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Wandering woodpeckers: foray behavior in a social bird

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Citation: Barve, S., N. D. G. Hagemeyer, R. E. Winter, S. D. Chamberlain, W. D. Koenig, D. W. Winkler, and E. L. Walters. 2020. Wandering woodpeckers: foray behavior in a social bird. *Ecology* 00(00):e02943. 10.1002/ecy.2943

Abstract. In many cooperatively breeding taxa, nonbreeding subordinates, or helpers, use extra-territorial forays to discover dispersal opportunities. Such forays are considered energetically costly and foraging birds face aggression from conspecific members of the territories they visit. In contrast, breeders in cooperatively breeding taxa are expected to foray seldomly. We used novel tracking technologies to follow 62 acorn woodpeckers (*Melanerpes formicivorus*), a cooperatively breeding bird, to study extra-territorial foray behavior. Both helpers and breeders engaged in extra-territorial forays routinely and often several times per day. Helpers forayed earlier in the day and invested more time when foraging to high-quality territories. Unexpectedly, breeders forayed as often and as far as helpers. Breeders from high-quality territories forayed closer to their home territories than breeders from low-quality territories, reflecting a potential trade-off between foraging and territory defense. Such a routine pattern of extra-territorial forays in both helpers and breeders suggests that the motives behind forays differ by sex and social status and involve more than simply searching for dispersal opportunities.

Key words: Acorn woodpecker; automated radiotelemetry; breeders; cooperative breeding; dispersal; extra-territorial movements; helpers.

INTRODUCTION

Many cooperatively breeding taxa live in social groups with nonbreeding helpers or subordinate individuals that forfeit breeding while part of the group (Cockburn 1998). Staying in a group as a helper may increase survival probability, provide inclusive fitness benefits, and facilitate the opportunity to inherit or otherwise attain breeder status (Emlen 1982a, 1982b, Stacey and Ligon 1991). To increase their chance of dispersing to a group where they can breed, or find extra-group mating opportunities, helpers may undertake extra-territorial forays, relatively short-duration movements to surrounding territories, eventually returning to their home group (Kesler et al. 2007, Hodge et al. 2008). When conducted specifically to discover a dispersal opportunity, this strategy has been termed “stay-and-foray” (Walters et al. 1992).

Forays provide critical social information and improve dispersal outcomes (Conradt et al. 2003). Yet, depending

on their spatial extent, forays can be energetically costly and physiologically stressful (Young and Monfort 2009, Cram et al. 2018), and intruding individuals are often expelled aggressively by resident territory holders, prompting foraging individuals to be behaviorally cryptic (Eikenaar et al. 2008). Forays thus entail a trade-off between physiological and energetic costs versus improved dispersal and fitness outcomes.

The potential fitness benefits of foray behavior for individuals that have already attained breeding status are not as obvious as they are for nonbreeding helpers, and thus foray behavior is thought to be rare among breeders. Potential motivations for breeders to foray include soliciting or obtaining extra-group mating opportunities (Double and Cockburn 2000, Young et al. 2007, Ward et al. 2014), assessing territory quality of other groups as part of a strategy to “trade up” (van Dongen et al. 2013), or for secondary dispersal opportunities (Ridley 2012). Like helpers, however, breeders no doubt also suffer physiological and energetic costs while foraging. Hence, variation in foray strategies will provide clues as to the selective factors driving group-living in social organisms.

Manuscript received 9 April 2019; revised 17 September 2019; accepted 18 October 2019. Corresponding Editor: John R. Sauer.

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Until recently, research on small animal movement, and especially that of birds, has been limited by the availability of suitable tracking technologies. In particular, the need for manually tracking birds individually limits not only the number of animals monitored but the distance over which birds can be followed (Kays et al. 2011). Tags used in tracking are also constrained by battery size and battery life and thus small, fast, and far-ranging animals like birds have only been trackable with high temporal resolution for short periods (Bridge et al. 2011, Taylor et al. 2017). The ability to test hypotheses about difficult-to-study but biologically critical behaviors such as forays and the relationship between environmental conditions and the evolution of social systems has therefore been significantly limited (Koenig et al. 1996, Handley and Perrin 2007). Here, we use newly developed solar-powered radio-tags, coupled with an array of automated receiver stations, to test long-standing hypotheses (Table 1) for the ecological and demographic drivers of extra-territorial movements in a population of cooperatively breeding acorn woodpeckers (*Melanerpes formicivorus*).

Acorn woodpeckers live in polygynandrous social groups with nonbreeding helpers of both sexes (Koenig et al. 2016). Cobreeding males and females are closely related within sex, and mating outside the group or between breeders and helpers is rare (Haydock and Koenig 2003). Helpers can become breeders by inheriting their natal territories after the death or disappearance of the opposite sex parent, by dispersing to a territory with a breeding vacancy, or by founding a new territory (Koenig et al. 2000). Mean tenure as breeders and helpers varies by sex (mean breeder tenure \pm SE, males: 2.33 ± 0.09 yr [$N = 920$], and females: 1.86 ± 0.09 yr [$N = 603$]; mean helper tenure, males: 1.35 ± 0.03 yr [$N = 1499$], and females: 1.26 ± 0.03 yr [$N = 1292$]; unpublished data). Acorn woodpeckers are found in a matrix of oak (*Quercus* spp.) woodland and savannah, are known to disperse up to 15 km from their natal territories (Hooge 1995), and are not restricted by barriers such as small gaps in habitats. Females disperse farther than males (Koenig et al. 1996), while males are more likely to inherit natal territories (Koenig et al. 1998). Thus, we predicted that helpers, particularly helper females, would foray farther than breeders.

Acorn woodpeckers rely on stored acorns for overwinter survival, and thus territory quality is measured by the size of the “granary,” a specialized acorn-storage structure that may consist of thousands of holes into which individual acorns are cached (Koenig et al. 2019). Acorns are stored in the autumn, mostly harvested from trees within a 150-m radius around the granary, and all members of the group contribute to granary and territory defense (Koenig et al. 2008). Birds, hence, face a trade-off between staying and defending their home territory against intruders vs. pursuing the advantages to be potentially gained by foraging off-territory (Woolfenden and Fitzpatrick 1978, Baglione et al. 2006, Young and Monfort 2009). Such a trade-off leads to the prediction that birds on high-quality territories should foray shorter distances or for shorter periods than birds on low-quality territories to minimize the risk of their home territory being usurped while they are away (Russell and Rowley 2000, Fedy and Stutchbury 2004). We further predicted that members of small social groups would spend a larger proportion of their time in their home territory than members of large groups.

Finally, given that secondary breeding dispersal in this population is relatively frequent, especially among females (N.D.G. Hagemeyer, unpublished data), and extra-group matings are absent in our population (Haydock and Koenig 2003), forays by breeders may be conducted as a means to trading up to a better quality territory or for secondary dispersal to avoid reproductive competition with same-sex cobreeders (Barve et al. 2019). In such a scenario, we predicted that breeders from low-quality territories would foray farther and for longer durations and that breeders of both sexes belonging to a breeding coalition would foray more frequently than singleton breeders. All hypotheses and their predictions for the Acorn woodpecker system are presented in Table 1.

METHODS

Study area and study species biology

We studied foray behavior of Acorn woodpeckers at Hastings Reservation (36.387° N, 121.551° W) in central coastal California, USA. Adults on their natal territory with their social (and genetic) parents were categorized

TABLE 1. Hypotheses for foray behavior in cooperative breeders with predictions adapted to the acorn woodpecker system.

Hypothesis	Predictions
Helpers foray more than breeders	Mean daily distance to non-home territories visited is larger in helpers than breeders; mean time spent at non-home territories is higher in helpers than breeders; helpers foray earlier in the day than breeders.
Territory quality influences foray behavior	Mean time spent at non-home high-quality territories is higher than at low-quality territories in helpers; home territory quality is negatively associated with foray distance
Territory defense drives foray behavior	Group size drives proportion of time spent on territory.
Intra-group reproductive competition drives breeder forays	Duration of time spent at non-home territories varies positively with the number of same-sex cobreeders; foray distance varies positively with the number of same-sex cobreeders.

as nonbreeding helpers, whereas group members not living on their natal territories, or living with birds of the opposite sex that were nonrelatives, were considered putative breeders (Koenig et al. 1998). Since 1973, the majority of the woodpecker population has been color-banded ($N = 6,184$) and monitored continuously for group size and composition. Acorn woodpecker territory quality was assigned to each social group in each year based on the size of the group's granary (1: <1,000 storage holes [low quality], 2: 1,000–2,500 [medium quality], 3: >2,500 [high quality]) (Koenig et al. 2011).

Automated telemetry system

A total of 62 Acorn woodpeckers were caught opportunistically and fitted with dorsally mounted solar-powered nanotags (Pegan et al. 2018) with leg loop harnesses adjusted for body size (Rappole and Tipton 1991). All tags weighed <1% of the bird's body mass and all birds tagged were of known sex and social status within each social group. Radio-tagged birds were detected by a permanently installed array of 43 autonomous, solar-powered base stations during daylight hours (Pegan et al. 2018). Base stations were placed at the center of active territories, generally near the granary, or within the centroid of a cluster of territories where territories were <100 m apart.

Tags produced an encoded 64-bit, 2.5 ms, radio ping every 1.5 s during the day, even in cloudy weather. Each detection of an individual at each base station was accompanied with a date, time, and signal strength stamp. All detections were stored in files created every 15 minutes and stored on removable memory drives that were collected every 7 d. Date and time precision for base stations were checked each week and maintained within 30 s among the array. This system thus had the ability to simultaneously track all tagged birds during daylight hours.

When a bird was detected at two base stations simultaneously, we assigned the bird to a location based on greatest signal strength. We binned each detection into 30-minute time intervals after the first detection of any bird for a given day to quantify differences in the timing of forays. This measure was thus corrected for the time relative to sunrise throughout the study period. Then, for each tagged individual, we calculated the following variables on a daily basis for all days the bird was tracked between 1 May and 31 October 2018. This period covered both breeding (May–July) and nonbreeding periods (August–October) in the acorn woodpecker annual cycle at Hastings (Koenig and Mumme 1987). We calculated (1) frequency of visitation of each bird to each non-home group, (2) quality and distance of the territory visited relative to the bird's home territory, (3) mean time spent at each non-home territory (number of pings for each individual at each territory per day, converted to minutes), and (4) the proportion of time spent on the home territory each day.

Proportion of time spent on the home territory was calculated by partitioning the time between 05:00 and 21:00 (the widest potential window of woodpecker activity during the study period) into 15-minute intervals, which corresponds to the mean duration of forays in this population (Hooge 1995). The bird was “at home” if detected most frequently by a base station on or within 250 m (for clustered territories that shared a base station) of the home territory of the bird during any particular 15-minute interval. Otherwise, the bird was considered “away” from its home territory for that 15-minute period. We calculated the proportion of 15-minute intervals that the bird was “at home” or “away” for each day for days when the bird was detected at least once on the home territory. In all analyses, we included only individuals that were tracked for >6 d.

Statistical analyses

All analyses were conducted in R 3.5.1 (R Core Team 2018). We used the packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2015) for model building and evaluation. We tested for statistically significant ($P < 0.05$) variation in foray behavior by means of linear mixed models using individual bird and territory identity as random factors. To test whether helpers forayed farther and earlier in the day than breeders, we examined whether status was a significant predictor of the mean distance to territories visited per day and the relative time interval during the day, respectively. To examine whether helpers made forays of shorter duration, we tested whether social status was a significant predictor of the mean time spent on non-home territories per day. To understand whether home group size determined the proportion of time spent foraging, we tested whether home group size was associated with proportion of time on the home territory per day.

We examined the relationship between forays and home territory quality by testing whether birds from high-quality territories forayed shorter distances than birds from low-quality territories. Because there were no helpers in the lowest territory quality category in this data set, we merged birds into those on high-quality territories (territory quality 3) or low-quality territories (territory quality 1 and 2) for this analysis. Finally, to understand whether reproductive competition with cobreeders influenced breeder forays, we tested whether the number of same-sex cobreeders was associated with time spent at non-home territories and the distance to non-home territories visited by a breeder. All hypotheses are outlined in Table 1. We report relative differences in foray metrics as calculated from linear mixed model estimates to facilitate interpretation of our results. The t statistic and P value reported for all mixed models were obtained from the output in the package lmerTest. Figures are, however, plotted with raw means and standard errors.

Other factors relating to both our receiver station array (density and spatial extent) and the biology of

individuals (age and familiarity with surrounding social groups) may also have influenced our estimates of foray behavior. We report the effects of such potential confounding factors in Appendix S1.

RESULTS

We compiled a radiotracking data set of 7,106 bird days including data from 19 female breeders, 9 female helpers, 18 male breeders, and 16 male helpers (Fig. 1).

Helpers did not foray farther than breeders

There was no significant difference in the mean daily foray distance of birds based on sex (among male and female breeders, 105 ± 69 m, $t = 1.53$, $df = 23$, $P = 0.14$; and helpers, 48 ± 92 m, $t = 0.53$, $df = 19$, $P = 0.6$) or social status (among breeders and helpers [sexes combined within sex], 10 ± 58 m, $t = 0.17$, $df = 53$, $P = 0.87$; Fig. 2a).

Birds on high-quality territories forayed closer to home

The mean daily distance to groups visited by birds from high-quality territories was 293 ± 92 m shorter than for birds on low-quality territories ($t = 3.05$,

$df = 50$, $P = 0.01$), largely explained by breeder forays, mean foray distance among breeders from high-quality territories was 342 ± 141 m shorter than for breeders from low-quality territories ($t = 2.35$, $df = 11$, $P = 0.03$) (Fig. 2b). In contrast, mean foray distance among helpers did not vary with home territory quality.

Birds in large social groups made forays of longer duration

Birds spent 20 ± 7 minutes less per day on the home territory for every additional member in their group (range of group size = 2 to 13; $t = 2.56$, $df = 28$, $P = 0.03$, Fig. 2c). Thus, home group size was a significant predictor of the proportion of time spent on the home territory.

Breeders spend more time away than helpers

Mean time spent at each non-home group was significantly less among helpers (14.1 ± 0.2 minutes) than breeders (26.3 ± 0.3 minutes, $t = 2.37$, $df = 76$, $P = 0.01$). There was no significant difference in the foray duration among the sexes within breeders (2 ± 7 minutes, $t = 0.31$, $df = 45$, $P = 0.75$) and helpers (3.6 ± 4.5 minutes, $t = 0.82$, $df = 29$, $P = 0.43$; Fig. 2d). In helpers, individuals spent significantly longer (5.8 ± 0.2 minutes, $t = 2.80$, $df = 418$, $P = 0.03$, Fig. 2e.) foraying to higher compared to lower quality territories. Mean foraying time of helpers to non-home territories was 36 ± 18 minutes earlier than it was for breeders ($t = 2.85$, $df = 48$, $P = 0.05$; Fig. 2f).

Foray behavior of breeders did not vary with number of cobreeders in the group

The number of cobreeders in the group did not predict the mean duration spent at a group while foraying (breeder females [range 1–3]: 7 ± 5 minutes, $t = 1.42$, $df = 21$, $P = 0.17$; breeder males [range 1–4]: 2 ± 9 minutes, $t = 0.24$, $df = 17$, $P = 0.81$), or the distance to the group visited (breeder females, 88 ± 107 m, $t = 0.14$, $df = 9$, $P = 0.43$; breeder males, 28 ± 67 m, $t = -0.42$, $df = 12$, $P = 0.68$).

DISCUSSION

Our analyses revealed many previously unsuspected foray patterns. Most surprisingly, we found that breeders forayed regularly and spent more time foraying than helpers. Overall patterns of foray behavior were driven by a combination of the distance to the territories visited, home territory quality, and differences in sex and social status of the bird. Mean daily foray distances were 500–600 m from an individual's home territory (Fig. 2a), which is within the range of previously reported within-population dispersal distances for both males (220 m) and females (530 m; Koenig et al. 2000). These dispersal distances, and the fact that power

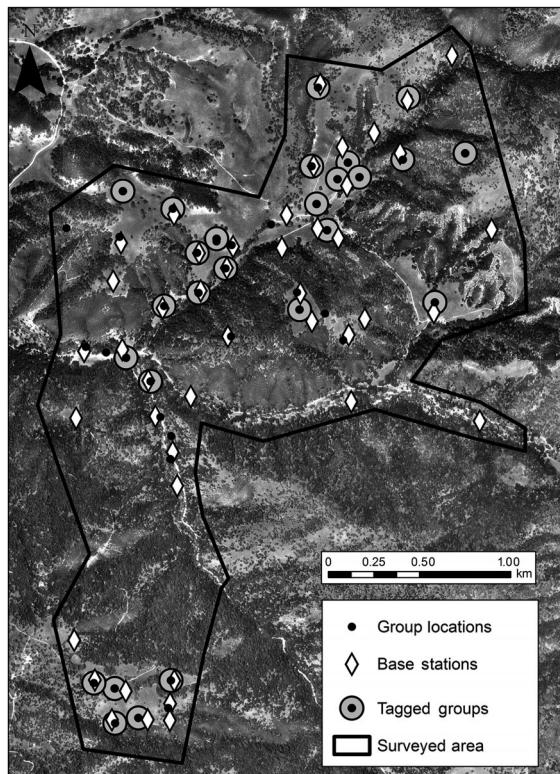


FIG. 1. Map of study area showing the spatial extent of the automated radiotelemetry array and the social groups with tagged birds. Black line represents the boundary of the permanent study area.

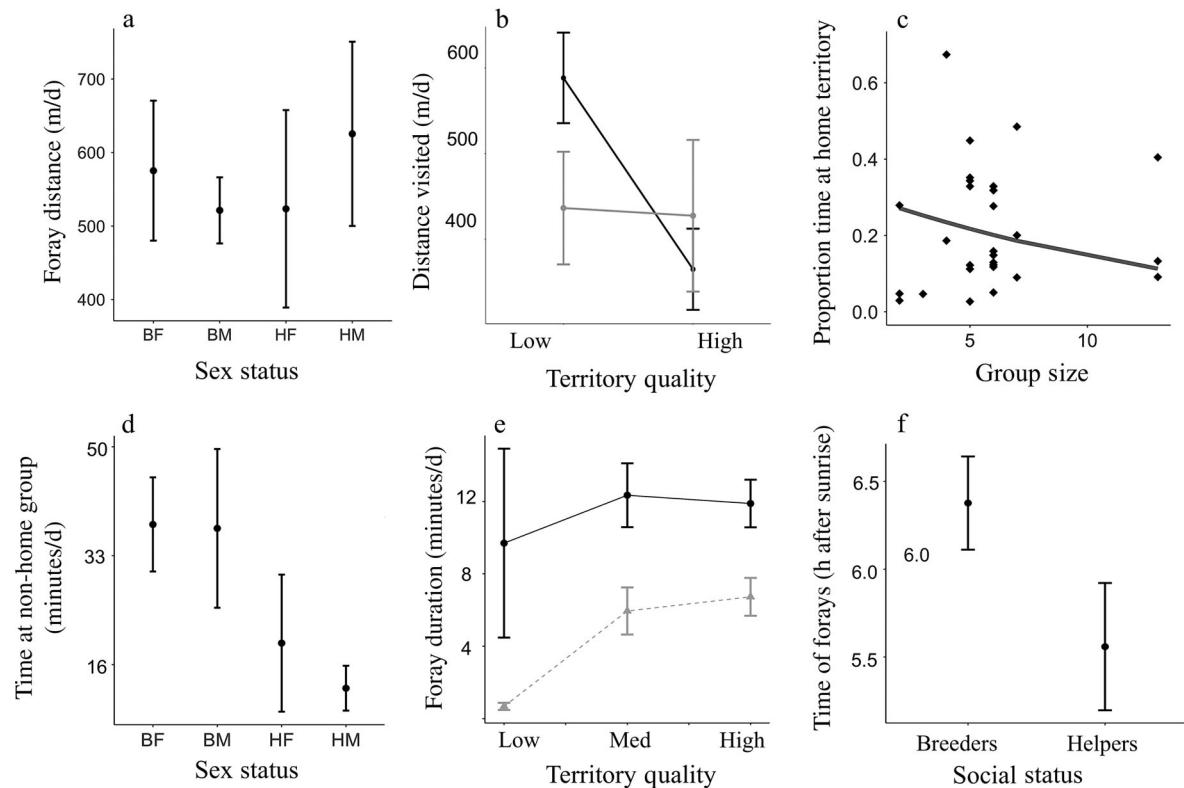


FIG. 2. Drivers of foray behavior of acorn woodpeckers: (a) mean daily foray distance does not vary by sex or status of the individual (BF, breeder females; BM, breeder male; HF, helper female; HM, helper male); (b) mean distance to territories visited decreases significantly with home territory quality for breeders (black symbols) but not for helpers (gray symbols); (c) proportion of time spent on the home territory decreases with increasing group size (line represents predicted values of a logistic regression model between proportion time on home territory and group size); (d) mean duration (minutes) spent at each non-home group per day is significantly smaller in helpers than breeders; (e) mean duration spent foraging based on quality of territory visited is higher for breeders (black symbols and line) than helpers (gray symbols and lines); and (f) mean timing of extraterritorial forays is significantly earlier in the day in helpers than breeders. Error bars denote SE. All means and standard errors are based on the raw data and not the mixed-model estimates.

struggles for available breeding vacancies can be initiated within minutes of the disappearance of breeders (Hannon et al. 1985), suggest that individuals monitor near territories more regularly than more distant territories (Fig. 2a), presumably to allow detection of breeding vacancies more readily while balancing foraging with defense of the home territory. Similar stay-and-foray strategies are known in other cooperatively breeding taxa including Red-cockaded woodpeckers (*Picoides borealis*; Walters et al. 1992), cooperative cichlids (*Neolamprologus pulcher*; Jungwirth et al. 2015), and banded mongooses (*Mungos mungo*; Cant et al. 2002).

Up until now, studies have generally assumed that breeders should remain on the territory to guard mates and defend the territory from intruders, while helpers should foray more often and farther than breeders, a pattern recorded in cooperatively breeding meerkats (*Suricata suricatta*) (Cram et al. 2018). In cooperatively breeding taxa where breeders are known to foray regularly, this behavior is conducted primarily to seek extra-group matings (Dunn and Cockburn 1999, Kesler et al.

2007, Johnson and Pruett-Jones 2018), a behavior that is rare in acorn woodpeckers (Haydock and Koenig 2003) and thus cannot explain the breeder foray behavior reported here. Breeders in this study forayed as much as helpers: mean daily foray distances did not differ between breeders and helpers, and breeders forayed regularly throughout both the breeding and nonbreeding periods of the study. Breeder forays were also of longer duration. As predicted, however, breeders from high-quality territories forayed shorter distances than breeders from low-quality territories, suggesting a trade-off between defending a high-quality territory and looking to trade up for a new breeding opportunity at a higher quality territory.

The motives behind breeder foray ecology in this population remain unknown. Breeder foray behavior may be driven by reproductive conflict between same-sex cobreeders in a coalition. When breeders are part of a large cobreeding coalition, individual reproductive success is reduced and reproductive skew among breeders can be high (Haydock and Koenig 2003, Barve et al.

2019). Thus, breeders may be motivated to foray to find independent secondary dispersal opportunities. Our results, however, failed to support this prediction. There was no relationship between mean foray distance or foray duration and number of same-sex cobreeders in the group. Thus, we suggest the following two potential drivers that likely motivate foray behavior among breeders:

- 1.. Acorn woodpeckers live in a complex social network where individuals identify one another by sight and through their vocalizations (Pardo et al. 2018). Breeders may thus foray to track group membership in surrounding groups and assess territory quality and reproductive success of neighboring groups to inform decisions about whether to attempt to trade up to a better territory.
- 2.. Breeders are often present at power struggles (Hannon et al. 1985) and are known to engage in agonistic interactions alongside related helpers before returning to their home territory (N.D.G. Hagemeyer, *unpublished data*). Breeders may thus foray frequently to detect breeding vacancies and facilitate dispersal of their offspring.

Helper foray behavior is affected by both ecological and social factors. Helper male acorn woodpeckers, as in many other avian cooperative breeders, inherit their natal territories more often and typically disperse closer to their natal territory than females (Koenig et al. 2000, Downing et al. 2018). However, we found no difference in foray distance or foray duration between helper males and females, a pattern that may be an artifact of the spatial extent of our receiver array, whose limits are substantially less than many female foray movements (Koenig et al. 1996).

Helper forays differed from breeder forays in three important aspects. First, foray distances in helpers did not vary with home territory quality, which likely demonstrates the importance of forays in maximizing the probability of successful dispersal for helpers. This suggests that while breeders may only foray close to their territory to facilitate territory defense, helpers are motivated by other factors. Second, helpers varied their temporal investment by spending more time on high-quality territories. Third, helpers forayed to territories earlier in the day than breeders. Taken together, these differences suggest that, while helper forays are not constrained by the quality of their home territory, they foray early in the day when territory vacancies are likely to first be apparent, and spend more time in the territories of groups to which they would gain the most from joining.

The foray behavior of acorn woodpeckers also appears to be influenced by characteristics of the home territory and group composition. Overall, home territory quality was a significant predictor of the mean distance of daily forays, with birds, especially breeders, from low-quality territories foraying farther than birds from high-quality

territories (Fig. 2b). Birds from high-quality territories may foray closer to home and invest more time in territory defense than birds from low-quality territories since high-quality territories likely attract not only more unrelated foraging woodpeckers but also California ground-squirrels (*Otospermophilus beecheyi*) and California scrub-jays (*Aphelocoma californica*), species known to pilfer acorns from woodpecker granaries (Koenig et al. 2019).

Our results revealed that the proportion of time spent on the home territory by an individual varied inversely with group size. This finding may be driven by birds undertaking forays for dispersal but also competition for resources on the territory. That is, large home group sizes may allow birds to foray more frequently, but may also increase competition for food and thus the motivation to forage outside the territory for food (Mayer et al. 2017).

Despite living on permanent year-round territories, acorn woodpeckers forayed outside their territory on a routine basis. Surprisingly, breeders forayed at frequencies and distances similar to those of helpers. This suggests that forays in group-living animals that live on year-round territories may be motivated by a variety of factors beyond providing an avenue to dispersal or extra-group breeding opportunities. Such movements may facilitate other behaviors such as information gathering, resource exploitation, and secondary dispersal. Continued monitoring of individual movement patterns can help tease apart how variation in the socioecological background of an individual drives its movement ecology, ultimately allowing social organisms to live in close-knit social networks.

ACKNOWLEDGMENTS

We thank our colleagues, the 150+ field and lab assistants that have assisted with the project since 1979, and Rich Gabrielson, who helped design the radio tags and base stations. We also thank the Hastings Natural History Reservation for logistic support. This study was conducted under the auspices of the Animal Care and Use Committees of the University of California, Berkeley (protocol R010-0412), Cornell University (protocol 2008-0185), and Old Dominion University (protocol 12-001).

LITERATURE CITED

- Baglione, V., D. Canestrari, J. M. Marcos, and J. Ekman. 2006. Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. *Proceedings of the Royal Society B* 273:1529–1535.
- Barve, S., W. D. Koenig, J. Haydock, and E. L. Walters. 2019. Habitat saturation results in joint-nesting female coalitions in a social bird. *American Naturalist* 193:830–840.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bridge, E. S., et al. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. *BioScience* 61:689–698.

- Cant, M. A., E. Otali, and F. Mwanguhya. 2002. Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. *Ethology* 108:541–555.
- Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics* 29:141–177.
- Conradt, L., P. A. Zollner, T. J. Roper, K. Frank, and C. D. Thomas. 2003. Foray search: an effective systematic dispersal strategy in fragmented landscapes. *American Naturalist* 161:905–915.
- Cram, D. L., P. Monaghan, R. Gillespie, B. Dantzer, C. Duncan, H. Spence-Jones, and T. Clutton-Brock. 2018. Rank-related contrasts in longevity arise from extra-group excursions not delayed senescence in a cooperative mammal. *Current Biology* 28:2934–2939.
- Double, M., and A. Cockburn. 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proceedings of the Royal Society B* 267:465–470.
- Downing, P. A., A. S. Griffin, and C. K. Cornwallis. 2018. Sex differences in helping effort reveal the effect of future reproduction on cooperative behaviour in birds. *Proceedings of the Royal Society B* 285:20181164.
- Dunn, P. O., and A. Cockburn. 1999. Extrapair mate choice and honest signaling in cooperatively breeding superb fairy-wrens. *Evolution* 53:938–946.
- Eikenaar, C., D. S. Richardson, L. Brouwer, and J. Komdeur. 2008. Sex biased natal dispersal in a closed, saturated population of Seychelles warblers *Acrocephalus sechellensis*. *Journal of Avian Biology* 39:73–80.
- Emlen, S. T. 1982a. The evolution of helping. I. An ecological constraints model. *American Naturalist* 119:29–39.
- Emlen, S. T. 1982b. The evolution of helping. II. The role of behavioral conflict. *American Naturalist* 119:40–53.
- Fedy, B. C., and B. J. Stutchbury. 2004. Territory switching and floating in white-bellied antbird *Myrmeciza longipes*, a resident tropical passerine in Panama. *Auk* 121:486–496.
- Handley, L. J. L., and N. Perrin. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16:1559–1578.
- Hannon, S. J., R. L. Mumme, W. D. Koenig, and F. A. Pitelka. 1985. Replacement of breeders and within-group conflict in the cooperatively breeding acorn woodpecker. *Behavioral Ecology and Sociobiology* 17:303–312.
- Haydock, J., and W. D. Koenig. 2003. Patterns of reproductive skew in the polygynandrous acorn woodpecker. *American Naturalist* 162:277–289.
- Hodge, S. J., A. Manica, T. P. Flower, and T. H. Clutton-Brock. 2008. Determinants of reproductive success in dominant female meerkats. *Journal of Animal Ecology* 77:92–102.
- Hooge, P. N. 1995. Dispersal dynamics of the cooperatively breeding acorn woodpecker. Thesis. University of California, Berkeley, California, USA.
- Johnson, A. E., and S. Pruett-Jones. 2018. Reproductive promiscuity in the variegated fairy-wren: an alternative reproductive strategy in the absence of helpers? *Animal Behaviour* 139:171–180.
- Jungwirth, A., J. Walker, and M. Taborsky. 2015. Prospecting precedes dispersal and increases survival chances in cooperatively breeding cichlids. *Animal Behaviour* 106:107–114.
- Kays, R., et al. 2011. Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. *Computer Journal* 54:1931–1948.
- Kesler, D. C., S. M. Haig, and M. Brittingham. 2007. Territoriality, prospecting, and dispersal in cooperatively breeding Micronesian kingfishers (*Todiramphus cinnamominus reichenbachii*). *Auk* 124:381–395.
- Koenig, W. D., and R. L. Mumme. 1987. Population ecology of the cooperatively breeding acorn woodpecker. Princeton University Press, Princeton, New Jersey, USA.
- Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution* 11:514–517.
- Koenig, W. D., J. Haydock, and M. T. Stanback. 1998. Reproductive roles in the cooperatively breeding acorn woodpecker: incest avoidance versus reproductive competition. *American Naturalist* 151:243–255.
- Koenig, W. D., P. N. Hooge, M. T. Stanback, and J. Haydock. 2000. Natal dispersal in the cooperatively breeding acorn woodpecker. *Condor* 102:492–502.
- Koenig, W. D., J. P. McEntee, and E. L. Walters. 2008. Acorn harvesting by acorn woodpeckers: annual variation and comparison with genetic estimates. *Evolutionary Ecology Research* 10:811–822.
- Koenig, W. D., E. L. Walters, and J. Haydock. 2011. Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. *American Naturalist* 178:145–158.
- Koenig, W. D., E. L. Walters, and J. Haydock. 2016. Acorn woodpeckers: helping at the nest, polygynandry, and dependence on a variable acorn crop. Pages 217–236 in W. D. Koenig and J. L. Dickinson, editors. *Cooperative breeding in vertebrates: studies of ecology, evolution and behavior*. Cambridge University Press, Cambridge, UK.
- Koenig, W. D., E. L. Walters, P. B. Stacey, M. T. Stanback, and R. L. Mumme. 2019. Acorn woodpecker (*Melanerpes formicivorus*). *The Birds of North America Online* version 2.0. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2015. Package lmerTest. R package version 2. <https://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf>
- Mayer, M., A. Zedrosser, and F. Rosell. 2017. Extra-territorial movements differ between territory holders and subordinates in a large, monogamous rodent. *Scientific Reports* 7:15261.
- Pardo, M. A., E. A. Sparks, T. S. Kuray, N. D. Hagemeyer, E. L. Walters, and W. D. Koenig. 2018. Wild acorn woodpeckers recognize associations between individuals in other groups. *Proceedings of the Royal Society B* 285:20181017.
- Pegan, T. M., D. P. Craig, E. R. Gulson-Castillo, R. M. Gabrielson, W. Bezner Kerr, R. MacCurdy, S. P. Powell, and D. W. Winkler. 2018. Solar-powered radio tags reveal patterns of post-fledging site visitation in adult and juvenile tree swallows *Tachycineta bicolor*. *PLoS ONE* 13:e0206258.
- R Core Team. 2018. R 3.5.1: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- Ridley, A. R. 2012. Invading together: the benefits of coalition dispersal in a cooperative bird. *Behavioral Ecology and Sociobiology* 66:77–83.
- Russell, E., and I. Rowley. 2000. Demography and social organisation of the red-winged fairy-wren, *Malurus elegans*. *Australian Journal of Zoology* 48:161–200.
- Stacey, P. B., and J. D. Ligon. 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *American Naturalist* 137:831–846.
- Taylor, P., et al. 2017. The Motus wildlife tracking system: a collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology* 12:8.

- van Dongen, W. F. D., J. White, H. B. Brandl, Y. Moodley, T. Merklng, S. Leclaire, P. Blanchard, É. Danchin, S. A. Hatch, and R. H. Wagner. 2013. Age-related differences in the cloacal microbiota of a wild bird species. *BMC Ecology* 13:11.
- Walters, J. R., P. D. Doerr, and J. H. Carter III. 1992. Delayed dispersal and reproduction as a life-history tactic in cooperative breeders: fitness calculations from red-cockaded woodpeckers. *American Naturalist* 139:623–643.
- Ward, M. P., M. Alessi, T. J. Benson, and S. J. Chiavacci. 2014. The active nightlife of diurnal birds: extraterritorial forays and nocturnal activity patterns. *Animal Behaviour* 88:175–184.
- Wolfenden, G. E., and J. W. Fitzpatrick. 1978. The inheritance of territory in group-breeding birds. *BioScience* 28:104–108.
- Young, A. J., and S. L. Monfort. 2009. Stress and the costs of extra-territorial movement in a social carnivore. *Biology Letters* 5:439–441.
- Young, A. J., G. Spong, and T. Clutton-Brock. 2007. Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society B* 274:1603–1609.

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