & Brown, 1984; Kingma, 2017; Lindström, 1986).

In Seychelles warblers, *Acrocephalus sechellensis*, for example, birds that partition part of their natal territory by budding initially



**Figure 2.** Mean  $\pm$  SE (a) direct fitness and (b) indirect fitness of acorn woodpeckers that inherited their natal territory ('inherited'), dispersed from their natal territory to another territory within the study area ('dispersed') and both inherited their natal territory and dispersed to another territory within the study area ('both'). All comparisons were nonsignificant ( $P > 0.025$ ).

reproduce poorly but live longer and eventually gain a high-quality territory through site dominance. The birds engaging in this strategy consequently achieve higher lifetime reproductive success than birds dispersing to low-quality territories (Komdeur & Edelaar, 2001). In Florida scrub-jays, *Aphelocoma coerulescens*, older and more dominant males are more likely to inherit their natal territory,

**Table 1**  
Comparison of acorn woodpeckers that inherited versus dispersed, and between those that inherited versus both inherited and dispersed

Variable	(1) Inherited	(2) Dispersed	(3) Both inherited and dispersed	P	
				(1 vs 2)	(1 vs 3)
<b>Males</b>					
N years as a helper	1.58 $\pm$ 0.13	1.19 $\pm$ 0.09	2.00 $\pm$ 0.30	0.035	0.18
Mean helper cohort size	2.43 $\pm$ 0.16	3.04 $\pm$ 0.14	2.98 $\pm$ 0.44	<b>0.002</b>	0.43
Mean age at first siring	3.78 $\pm$ 0.21	3.11 $\pm$ 0.18	4.18 $\pm$ 0.49	<b>&lt;0.001</b>	0.28
N years as a breeder	5.95 $\pm$ 0.36	5.76 $\pm$ 0.33	8.05 $\pm$ 0.72	0.49	<b>0.004</b>
Mean breeder territory quality	2.87 $\pm$ 0.04	2.46 $\pm$ 0.07	2.67 $\pm$ 0.11	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Mean co-breeder coalition size	2.94 $\pm$ 0.14	2.17 $\pm$ 0.08	2.70 $\pm$ 0.22	<b>&lt;0.001</b>	0.74
Direct fitness	3.32 $\pm$ 0.44	3.34 $\pm$ 0.35	3.63 $\pm$ 0.79	0.32	0.19
Indirect fitness	1.18 $\pm$ 0.12	1.11 $\pm$ 0.13	2.21 $\pm$ 0.47	0.14	0.037
N birds	110	136	22	–	–
<b>Females</b>					
N years as a helper	1.46 $\pm$ 0.31	0.99 $\pm$ 0.10	2.00 $\pm$ 0.82	0.17	0.62
Mean helper cohort size	1.81 $\pm$ 0.19	1.93 $\pm$ 0.11	2.03 $\pm$ 0.26	0.99	0.80
Mean age at first reproduction	3.44 $\pm$ 0.45	2.73 $\pm$ 0.16	4.67 $\pm$ 0.56	0.16	0.17
N years as a breeder	5.32 $\pm$ 0.77	4.69 $\pm$ 0.28	9.43 $\pm$ 1.86	0.66	0.06
Mean breeder territory quality	2.88 $\pm$ 0.08	2.57 $\pm$ 0.07	2.77 $\pm$ 0.15	<b>0.015</b>	0.27
Mean co-breeder coalition size	1.91 $\pm$ 0.17	1.73 $\pm$ 0.07	1.36 $\pm$ 0.14	0.41	0.18
Direct fitness	3.04 $\pm$ 0.90	3.36 $\pm$ 0.36	7.82 $\pm$ 2.34	0.51	0.06
Indirect fitness	0.81 $\pm$ 0.19	0.57 $\pm$ 0.09	0.96 $\pm$ 0.45	0.13	0.85
N birds	28	121	7	–	–

Values are means  $\pm$  SE. P values by Wilcoxon signed-rank tests. Statistically significant differences ( $P \leq 0.025$ ) are shown in bold.

consistent with the hypothesis that inheritance yields superior fitness benefits (Suh et al., 2020). More generally, in a meta-analysis, Kingma (2017) found that the direct fitness benefits associated with the probability of territory inheritance were associated with the amount of helping behaviour provided by helpers, supporting the hypothesis that the direct fitness benefits of inheritance play a key role in the evolution of cooperative breeding.

The alternative to territory inheritance is dispersal, a behaviour that, although risky, can yield fitness benefits that outweigh those of remaining philopatric (Green & Hatchwell, 2018; MacColl & Hatchwell, 2004). In some cases, dispersal is thought to be a decision made early in life in response to factors such as resources and family ties, as is the case for western bluebirds, *Sialia mexicana* (Dickinson et al., 2014). In red-cockaded woodpeckers, *Dryobates borealis*, about one-third of individuals disperse in search of a breeding vacancy ('depart-and-search'), in some cases after jumping to locations far from their natal group (Kesler et al., 2010), while two-thirds delay dispersal and compete for breeding vacancies in the vicinity of the natal territory ('stay-and-foray'), alternative strategies that appear to yield roughly equivalent lifetime fitness (Walters et al., 1992).

In acorn woodpeckers, young delay dispersal through at least their first winter (Koenig & Mumme, 1987). At that point, it is unclear to what extent young actively choose to leave their natal group; that is, depart-and-search rather than delay dispersal and stay-and-foray, as the fate of birds disappearing on or after their first spring is unknown unless they move within the study area or are seen on the study area at a later time (often when competing for a vacancy at a power struggle). We suspect that few birds choose a depart-and-search strategy, permanently leaving their natal territory to search for reproductive vacancies, although some helpers leave (or may be forced from) their natal group following a breeding vacancy of the same sex as themselves once that vacancy is filled by an unrelated bird from elsewhere (Koenig et al., 1998). Rather than 'depart-and-search', helpers regularly engage in forays averaging 0.5–0.6 km away from their natal territory in search of vacancies (Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020). Those that are successful at finding and competing for a reproductive vacancy before a turnover of the opposite sex occurs in their home group become dispersers, whereas those that are unsuccessful at dispersing before a turnover of the opposite sex occurs inherit and become co-breeders with their same-sex parent and related same-sex co-breeders.

This scenario, in which all offspring are searching for reproductive vacancies and either become dispersers or inheritors depending on their competitiveness and timing (i.e. when a turnover of the opposite sex in their natal group occurs), is consistent with inheritors remaining as helpers longer than dispersers (Koenig & Walters, 2011), thereby producing their first offspring later in life. Furthermore, because larger coalitions are more competitive and more likely to win power struggles (Hannon et al., 1985), dispersers should be part of a larger cohort of same-sex helpers more often than inheritors.

No such differences were detected among females. Among males, however, for which inheritance is a more frequent strategy, the cohort of same-sex helpers was larger for dispersers while the mean age dispersers first produced an offspring was younger, as predicted (Table 1).

The scenario in which all offspring are searching for reproductive vacancies and the difference between inheritors and dispersers is largely one of timing also envisions inheritance and dispersal as being two ends of a spectrum rather than distinct alternative

strategies for obtaining a reproductive position in the population. Prior analyses found no evidence that larger, socially dominant offspring within a brood were more likely to inherit (Koenig et al., 2011), countering the hypothesis that inheritance is a preferred or superior strategy.

Although most acorn woodpecker offspring that remained in the study area attained breeding status via dispersal or inheritance, a small proportion inherited their natal group territory but later dispersed to another territory, or, conversely, dispersed to another territory but later returned to inherit and become a breeder in their natal territory. These cases are indicative of two key features of the acorn woodpecker system. First, birds continue to search for superior breeding opportunities, either in terms of territory quality or number of co-breeders, and will potentially disperse even after inheriting breeding status on their natal territory. In conjunction with secondary dispersal by breeders, a relatively common occurrence (Koenig, Walters et al., 2016), such cases may explain the unexpectedly common foray behaviour exhibited by breeders in the population (Barve, Hagemeyer, et al., 2020).

Second, these cases demonstrate that dispersal does not preclude the possibility of later returning and inheriting one's natal territory should the opportunity arise. Inheritance and dispersal are not mutually exclusive strategies in acorn woodpeckers. Such flexibility reduces whatever fitness benefits there may be to delayed dispersal, thus increasing the relative importance of ecological constraints and kin-based benefits as drivers of delayed dispersal and helping behaviour.

The territory inheritance hypothesis predicts that the fitness of inheritors should exceed that of dispersers, usually because territories that are inherited are of higher quality, on average, than those to which birds disperse. For both males and females, inheritors benefited by breeding on higher-quality territories than did dispersers; additionally, male inheritors bred in larger coalitions (Table 1). These life-history differences failed to result in higher direct or indirect fitness of inheritors, however.

For males, which inherit their natal territory more frequently than females, this result may partly be due to the opposing effects of some factors. For example, the fitness advantage of greater mean breeder territory quality enjoyed by inheritors may be offset by the younger age that dispersers produce their first offspring. Birds that inherit are often part of a large co-breeding coalition, but the number of birds in a breeding coalition is only advantageous up to coalitions of intermediate size (Barve et al., 2021; Koenig et al., 2023).

Our results indicate that territory inheritance corresponds to several differences in life histories but does not yield higher inclusive fitness relative to birds that become breeders via dispersal. One interpretation of this result is that it fails to support the territory inheritance hypothesis: despite the superior territory quality enjoyed by inheritors, inheritors do not achieve greater fitness than dispersers. Alternatively, the fact that territory inheritance appears to yield a fitness payoff equivalent to dispersal suggests that inheritance is a successful alternative route to attaining breeding status that is generally unavailable in noncooperatively breeding species. To the extent that the latter interpretation is appropriate, territory inheritance is an important benefit of cooperative breeding, particularly for male acorn woodpeckers.

Conversely, birds that dispersed did not necessarily suffer decreased reproductive success compared to inheritors, a finding that parallels results in long-tailed tits, *Aegithalos caudatus*, and meerkats, *Suricata suricatta*, in which no, or conflicting, fitness costs to dispersal were detected (Green & Hatchwell, 2018; Maag et al.,

2022; Sharp et al., 2008). Two other examples include the southern pied babbler, *Turdoides bicolor*, where the fitness cost of dispersal is dependent on social circumstances (Nelson-Flower et al., 2018), and the superb starling, *Lamprolornis superbus*, in which dispersal and philopatry have been found to yield equivalent inclusive fitness (Shah & Rubenstein, 2022). In our case, however, the conclusion that there is no fitness cost to dispersal relative to inheriting is subject to two caveats. First, the limitations of our study area meant that we could only detect dispersal events shorter than ~4 km. Acorn woodpeckers, however, are relatively good dispersers, as indicated by having established several new populations up to ~200 km outside their core range within historic times (Koenig et al., 2020; Rusk et al., 2013). The potential fitness consequences of longer-distance dispersal remain to be determined.

Second, we measured fitness following successful dispersal, and thus avoided assessing the potential risk of dispersal itself. With the relatively rare exceptions of birds dispersing following acorn crop failures (Hannon et al., 1987) and of helpers being forced from their group following replacement of same-sex breeders, relatively few birds appear to leave their natal territory to search for reproductive vacancies elsewhere. Rather, most birds retain their natal territory as a base from which they 'stay-and-foray' in search of potential breeding opportunities (Barve, Hagemeyer, et al., 2020; Koenig et al., 1996). Thus, we suspect that mortality of birds in the process of dispersal is relatively low. This is clearly an assertion that needs to be tested, however.

If territory inheritance does not yield fitness benefits to delayed dispersal in acorn woodpeckers, are there other factors that may confer direct fitness benefits favouring delayed dispersal? Prior analyses have failed to support the importance of skill acquisition or the hypothesis that young help as payment in return for being allowed to remain in their natal group (Koenig & Walters, 2011). Still to be tested are the extent to which young gain enhanced survivorship due to living on a familiar territory or in larger groups (the 'safe haven' and 'group augmentation' hypotheses; Kokko & Ekman, 2002; Kokko et al., 2001). Thus, direct fitness benefits cannot be ruled out as being important to delayed dispersal and helping behaviour. However, in acorn woodpeckers, as well as in other cooperative breeders in which helpers are close relatives, there is strong support for ecological constraints and indirect fitness benefits of helping behaviour to be the primary drivers of delayed dispersal (Dickinson & Hatchwell, 2004; Ekman et al., 2004).

### Author Contributions

Analyses were performed by W.D.K. Field work was done by W.D.K, J.H. and E.L.W. Genetic analyses was done by J.H. and H.L.D. The manuscript was written by W.D.K. All authors reviewed and edited drafts of the paper.

### Data Availability

Data used in the analyses are provided as Supplementary Material.

### Declaration of Interest

None.

### Acknowledgments

We thank the reviewers for comments and Hastings Reservation (<https://doi.org/10.21973/N33Q0G>) for hosting the project since it was started by Michael and Barbara MacRoberts in 1968. We

particularly thank our colleagues and the 250+ field and assistants who have contributed to the project over the years. This work was supported by U.S. National Science Foundation grants IOS-1455881 to W.D.K., IOS-1455949 to J.H. and IOS-1455900 to E.L.W. and by Natural Environment Research Council (NERC) fellowship NE/1021748/1 to H.L.D.

### Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2023.08.021>.

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## Appendix

### Details of Genetic Analyses

Young parented by individual breeders were determined by genetic parentage analyses using the blood samples taken when birds were banded. Blood was stored in Longmire's solution (Longmire et al., 1988) at  $-20^{\circ}\text{C}$  until DNA extraction and analysis. Microsatellite loci (8–18) were developed based on standard protocols (Armour et al., 1994; Gibbs et al., 1997; Jones et al., 2002). Amplicons for each locus were produced in up to six multiplexed polymerase chain reactions (Qiagen Multiplex Plus, Venlo, The Netherlands) and sized on an Applied Biosystems (Waltham, MA, U.S.A.) 3730 DNA analyzer using Liz 500 as a molecular weight standard. We tested the loci used in our parentage assignments for deviations from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium using GenePop 4.7.5 (Rousset, 2008). Given that acorn woodpeckers have a mean life expectancy of ~5 years (males)

and ~4 years (females) (Koenig & Mumme, 1987), we ran the analyses for every 5-year span (1990, 1995, 2000, 2005, 2010, 2015) using 52–78 candidate parents in each.

Deviation caused by the presence of relatives was reduced by selecting one male and one female candidate parent (usually individuals with breeding status) from each social group and then eliminating individuals that were confirmed first-order relatives, usually because they were from the same natal group. Of the 18 loci we commonly used in determining parentage, eight deviated from HWE in at least one year. Consequently, we examined assignments for all offspring paying particular attention to two loci that were difficult to score accurately. Genotypes were either corrected by examining Mendelian transmission across generations for an allele or deleted if we suspected a null allele. False discovery rate was controlled for in the linkage disequilibrium tests due to the large number of pairwise loci comparisons (Benjamini & Hochberg, 1995). We included all 18 loci in parentage assignments, as no locus was in disequilibrium in more than one year.

Parentage was determined using CERVUS 3.0.7 (Marshall et al., 1998). The following simulation criteria were used: number of offspring = 10 000; proportion of loci typed = 0.75; *N* candidate mothers = 5; *N* candidate fathers = 10; proportion of candidate parents genotyped = 1.0; and proportion of loci mistyped = 0.02 (Marshall et al., 1998). We accepted assignments that produced at least 95% confidence for a single father–offspring dyad and excluded every possible male group member with putative breeding status within the previous 2 years. At most, two mismatches were allowed in the assigned parent–offspring triad for all parental assignments. We were not necessarily able to exclude all possible helper–offspring dyads with 95% confidence, but most (>90%) could be excluded based on assigned parental triads. Some helpers that were most likely full siblings of offspring could not be excluded due to having been genotyped at too few loci. This was unlikely to alter the assignments used here, as reproduction by helpers is extremely rare (Dickinson et al., 1995; Koenig et al., 1998). Overall, paternity was assigned for 85.0% of 3460 offspring sampled.

#### Estimating the Coefficient of Relatedness Between Co-breeders

Co-breeders are almost always close relatives, either siblings or ‘parents’ and their offspring, where the ‘parent’ may or may not be the genetic parent but is itself a close relative of the genetic parent (Koenig et al., 1998; Koenig & Pitelka, 1979). As such, co-breeders vary in relatedness ( $r_{co}$ ) from 0.25 (half-siblings) to 0.5 (full siblings or parents and their genetic offspring) (Koenig et al., 1998). We estimated coefficients of relatedness between co-breeders using pedigrees going back, whenever possible, two generations. When co-breeders shared the same genetic parents, we set  $r_{co} = 0.5$  (full siblings); when co-breeders had the same genetic mother but different fathers who were either full siblings or a father and son, or had the same genetic father but different mothers who were either full siblings or a mother and daughter, we set  $r_{co} = 0.375$ ; and when co-breeders had different mothers and different fathers, but both potential mothers and potential fathers were either full siblings or father–son/mother–daughter, we set  $r_{co} = 0.25$ . Averaged across all co-breeder-years and weighted according to the number of young parented, overall mean  $r_{co}$  values between co-breeder males were 0.40 (0.20 via fathers and 0.20 via mothers) and 0.43 between co-breeder females (0.23 via fathers and 0.20 via mothers); these estimates were used when pedigrees were unknown. We did not adjust for

incest, which is rare in this population (~3.5% of offspring; Haydock et al., 2001).

Excluding immigrants, the pedigrees of 46.9% of pairs of co-breeder males and 31.9% of pairs of co-breeder females could be estimated from genealogies. At least one parent was estimated from genealogies for 59.8% of co-breeder male pairs and 54.9% of co-breeder female pairs. The smaller number of female co-breeders being of known relatedness is a consequence of the greater dispersiveness of females (Koenig et al., 2000).

**Table A1**

Comparison of acorn woodpeckers that inherited and then dispersed within the study area versus those that dispersed and later inherited their natal territory

Variable	Inherited first	Dispersed first	<i>P</i>
<b>Males</b>			
<i>N</i> years as a helper	1.44±0.53	2.38±0.33	0.11
Mean helper cohort size	3.17±0.95	2.89±0.49	1.00
Mean age at first siring	3.71±0.75	4.50±0.650	0.44
<i>N</i> years as a breeder	7.78±0.68	8.23±1.14	0.97
Mean breeder territory quality	2.55±0.32	2.72±0.09	1.00
Mean co-breeder coalition size	2.93±0.35	2.55±0.28	0.50
Direct fitness	3.11±1.20	3.98±1.07	0.74
Indirect fitness as a breeder	3.19±0.94	1.53±0.39	0.12
<i>N</i> birds	9	13	–
<b>Females</b>			
<i>N</i> years as a helper	0.33±0.33	3.25±1.03	0.07
Mean helper cohort size	2.00	2.04±0.34	1.00
Mean age at first reproduction	4.00±1.00	5.00±0.71	0.63
<i>N</i> years as a breeder	8.00±2.52	10.50±2.84	0.63
Mean breeder territory quality	3.00	2.71±0.17	–
Mean co-breeder coalition size	1.46±0.11	1.29±0.24	0.37
Direct fitness	9.02±4.54	6.93±2.86	1.00
Indirect fitness as a breeder	1.21±0.89	0.77±0.53	0.59
<i>N</i> birds	3	4	–

Values are means ± SE. *P* values by Wilcoxon signed-rank tests. No comparison was statistically significant at the  $P \leq 0.025$  level.

**Table A2**

Comparison of life histories and fitness of acorn woodpeckers that dispersed <1 km and >1 km within the study area

Variable	Short-distance dispersers	Long-distance dispersers	<i>P</i>
<b>Males</b>			
<i>N</i> years as a helper	1.24±0.10	0.64±0.24	0.07
Mean helper cohort size	3.03±0.15	3.20±0.12	0.63
Mean age at first siring	3.11±0.19	3.00±0.69	0.76
<i>N</i> years as a breeder	3.89±0.31	5.18±1.35	0.33
Mean breeder territory quality	2.47±0.07	2.40±0.22	0.55
Mean co-breeder coalition size	2.21±0.09	1.74±0.17	0.15
Direct fitness	3.20±0.37	4.84±1.36	0.19
Indirect fitness	1.10±0.14	1.17±0.58	0.55
<i>N</i> birds	125	11	–
<b>Females</b>			
<i>N</i> years as a helper	0.91±0.11	1.36±0.25	0.06
Mean helper cohort size	1.88±0.11	2.12±0.34	0.86
Mean age at first reproduction	2.70±0.18	2.92±0.43	0.44
<i>N</i> years as a breeder	3.07±0.28	2.64±0.61	0.24
Mean breeder territory quality	2.51±0.08	2.85±0.11	0.09
Mean co-breeder coalition size	1.80±0.08	1.34±0.11	<b>0.015</b>
Direct fitness	3.38±0.40	3.25±0.85	0.57
Indirect fitness	0.60±0.10	0.43±0.20	0.053
<i>N</i> birds	99	22	–

Values are means ± SE. *P* values by Wilcoxon signed-rank tests. Statistically significant differences ( $P \leq 0.025$ ) are shown in bold.



**Table A3**

Results of linear models comparing the lifetime breeding fitness of dispersers versus inheritors

Response variable	Explanatory variables				$R^2_{\text{adj}}$	Model $P$
	Dispersers	Mean breeding territory quality	Mean $N$ co-breeders	Mean $N$ co-breeders <sup>2</sup>		
<b>Males</b>						
Direct fitness	0.059±0.702 (0.93)	<b>1.720±0.618 (0.006)</b>	<b>-1.044±0.294 (&lt;0.001)</b>	–	0.08	<b>&lt;0.001</b>
Indirect fitness	0.152±0.241 (0.53)	0.241±0.212 (0.26)	<b>1.957±0.442 (&lt;0.001)</b>	<b>-0.249±0.075 (0.001)</b>	0.20	<b>&lt;0.001</b>
<b>Females</b>						
Direct fitness	-0.136±1.167 (0.91)	1.661±0.927 (0.08)	<b>-2.131±0.711 (0.004)</b>	–	0.10	<b>0.015</b>
Indirect fitness	0.169±0.266 (0.53)	0.444±0.212 (0.040)	<b>3.174±0.651 (&lt;0.001)</b>	<b>-0.636±0.151 (&lt;0.001)</b>	0.28	<b>&lt;0.001</b>

Values are mean effect sizes ± SE of dispersers relative to inheritors; quadratic co-breeder term included only when  $P < 0.05$ . Statistically significant differences ( $P \leq 0.025$ ) are shown in bold.

**Table A4**

Results of linear models comparing the lifetime breeding fitness of acorn woodpeckers that both inherited their natal territory and dispersed at some point in their lives (category 'both') compared to inheritors

Response variable	Explanatory variables				$R^2_{\text{adj}}$	Model $P$
	Both	Mean breeding territory quality	Mean $N$ co-breeders	Mean $N$ co-breeders <sup>2</sup>		
<b>Males</b>						
Direct fitness	0.461±1.057 (0.66)	1.215±1.093 (0.27)	<b>-1.088±0.355 (0.003)</b>	–	0.07	<b>0.025</b>
Indirect fitness	0.457±0.358 (0.20)	0.251±0.198 (0.21)	<b>2.099±0.435 (&lt;0.001)</b>	<b>-0.280±0.073 (&lt;0.001)</b>	0.19	<b>&lt;0.001</b>
<b>Females</b>						
Direct fitness	3.064±1.913 (0.11)	<b>1.855±0.901 (0.043)</b>	<b>-2.183±0.705 (0.003)</b>	–	0.15	<b>0.002</b>
Indirect fitness	0.507±0.369 (0.17)	0.126±0.381 (0.74)	<b>2.188±0.559 (&lt;0.001)</b>	<b>-0.288±0.090 (0.002)</b>	0.20	<b>&lt;0.001</b>

Values are mean effect sizes ± SE of birds in category 'both' relative to inheritors; quadratic co-breeder term included only when  $P < 0.05$ . Statistically significant differences ( $P \leq 0.025$ ) are shown in bold.