POPULATION DYNAMICS AND DISPERSAL COALITIONS IN THE COOPERATIVELY BREEDING ACORN WOODPECKER

by

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ABSTRACT

POPULATION DYNAMICS AND DISPERSAL COALITIONS IN THE COOPERATIVELY BREEDING ACORN WOODPECKER

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Dispersal is a critical life-stage with consequences not only for the individual, but for population dynamics and thus the fate of the whole species. The creation of dispersal coalitions can lead to complex outcomes and affect how changes in abundance occur on the landscape. I examined population dynamics and dispersal coalitions in a population of cooperatively breeding acorn woodpeckers in central California, USA. Using a 34-year dataset on occupancy and abundance, I determined that increases in abundance were determined by dispersal to new locations. This resulted in increased occupancy, rather than increases in group size and larger coalitions. I then examined vocal recruitment via simulated breeding vacancy conflicts to determine whether vocal signaling was sufficient to recruit individuals to a simulated conflict. Despite using recordings of conflict vocalizations, individuals exhibited a territorial response to these simulations, rather than responding as if to a breeding vacancy. Finally, I examined observed coalition sizes during breeding vacancy conflicts relative to those inferred from historical records of group composition following breeder turnover. Coalition dissolution after the conclusion of an observed conflict was common in non-breeders, suggesting that indirect fitness benefits are a major driver of coalition participation. Surprisingly, individuals with breeding positions often participated in these conflicts but did not remain with the coalition following the successful acquisition of the new breeding position. This flips the paradigm of cooperative breeding, with helping behavior directed from breeders to their non-breeding kin and offspring, thus leading breeders to gain indirect and direct fitness benefits through improving the reproductive success of their so-called "helpers". Overall, as resources increase, the population expands by taking advantage of previously marginal habitat in non-combative dispersal events, primarily by single individuals rather than coalitions. Marginal habitat does not appear to attract coalition visits, even with simulated vocalizations of dispersal conflicts. Dispersal conflicts occur primarily at high-quality habitat and involve the majority of same-sex relatives residing at the home territory, even those with breeding positions.

Dedicated to Almost the Acorn Woodpecker, who touched hundreds of lives.

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INTRODUCTION

Dispersal is one of the most important, yet least understood, life history stages (Wiens 2001). By the simple act of moving from one location to another, the dispersal of an individual has consequences not only for the fate of the individual, but for population dynamics and even the fate of the species (Bowler and Benton 2005). Though the ramifications of dispersal can be complex, at its core dispersal is a relatively basic process: a permanent or near-permanent movement of an individual from one location to another (Greenwood and Harvey 1982).

This movement can occur both when an individual leaves its natal site and when an individual leaves a breeding site (Bowler and Benton 2005). Natal dispersal is the permanent movement made by an individual from its natal site to a new location, while breeding dispersal is movement from one "permanent" location to another between reproductive attempts (Endler 1976; Greenwood and Harvey 1982; Bowler and Benton 2005). Other forms of movement, such as nomadic travel or migration, are not considered forms of dispersal (Greenwood and Harvey 1982).

Natal dispersal can be subdivided into three behaviorally distinct phases: (1) “departing,” when an individual leaves its home range; (2) “floating,” a variable time period during which an individual explores other areas; and (3) “settling,” when an individual settles in appropriate habitat, either as a temporary settlement or on a breeding territory (Ronce 2007; del Mar Delgado and Penteriani 2008). These three phases are sequential and comprise the “depart-and-search” dispersal strategy (Kokko and Ekman 2002). Individuals may float for some time, as waiting for an opportunity to settle in high-quality habitat can be worth the potential dangers of floating (Kokko and Sutherland 1998). Floating may be further complicated by “jumping” strategies, in which an individual first makes a long-distance “jump” to a distant location, where the individual then searches for settlement options (Kesler et al. 2010).

Conversely, an individual may choose to delay natal dispersal and “stay-and-foray,” restricting themselves to a smaller search area, and potentially foregoing breeding by remaining at their natal site (Walters et al. 1992). In the case of delayed dispersal, a different set of three behavioral phases may occur: (1) “foraying,” where an individual visits neighboring territories until a breeding vacancy becomes available; (2) departing; and (3) settling. Importantly, in species with delayed dispersal, an individual may sometimes also be able to inherit the natal territory or part of the natal territory, in which case an individual would never disperse (Kokko and Ekman 2002).

With the added behavioral complexity of delayed dispersal, one can then posit a form of “reverse dispersal,” whereby an individual returns to a previous home range after an attempt at reproduction, whether or not reproduction is successful. It is possible to imagine both a reverse natal dispersal, where an individual returns to its natal site after an attempt at reproduction (effectively returning to a state of delayed dispersal), and a reverse breeding dispersal, where an individual returns to a former breeding site after an attempt at reproduction elsewhere.

None of these dispersal types are mutually exclusive and dispersal is often plastic (Ronce 2007; Clobert et al. 2009). The conditional expression of dispersal types may reflect both constraints on the process of dispersal and plasticity in the individual’s response to various cues in the environment, a phenomenon termed “informed dispersal” (Ronce 2007). Much of condition-dependent dispersal is due to informed dispersal of individuals rather than physical constraints upon dispersing individuals (e.g. starvation, Bowler and Benton 2005); moreover, dispersal decisions need not be immediate or permanent, and dispersal can play out over extended periods of time (Roper et al. 2003).

Social factors may be major influences on dispersal decisions. During foray or floating periods, individuals may also make assessments as to the social environments available, such as differences in densities of each sex or the frequency of signal phenotypes, and adjust dispersal decisions accordingly (Nicolaus et al. 2012; Vercken et al. 2012). Dominance and sibling competition can also affect an individual’s choice of dispersal strategy (Pasinelli and Walters 2002), as can cooperative interactions such as participation in social groups (Cockburn 1998). For example, dominant individuals may drive out subordinate individuals when conditions are poor, thereby forcing subordinates to disperse (Pasinelli and Walters 2002; Jack et al. 2012); conversely, individuals may choose to disperse when sibling competition for resources is high, potentially to avoid these competitive kin interactions (Pasinelli and Walters 2002).

Similarly, dispersal rates can be influenced by social status, leading to bimodal dispersal states where more cooperative individuals disperse short distances while poor cooperators or “freeloaders” disperse outside of their social neighborhood (Kesler et al. 2010; Parvinen 2013). Changes in social status or the composition of social groups may lead to eviction or voluntary emigration from a group, such as in the case of turnovers in the dominant breeding individuals (Heinsohn et al. 2000; Jack et al. 2012).

In cooperatively breeding species, some individuals within a social group do not reproduce, and instead provide alloparental care (“nonbreeding helpers,” Hatchwell and Komdeur 2000; Kokko et al. 2001; Clutton-Brock 2002). These helper individuals may be unrelated to the breeding individuals (and thus potential breeders themselves), but are most often offspring that remain philopatric by delaying dispersal (Clutton-Brock 2002; Koenig and Dickinson 2004).

Philopatric young may inherit breeding positions in the natal group only when an unrelated breeding partner is present (Koenig et al. 1998), creating a bimodal set of strategies: stay-and-help with the hope to inherit, or disperse. Young may be more likely to remain philopatric when there is a higher likelihood of opposite-sex turnover in the breeding positions of the group (Berg et al. 2009), particularly as the fitness costs of helping versus breeding are often high (Reyer 1986; Heinsohn and Cockburn 1994; Clutton-Brock et al. 1998; Heinsohn and Legge 1999).

External constraints on dispersal may also encourage high rates of philopatry (Selander 1964; Blackmore et al. 2011). Site isolation and lack of short-distance dispersal opportunities encourages natal philopatry (Russell 2001). Similarly, high predation pressures may constrain individuals to remain in their natal group, either because lone individuals are more likely to be depredated, or because individuals must spend more time avoiding predators (Heg et al. 2004). In some species, all available or high-quality breeding locations may be filled, an ecological constraint forcing individuals to wait until a breeding position becomes vacant before dispersing (Koenig and Pitelka 1981; Emlen 1982, Arnold and Owens 1998; Hatchwell and Komdeur 2000).

Constraints, however, are not the only factors encouraging philopatry. Inheritance of breeding positions in the group leads to significant fitness benefits (Nelson-Flower et al. 2012). Similarly, nonbreeding helpers may wait for breeding opportunities to arise on specific, adjacent territories of high quality, thereby gaining direct fitness benefits (Zack 1990). These philopatric benefits are highest when territory quality is highly variable across the landscape, or when group size leads to large variance in fitness (Stacey and Ligon 1991). “Site tenacity” from prior experience on or near a site improves the chance of acquiring that territory, leading to direct benefits for philopatry at natal territories bordering high-quality sites (Zack and Stutchbury 1992) – indeed, advantages of proximity in gaining a breeding opportunity likely promotes the delayed short-distance dispersal characteristic of many cooperative species (Zack and Rabenond 1989).

Similarly, group augmentation, where individuals survive or reproduce better in larger groups, may provide a benefit to philopatry (Kokko et al. 2001). These benefits to philopatry may be strong enough that delayed dispersal may be the preferred option, with sibling rivalry preceding dispersal and forcing subordinate individuals to leave (Stacey and Ligon 1991; Ekman et al. 2002).

Beyond the decision to stay or disperse, individuals must determine whether to disperse as a lone individual or in parallel (to join a relative or social partner breeding elsewhere at an existing group, or to disperse in a coalition with other individuals). The benefits of group augmentation provide immediate incentive for an individual to cooperate (Kokko et al. 2001; Zhang and Hui 2011). A group may be able to deter predators (Heg et al. 2004), gain and maintain control of a breeding territory (Williams and Rabenold 2005), or otherwise face lower costs to dispersal than an individual would alone (Ridley 2012).

When dispersing with kin, an individual also gains indirect fitness benefits from helping kin to gain a breeding position (Zhang and Hui 2011). In models of dispersal, dispersal of kin in coalitions helps to maintain cooperation, even in the absence of group augmentation effects such as predator deterrence (Sharp et al. 2008). Individuals that participate in pre-dispersal coalitions are more likely to disperse in a coalition (Schoof et al. 2009), and individuals may advertise their willingness to join coalitions through risky behaviors such as predator deterrence, suggesting a major benefit to dispersing in a coalition (Maklakov 2002).

Dispersing with kin as opposed to non-kin increases both the likelihood of gaining a breeding territory and the length of breeding tenure (Woodroffe et al. 1995; Doolan and Macdonald 1996), potentially because kin are more cooperative than non-kin, due to the indirect fitness benefits from assisting kin. Similarly, reproductive success in a breeding coalition increases with relatedness, likely due to the same mechanism of indirect fitness benefits increasing the level of cooperation (Pope 2000).

Nevertheless, coalitions can be costly. Dispersal costs may be levied before dispersal via investments into altruistic behavior, or during dispersal via energetic costs of movement, competitive behaviors, and increased risks (Bonte et al. 2012). After dispersal, large breeding coalitions may be unable to sustain themselves on low-quality territories (Zack and Stutchbury 1992), or on highly fragmented habitat, due to decreased resources and increased risks (Blackmore et al. 2011); dispersal by coalitions to lower-quality habitat is therefore more costly than dispersal by single individuals.

The presence of non-breeding individuals may also reduce the overall fitness of breeders by costing more in resources than they return in helping benefits (Hamilton and Taborsky 2005). Furthermore, coalitions are dynamic, with coalitions forming, dissolving, and reforming based on environmental factors such as food availability or habitat saturation (Konishi and Debraj 2003). Thus, one would expect to see higher rates of cooperative dispersal in the presence of ecological constraints to high-quality territories, and lower rates of parallel dispersal to low-quality territories.

Post-dispersal, individuals breeding in a coalition may face high reproductive skew (Vehrencamp 1983; Richardson et al. 2002; Nelson-Flower et al. 2011) or constraints on the number of young produced (Gerlach and Bartmann 2002), both of which may reduce or eliminate direct fitness benefits to coalition dispersal (Barve et al. 2019). Coalition members may share breeding near-equitably, or one or a few members may dominate breeding; in extreme cases, subordinate individuals may be evicted from the coalition (Jennions and Macdonald 1994; Cant et al. 2001; Sharp et al. 2008). Participation in coalition dispersal by subordinate individuals unlikely to secure a breeding position is likely driven by indirect fitness benefits from helping kin to secure a breeding position (Heinsohn et al. 2000).

The cooperatively breeding acorn woodpecker is a model system for investigating cooperative dispersal. The acorn woodpecker exhibits both flexible polygynandry and philopatry (MacRoberts and MacRoberts 1976). A breeding group may contain up to 4 breeding females that nest jointly, and up to 7 breeding males (Koenig et al. 2020). Cobreeders of the same sex are usually closely related, either siblings or parent-offspring, and incest is rare (Koenig and Pitelka 1979; Haydock et al. 2001). Each group may also have a variable number of non-breeding offspring from previous nests that help by provisioning non-descendant offspring, defending the territory from both conspecific and heterospecific intruders, and tending the granary or granaries (Stacey 1979; Koenig et al. 1984).

Nearly all (97.6%) groups contain at least one pair of unrelated breeding individuals, and monogamous pairs are common (Koenig and Mumme 1987). Mean group size at Hastings Natural History Reservation (Carmel Valley, CA, USA, hereafter "Hastings") is 4.4 individuals, while in the U.S. Southwest, groups are most commonly pairs, with a mean group size of only 2.6 (Koenig and Stacey 1990).

Broodmates may remain together on the natal territory for at least one year (Stanback 1994), though they sometimes disperse sooner (Keonig et al. 2000). In addition to helping at their natal territory, nonbreeding individuals conduct extensive forays up to at least 15 km away from their natal group, with females foraying further than males, occasionally traveling together with relatives (Hooge 1995). These forays are in search of breeding vacancies at other territories, and may occur as frequently as once per hour or take as long as several days to complete.

The majority of breeding vacancies are resolved when unrelated immigrants fill the vacancy to the exclusion of resident same-sex helpers, with the latter almost always emigrating or being evicted after the vacancy is filled (Koenig et al 1998). Though incest avoidance predicts the emigration of these resident same-sex helpers, the time required to resolve reproductive vacancies is significantly longer in groups with helpers of the same sex as the vacancy, suggesting reproductive competition serves a role in determining when a vacancy is filled (Hannon et al. 1985; Koenig et al. 1999). Though helpers in this situation will avoid committing incest, they attack potential replacements, while the remaining parent advertises for a new mate, indicating parent-offspring conflict (Hannon et al. 1985).

When a vacancy is discovered, potential unrelated immigrants will invade the territory, sometimes in large numbers (Koenig 1981). These invasions are usually conflicts between groups of potential immigrants (coalitions) for the breeding vacancy, leading to the term "power struggle," and indicate intense, risky, and energetically costly competition among individuals attempting to disperse from their natal group (Koenig 1981). These territory conflicts are most common in March–April and August–September (MacRoberts & MacRoberts 1976). In general, these conflicts are associated with recolonization of abandoned territories (MacRoberts & MacRoberts 1976) and an increase in frequency of forays and movement between territories

(Hooge 1995). Dispersal conflicts, both within and between coalitions attempting to fill a breeding vacancy (Hannon et al. 1985), suggest that not all coalitions persist past initial dispersal.

Overall, acorn woodpeckers exhibit a long-tailed distribution of dispersal distance, with the majority of individuals inheriting a territory or dispersing one or two territories away to breed, but with records of individuals traveling up to nearly 200 km away from their primary range (Rusk et al. 2013). Dispersal distances for short-distance dispersers range from 0.22 to 2.90 km for males and 0.53 to 9.57 km for females; the frequency or mean distance of long-distance dispersers is not known (Koenig et al. 2000).

Dispersal is sex-biased, where female acorn woodpeckers disperse sooner, farther, more solitarily, and more aggressively than males; as a result, females are likely to suffer greater mortality in the process of dispersal, contributing to a pronounced sex bias (Koenig et al. 1983). Inheritance is similarly biased, with only 8% of females inheriting the natal territory, while 15% of males inherit (Koenig et al. 1983). During dispersal, females generally emigrate as singletons or pairs, while males emigrate as singletons or in groups of up to 4 individuals (Koenig et al. 1983).

In this dissertation, I first examined the population dynamics of the population at Hastings, which has seen a paradoxical increase in population as the percent land cover of the preferred habitat has decreased. Increases in resources may lead to increased recruitment of young into the population or increased dispersal into the population (Koenig et al. 2011). In a cooperatively breeding species, this increase in the population may happen in two different ways: 1) increases in abundance may encourage dispersal and colonization of formerly marginal habitat, increasing occupancy of sites, or 2) increases in local resources may lead to recruitment of young into the natal group, leading to larger group sizes.

Next, I conducted a playback experiment to determine whether agonistic vocalizations are sufficient to attract dispersal coalitions to a given location. One important component for the formation of coalitions in terrestrial vertebrates is vocal recruitment. Vocal recruitment has been associated with many different types of coalition formation, including foraging groups (Evans 1982), predator defense (Krama and Krams 2005), fledgling recruitment (Radford and Ridley 2006), and conspecific agonistic encounters (Gouzoules et al. 1984). Vocalizations may include encoded information that allows receivers to determine whether to join the coalition (Goodwin and Podos 2014); such vocalizations may also be "eavesdropped" on by potential enemies (Szipl et al. 2018). I used agonistic vocalizations from breeding conflicts outside of the study area to test if dispersal coalitions use these vocalizations by strangers to recruit to a potential breeding vacancy, even when the callers are not part of their own group or coalition.

Finally, I documented dispersal conflicts in the acorn woodpecker, to understand what determined dispersal coalition participation. I included potential drivers for coalition size such as the number of available non-breeders and breeders, the size of the largest opposing coalition, and the distance to the breeding vacancy. When dispersing with kin, an individual may gain both direct fitness benefits (from obtaining a breeding position) and indirect fitness benefits (from helping relatives gain breeding positions). In acorn woodpeckers, the likelihood of winning a dispersal conflict and gaining a breeding position increases with increasing coalition size (Hannon et al. 1985). This indicates both direct selection benefits for coalition participation (the larger the coalition, the higher the likelihood of breeding, even if one must share reproduction) alongside powerful indirect selection, where individuals are helping kin to gain breeding positions, even if the individual did not remain to breed.

INVESTIGATING THE SPATIAL SCALES OF CHANGES IN HABITAT COMPOSITION AND RESOURCE AVAILABILITY THAT DRIVE INCREASING ABUNDANCE AND OCCUPANCY OF A COOPERATIVELY BREEDING BIRD

Introduction

A positive relationship between the abundance and site occupancy of a species is a fundamental pattern in ecology (Andrewartha and Birch 1954; Gaston et al. 2000), but the population dynamics underlying this relationship are poorly understood. In addition, local dynamics are strongly related to regional and large-scale population dynamics only when colonization of new habitat is high, as in continuous populations or those with high dispersal rates (Freckleton et al. 2005). Various mechanisms have been proposed to explain intraspecific abundance-occupancy relationships, but none has received unequivocal support (Gaston et al. 1997; Borregaard and Rahbek 2010). Species occupancy and abundance are often determined by resource availability, both locally and in regional populations (García and Ortiz-Pulido 2004; Prange et al. 2004; Saracco et al. 2004). Pulses of resources can result in large increases in abundance when organisms disperse to resource-rich locations and/or by increases in fecundity (Edworthy et al. 2011). Similarly, landscape-level changes in habitat associated with fragmentation or succession can affect the quality of that habitat, resulting in some patches becoming unsuitable (Vander Haegen et al. 2000; Vallecillo et al. 2008) and thus decreasing local abundance when organisms emigrate and/or by decreases in fecundity (Borregaard and Rahbek 2010). Thus, both local and landscape processes may affect occupancy and demography, potentially in competing ways (Pearson 1993; Koper and Schmiegelow 2006).

In addition to spatial variation, temporal variation in resource availability may also determine both abundance and occupancy (Hanski et al. 1993; Gaston et al. 1997). When resources are consistently available, yet temporally variable at a site, species with high resource tracking remain at high overall abundance on the landscape with variable occupancy at the site, while species with poorer resource tracking have lower overall abundance and more consistent site occupancy (Rey 1995; Afonso and Eterovick 2007). Conversely, when resource abundance varies temporally, the abundance and occupancy of species reliant on those resources is highest during or after the peak of the resource (Levey 1988; Beehler and Mulla 1995; Schnurr et al. 2002). Unfortunately, there has been a historical mismatch in the temporal and spatial scales at which population dynamics and landscape heterogeneity are quantified, potentially confounding the understanding of population-level processes (Wiens 1989; Lima and Zollner 1996; Wiegand et al. 1999). This relationship between occupancy and abundance is further complicated in cooperatively breeding taxa, as local abundance may be determined by changes in mean social group size and/or the number of social groups.

The cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*) has exhibited both range increases (Kirk and Kirk 2005) and local population size (McMahon et al. 2015) in recent years, indicating at least a limited positive intraspecific abundance-occupancy relationship. This species lives in variably-sized social groups and specializes on acorns (*Quercus* spp.) as a critical, yet highly variable, winter food source (Koenig et al. 2016). Population productivity is tied to variation in acorn crop size (Koenig et al. 2011), and this dependence is further illustrated by the extensive acorn hoards this species accumulates in storage trees known as "granaries" that provide a food source when flying insects, the preferred food, are not available (MacRoberts 1970; Koenig et al. 2016). Granaries likely serve as an ecological constraint on independent breeding, and because of their rarity on the landscape and effort required to construct, granaries are typically inherited or acquired in an existing territory when a breeding vacancy occurs (Koenig and Mumme 1987; Koenig et al. 1995).

Previous work has revealed a paradoxical relationship between acorn woodpeckers and oaks. At the landscape scale, an increase in the acorn woodpecker population size is positively associated with the closing of oak canopy cover (McMahon et al. 2015), while locally, habitat with closed canopy structure is less likely to be occupied by woodpeckers than open canopy habitat (MacRoberts and MacRoberts 1976). This paradox – an increase in population size despite a decrease in preferred habitat – may have arisen because dispersal and foraging activities occur at different spatial scales (Hooge 1995; Koenig et al. 1996; Koenig et al. 2008), suggesting that a combination of mechanisms acting on occupancy and social group size may drive this paradoxical response.

Here, I attempt to integrate both spatial and temporal occupancy-abundance relationships to understand how changes in resource availability affect these relationships and to disentangle the mechanisms leading to the apparently paradoxical relationship. At least some metrics of habitat composition have changed significantly, which may affect the abundance-occupancy relationship (McMahon et al. 2015); in acorn woodpeckers, important resources include overall acorn availability, habitat quality associated with tree cover, and access to granary trees (Koenig and Mumme 1987; Stacey and Ligon 1987).

Changes in these resources may lead to increases in population abundance via enhanced reproductive success and subsequent recruitment of young into the population (Koenig et al. 2011), with increases in acorn availability leading to increases in abundance. Increases in abundance may motivate individuals to disperse and colonize formerly marginal habitat when local abundance is high, thereby affecting occupancy of sites and leading to increases in group density (Rosenzweig 1991; Gaston et al. 2000), manifested by increases in occupancy of territories with higher tree cover when abundance is high. Conversely, increases in resources may lead to increases in group size due to recruitment of young into the natal group (Koenig et al. 2011), and would be evidenced by increasing group size associated with increased acorn availability and decreased tree cover. Thus, to determine which aspects of the biotic environment are responsible for the increase in abundance of acorn woodpeckers over time, I investigated whether population increases occurred through changes in the size or density of groups and, if so, determined potential mechanisms of change in both group size and density across three ecologically relevant spatial scales.

Methods

Data

I used long-term data from the 953-ha Hastings Natural History Reservation in central coastal California, USA (hereafter ‘Hastings Reserve’; 36° 23’ N, 121° 33’ W). This site is situated within the Pacific Coast population of acorn woodpeckers, which is a generally continuous population (Koenig and Haydock 1999). As the acorn woodpecker is a good colonizer with rapid dispersal into available habitat (Koenig et al. 1995; Koenig et al. 2000; Rusk et al. 2013), the dynamics of the abundance-occupancy relationship at Hastings Reserve are likely reflective of the Pacific Coast population as a whole (Freckleton et al. 2005).

To investigate potential mechanisms underlying the temporal abundance-occupancy relationship of acorn woodpeckers, I examined the relationship between changes in habitat composition (canopy and shrub cover), annual variation in acorn production, and population dynamics of acorn woodpeckers. Specifically, my analysis used three long-term datasets: i) annual estimates of changes in habitat composition interpolated from vegetation surveys conducted in 1979 and 2013 (McMahon et al. 2015); ii) annual acorn counts on 250 individual trees comprising five oak species (1980–2013); and iii) annual acorn woodpecker occupancy and group size (1980–2013). I considered three spatial scales: i) the local foraging scale of territories, estimated as a 150-m radius around the granary, which includes the area generally defended (MacRoberts 1970) and in which >95% of foraging occurs (Koenig et al. 2008); ii) the neighborhood scale, consisting of discrete collections of foraging territories where each territory overlapped another by ≥10%, producing 7 neighborhoods ranging in size from 4 to 18 territories and representing 17.4 – 50.6 ha (Fig. 1); and iii) the landscape scale, consisting of all habitat surveyed (198 ha; Fig. 1). I assumed that the local scale remained consistent (territory boundaries remained static) throughout the study period.

Habitat Composition

To estimate changes in habitat composition over the study period, I compared two vegetation surveys conducted in 1979 and 2013, respectively. The surveys were laid out in a grid pattern of 613 x 0.04-ha (11.3-m radius) circular habitat plots, spaced at 60-m intervals (Fig. 1). Basal area for each tree species, number of stems for each tree species, overall proportion of canopy cover, and overall proportion of shrub cover were recorded for each plot (McMahon et al. 2015). Habitat plots that did not include canopy and shrub cover measurements from both years were excluded from the analysis ($n = 6$). I conducted supplemental analyses using National Agricultural Imagery Program aerial photographs from 2005 to 2014 (U.S. Department of Agriculture, 2015), which showed a linear increase of canopy cover over time (see Appendix). For each plot, I calculated the relative change in habitat composition from 1979 to 2013 for all metrics and interpolated annual estimates of canopy cover, shrub cover, and basal area of each species based on the linear trend found using the aerial photographs.

To characterize the change of a territory's habitat composition over time, I assigned habitat plots to 1-ha circles around the granary tree (total n = 477 plots). When these idealized woodpecker foraging territories overlapped, habitat plots within the overlap were assigned to all overlapping territories. Although such overlap could be considered a form of pseudoreplication, spatial overlap of plots used to calculate habitat metrics typically has little effect on the error structure of statistical models (Zuckerberg et al. 2012). I thus assigned habitat plots to neighborhoods in a similar fashion. To capture habitat composition, canopy cover, shrub cover, and basal area of each oak species, I averaged these metrics across each territory, neighborhood, and all habitat plots.

Acorn Production

I used acorn production data provided by the California Acorn Survey (W. D. Koenig and J. Knops, unpublished data) to determine an index of annual seed production of 250 individuals of five oak species: 88 *Quercus lobata,* 63 *Q. agrifolia,* 57 *Q. douglasii,* 21 *Q. kelloggii,* and 21 *Q. chrysolepis.* Survey trees were selected in 1980 in proximity to existing acorn woodpecker groups. Each autumn, two observers counted as many acorns as they could find on a survey tree within 15 seconds and summed for each tree (N30). Taken together, the mean counts of all 250 trees provided an index of annual acorn production for the study site (Koenig et al. 1994). The count from each tree was subsequently *ln*-transformed (LN30 = *ln* (N30+1)) to reduce skew in the data. Because woodpecker group size data were enumerated on 15 May of each year, I used a one-year (the previous autumn's LN30) and two-year lag to investigate the drivers of changes in group size due to acorn crops, mediated through successful woodpecker reproduction the previous year (Koenig et al. 2011).

Population Dynamics

I used the number of granary sites occupied by acorn woodpeckers as a measure of the spatial distribution of social groups on the landscape (occupancy; Fig. 1), and the sum of all individuals over all social groups on 15 May as population size (total abundance). I defined group size as the number of adult (i.e., > 5 months old) individuals that were present on 15 May (i.e. midway through the breeding season) on an occupied territory. If group size varied across the breeding season (April – July), I used the minimum number of individuals present in the group for that year.

Annual acorn woodpecker territory occupancy and group size were determined by monitoring color-banded individuals during bi-monthly censuses at each granary site (Koenig and Mumme 1987). Only territories that were occupied at least once between 1980 and 2013 were used, including sites that were not inhabited by woodpeckers at the study outset but later became occupied. I restricted my analysis to only those areas monitored continuously over the duration of the study. Thus, any population increases during the duration of the study were due to increases in density of acorn woodpeckers within the study site, rather than an artifact of changing study site boundaries. This measure of territory occupancy was used to determine local distribution of acorn woodpeckers at the site. Because the oaks surveyed, habitat plots, and woodpecker territories did not always co-occur in space, I restricted my analysis to only those territories that contained a minimum of five habitat plots and three survey oaks within the 150-m territory buffer (total n = 59 locations; Fig. 1); these territories included the majority (i.e. >90%) of the study population.

Statistical Analyses

To investigate whether changes in acorn woodpecker abundance at the study site were driven by the number (occupancy) of groups or mean group size, I conducted an analysis of variance of the annual total number of birds on the study site as a function of group number and mean group size.

I then used an information-theoretic approach to investigate determinants of occupancy and group size and the spatial scale at which they acted (Burnham and Anderson 2002). To dissociate occupancy from group size, I used a ‘hurdle modelling’ approach, which assumed that different drivers account for the transition from zero to non-zero values than the drivers of variation among non-zero values (Zuur et al. 2009). First, I modelled the predictors of occupancy for the full data set (i.e. zero vs. non-zero values in group size), by constructing generalized linear mixed models (GLMMs) with binomial error distributions. I then investigated the drivers of variation in group size for sites occupied (for the subset of non-zero values) with GLMMs using zero-truncated Poisson error distributions with a log-link (Zuur et al. 2009). For each step, I compared sets of candidate models with occupancy (Appendix Table A1) or group size (Appendix Table A2) as dependent variables and habitat composition parameters and acorn crop estimates at different scales as fixed effects.

For both occupancy and group size, I assembled *a priori* candidate model sets with fixed effects that reflected changes in habitat composition, characterized by overall canopy cover or species-specific changes in basal area, as well as overall and species-specific acorn production and their one- and two-year lagged effects. To account for repeated sampling of territories, all models contained the territory identifier (“SITE ID”) as a random effect (Bolker et al. 2009). The models for occupancy considered drivers at the neighborhood and landscape scale, as dispersal occurs among territories. Similarly, models of group size only included territory- and neighborhood-level drivers, because preliminary analyses suggested a prominent role of local- over landscape-scale processes. Finally, I included an interaction term between canopy cover and acorn production in the models of occupancy but not group size. Because the measures of acorn crop were a metric of relative per-tree production, and not a measure of overall number of acorns on the landscape, this interaction term allowed us to infer potential changes in absolute acorn production, where, as surveyed oaks matured and increased in proportional cover of the study area, the number of acorns produced increased (McMahon et al. 2015). In contrast, initial analyses revealed that group size did not increase over the study period; rather, it fluctuated around a stable mean. Therefore, my models investigated short-term drivers of group size variation. Inclusion of the interaction term did not improve model fit for these models. I present the model selection results for the top five models in the text and full model selection results in the Appendix.

Analyses of the effect of species-specific acorn crops and changes in basal area were conducted only with the three most common oak species (*Q. agrifolia*, *Q. lobata*, and *Q. douglasii*) as the distribution of the other two species (*Q. kelloggii* and *Q. chrysolepis*) only overlapped with parts of the study area, where they made up a small proportion of oaks (McMahon et al. 2015). I also constructed models where I partitioned oaks into functional groups of ‘evergreen’ (*Q. agrifolia* and *Q. chrysolepsis*) versus ‘deciduous’ (*Q. douglasii*, *Q. kelloggii*, and *Q. lobata*) oak basal areas and acorn crops, but they were not considered further as these models failed to explain more variation than models that had overall acorn crop as fixed effects. Acorn production was only considered at the neighbourhood and landscape scales because the small number of trees sampled per territory was insufficient for territory-level estimates (Fig. 1).

Similarly, at the landscape scale, I investigated only changes in basal area of *Q. agrifolia* because linear interpolation between 1979 and 2013 resulted in high multicollinearity of estimates among all oak species and *Q. agrifolia* best represented the overall pattern of habitat change in the study area (McMahon et al. 2015).

All analyses were conducted in R 3.4.1 (R Development Core Team, 2017). Models were constructed with the package 'glmmTMB' (Brooks et al. 2017; Magnusson et al. 2017) and model selection conducted with the package 'bbmle' (Bolker and R Development Core Team, 2016). All models were checked for multicollinearity among predictors and model fit was assessed by inspecting residual distributions. Parameter definitions are provided in Table 1, while model sets are summarized in the Appendix. Unless noted otherwise, I report mean ± standard error.

Results

The acorn woodpecker population in the study area increased from 52 individuals in 1980 to 219 in 2013 (Fig. 1, 2a), and this change in abundance was most strongly associated with the number of occupied sites (ANOVA: $F_{1,32} = 112.1$, $p < 0.001$, Fig. 3) and with mean group size ($F_{1,32} = 17.6$, $p < 0.001$, Fig. 3).

Habitat composition at Hastings Reserve changed significantly from 1979 to 2013. Mean canopy cover in habitat plots increased from 21.8 ± 0.9 % to 41.5 ± 1.5 %, while shrub cover increased from 11.5 ± 1.0 % to 27.9 ± 1.4 % (n = 477 plots). The number of stems increased from 66.9 ha^{-1} to 78.2 ha^{-1}. Density of *Q. lobata*, the preferred nesting tree species for acorn woodpeckers at the study site (Hooge et al. 1999), decreased from 21.0 to 14.1 stems ha^{-1}. The density of the other oak species remained unchanged. In contrast, acorn production was highly variable among years and species and exhibited no long-term trend (Fig. 2b).

Occupancy of territories exhibited both spatial and temporal variation (Figs. 1, 2a). Of the 59 territories considered, the mean duration of occupancy was 14.9 ± 1.7 years, but 10 (16.9%) were occupied for all 34 years of the study, while 20 (33.9%) were occupied for less than 5 years. The likelihood of a territory being occupied by a woodpecker group increased significantly with year (GLMM: $B = 0.07 \pm 0.01$, df = 3, z = 10, $p < 0.001$, Fig. 2a).

Landscape-level changes in habitat composition and neighborhood acorn production were the most important predictors of woodpecker site occupancy, as evidenced by the top model ($w_i = 0.913$, Table 2a). The parameters of the top model supported a mechanistic role of overall acorn crop in the previous two years, while the confidence interval for both canopy and shrub cover overlapped with zero (Table 2b). The significant statistical interaction between mean canopy cover and the 1-year lag in acorn crop size (‘Acorn Crop [1-year lag] [N] x Canopy Cover [L]’, Table 2b) in predicting occupancy suggests that the likelihood of site occupation increased with the previous year’s acorn crop size in the neighborhood, and that this relationship became stronger as the mean proportion of canopy cover on the landscape increased (Fig. 4).

Individual group sizes ranged from 1 to 15 birds (mean = 4.8 ± 0.1 birds). While there was a positive relationship between acorn woodpecker abundance and mean group size at the population level (Fig. 3), mean group size did not increase significantly over the study period (Fig. 2a, GLMM: Year: $B = 0.003 \pm 0.002$, df = 4, z = 1.5, $p = 0.14$). The top model predicting group size in occupied sites ($w_i = 0.946$, Table 3a) was determined by neighborhood acorn crop and territory-level habitat. Within this model, acorn crop sizes in each of the two preceding years were important positive predictors of group size (Table 3b, Fig. 5a, Fig. 5b). Moreover, group size was inversely related to mean canopy cover in territories (Fig. 5c).

Discussion

My goal was to determine the mechanism that led to the paradoxical rapid growth in population size of acorn woodpeckers despite decreasing availability of preferred habitat. More broadly, I sought to understand how changes in resource availability affect spatial and temporal occupancy-abundance relationships, and particularly how this related to cooperatively breeding species. My findings indicate that the population grew mainly by expanding the number of groups across the landscape (Figs. 2a, 3). I also found a weaker, but significantly positive, relationship between bird abundance and mean group size at the population level (Fig. 3), but these changes took the form of short-term fluctuations and did not result in a significant increase in mean group size over the duration of the study period (Fig. 2a).

Occupancy of new sites increased with landscape-scale gains in proportional canopy cover and with the interaction of canopy cover and the previous year's acorn production within the neighborhood (Table 2b), supporting the role of increasing food availability driving increases in acorn woodpecker abundance. In contrast, the strongest predictor of short-term changes in individual group size was the size of the acorn crop two autumns earlier and, to a lesser extent, the size of the most recent acorn crop at the neighborhood scale, potentially offsetting the negative effect of increased canopy cover at the local scale (Table 3b).

These results suggest that recruitment is a response to annual fluctuations in food availability, as the size of the acorn crop two autumns prior was the main predictor of recruitment of helpers to a group (Koenig et al. 2011). Meanwhile, the paradoxical response of the acorn woodpecker population to the decrease in preferred breeding habitat, achieved by increasing the number of groups, rather than group sizes, was mediated by increased acorn availability at the landscape-scale.

The habitat changes observed at the Hastings Reserve mirror those found across much of the range of Pacific Coast acorn woodpecker populations. Throughout the coastal range and the foothills of the Sierra Nevada, evergreen oaks have been increasing in cover over the last few decades (McIntyre et al. 2015; Peréa et al. 2017). Similarly, the breeding range of the woodpeckers, as well the mean abundance in standardized citizen science surveys (i.e. breeding bird survey – BBS, and Christmas bird counts CBC) have been increasing (Koenig and Pesendorfer *unpublished data*). Therefore, I surmise that the landscape-scale pattern in my study is representative of range-wide dynamics.

Habitat preferences exist at a local scale, with woodpeckers defending a small area around the granary (MacRoberts and MacRoberts 1976). Canopy cover, however, increased at the local scale, and group size was negatively related to this increase – results that uphold previous findings that acorn woodpeckers prefer open canopy and that overall territory quality is lower in areas with more closed canopy (MacRoberts 1970). I found no support for woodpecker population dynamics changing in response to a single species of oak, nor that food variability alone drives woodpecker population dynamics. Instead, increases in acorn food abundance appeared to enable the population to establish more groups in what was previously marginal habitat, despite the adverse effect of canopy cover. In support of this contention, the recent growth in group numbers occurred over a period without near-complete acorn crop failures, a phenomenon that occurred on several occasions prior to 2005 (Fig. 2a) and, at one point early in the study (1983 – 1984), led to abandonment of several territories (Hannon et al. 1987).

Variation in habitat quality, including food resources, can affect both mean abundance within a habitat and the overall suitability of the habitat, which can cause a species to vary in both abundance and occupancy (Holt et al. 1997; Gaston et al. 2000; Freckleton et al. 2011). In species with high dispersal ability, dispersal effects are thought to be limited and abundance and occupancy are dependent on the quality of the habitat, rather than abundance-based colonization rates or source-sink dynamics (Freckleton et al. 2005). My results suggest that increases in food abundance should lead directly to both increases in abundance and site occupancy, with formerly marginal habitat becoming habitable due to food increases. Indeed, increases in food abundance appeared to be sufficient for increases in acorn woodpecker occupancy but, in other species, metrics of habitat quality may play an important role in determining occupancy and abundance (Östman 2011).

For acorn woodpeckers, acorn harvesting and storage is a predominantly local process (Koenig et al. 2008; Scofield et al. 2010). Consequently, this species does not show a strong foraging response to landscape-scale spatial variation in acorn abundance within years (Pesendorfer and Koenig 2016), even though the previous autumn's acorn crop is a critical food source for overwinter survival (Hannon et al. 1987). The long-term acorn crop data did not include enough trees to provide a relevant measure of acorn crop at the local scale; nevertheless, the more localized neighborhood-scale measure of acorn crop was a better predictor of occupancy than the landscape-wide measure.

The total number of acorns produced across the landscape, estimated by the statistical interaction between acorn crop and landscape canopy cover, also influenced woodpecker occupancy, which is, by definition, a landscape-level process because individuals must disperse from their natal groups to an unoccupied location to establish a new territory (Hooge 1995). When considering leaving a group and subsequently determining where to settle, individuals are likely to be influenced by the presence of resources across the landscape (Edworthy et al. 2011), dispersing and occupying locations in years of high acorn availability (Koenig et al. 2011) and abandoning marginal territories in years with acorn crop failure (Hannon et al. 1987).

Dispersal to new locations is critical for increasing occupancy, and ability to disperse into new locations may help explain abundance-occupancy relationships (Gaston 2000). Although acorn woodpeckers are limited in part by the presence of granaries (Koenig and Mumme 1987), an increased overall abundance of acorns on the landscape in combination with a sufficient local acorn crop may allow acorn woodpeckers to occupy locations lacking granaries through a combination of the persistence of acorns in the canopy (i.e. serotiny; Koenig et al. 2014) and storing acorns in cavities and other temporary sites (MacRoberts and MacRoberts 1976) while they begin the construction of more permanent storage facilities. As an abundant species with high dispersal, acorn woodpeckers have a high likelihood of colonizing new patches or exhibiting rescue effects for groups occupying low quality habitat (Freckleton et al. 2005). This may lead to more spatial synchronization in the population. In rarer species, or species with poorer dispersal, resources and habitat quality may have weaker effects on both abundance and occupancy, leading to patterns determined more by dispersal capability than responses to changing resources (Freckleton et al. 2005; Borregaard and Rahbek 2010). Indeed, responses to changes in habitat may be masked by habitat heterogeneity or time lags, and it is critical to consider these factors when examining abundance-occupancy relationships (Conrad et al. 2001; Holt et al. 2004).

Mean group size remained relatively constant and appeared to change only with population fluctuations at shorter time scales. The 2-year lag in acorn crop was the strongest predictor of the number of offspring from the previous year’s breeding season that remained philopatric, which in turn predicted larger group sizes. While resource fluctuations affect dispersal decisions, there is no evidence for long-term changes in the fitness benefits of dispersal versus philopatry. Rather, there may be an optimal group size that has remained unchanged over the course of the study period, potentially due to the limited benefits derived from having helpers in a group (Mumme and de Queiroz 1985; Koenig et al. 2011). Thus, increases in abundance in this population have resulted in an increase in group density rather than an increase in group size.

My investigation of the intraspecific abundance-occupancy relationship relied on assumptions whose role in population dynamics I plan to investigate in the future. By using the distribution of occupied granary sites as my measure of occupancy, for example, I assumed that territory sizes did not vary greatly with group size or habitat quality. Indirect evidence from foraging observations suggests, however, that space-use of individual groups may vary among years as a function of acorn production by different oak species (Koenig et al. 2008). Figure 1 illustrates that newly-formed groups expanded the species’ core use areas in the landscape, suggesting that the birds did not simply reduce territory size to cluster into previously used areas. Furthermore, I did not explicitly account for dispersal into and out of the study population, but my study site is part of a continuous population and emigration is likely equal to immigration (Koenig et al. 2000). Finally, I interpreted the interaction between changes in canopy cover and relative annual acorn production as changes in overall acorn availability, as seed production is proportional to tree canopy size (Greene and Johnson 1994).

Conclusion

My results support a prominent role for food abundance in driving the temporal abundance-distribution relationship in acorn woodpeckers. The interaction of the population response to temporal variation in food availability and habitat preferences led to a counterintuitive increase in population size despite decreases in overall habitat quality; such interactions may occur not only due to mechanistic drivers, but also due to the scale at which these mechanisms act (Pearson 1993; Koper and Schmieglow 2006; Gaillard et al. 2010). Most importantly, the effects of temporal heterogeneity may not be immediately apparent, as patterns may emerge months or even years later.

The response of individuals to changes in resources and habitat is critical in determining both occupancy and abundance (García and Ortiz-Pulido 2004; Prange et al. 2004; Saracco et al. 2004). Moreover, no single mechanism is necessarily responsible for even simple patterns, including the ubiquitously positive abundance-distribution relationship (Borregaard and Rahbek 2010). This observation particularly applies to cooperatively breeding species, where individuals may increase in abundance both by dispersing to occupy new locations or by increasing group size.

In the acorn woodpecker, occupancy and abundance were driven by two different mechanisms: occupancy was dependent on landscape food abundance that supported a larger population, while group size was driven primarily by recruitment of philopatric offspring. Given that mean group size was relatively constant, the temporal abundance-distribution relationship in acorn woodpeckers was likely driven by food abundance, as shown by the increase in occupancy due to increases in landscape food resources (Fig. 2). While responses to fluctuations in acorn production are important in explaining year-to-year variation in group size, the overall patterns in the temporal abundance-distribution relationship of this species can be attributed to increases in overall food abundance, supporting a larger population. Nonetheless, the present study emphasizes that the population dynamics underlying abundance-distribution relationships are complex and an approach that examines a variety of possible mechanisms across relevant scales is necessary to fully understand this fundamental ecological pattern.

Table 1.

The variable sets used to build the candidate models for predicting acorn woodpecker occupancy or group size.

Fixed effects included habitat composition and acorn crop; random effect included territory id. See *Methods* for the definition of each scale. Single-species models and single-lag models were used in preliminary analyses and performed very poorly compared to the full variable sets and are thus not reported here.

Variable sets used to build candidate models

Variable set	**Variables**	**Spatial Scales**
Overall Acorn Crop (OAC)	summed acorn count (1-year lag) + summed acorn count (2-year lag)	Neighborhood (N), Landscape (L)
Species Acorn Crop (SAC)	*Q. agrifolia* acorn count (1-year lag) + *Q. agrifolia* acorn count (2-year lag) + *Q. douglasii* acorn count (1-year lag) + *Q. douglasii* acorn count (2-year lag) + *Q. lobata* acorn count (1-year lag) + *Q. lobata* acorn count (2-year lag)	Neighborhood, Landscape
Habitat Cover (HC)	percent canopy cover + percent shrub cover	Territory (T), Neighborhood, Landscape
Species Basal Area (SBA)	basal area *Q. lobata* + basal area *Q. agrifolia* + basal area *Q. douglasii*	Territory, Neighborhood

Table 2.

Predictors of acorn woodpecker occupancy of territories.

See Table 1 for definitions of model variable sets. (a) Model selection table for the top five supported models out of a total of 15 candidate models (see Appendix Table A1 for full candidate set) where K is the number of parameters, AIC is the Akaike Information Criterion value, ΔAIC is the delta AIC relative to the top model, and w_i is the model weight. (b) Standardized parameter estimates (β) and 95 % confidence intervals for the top model. Predictors with confidence intervals that do not overlap with zero are marked in bold.

Top models of territory occupancy

(a) **Model***	**K**	**AIC**	**ΔAIC**	**w_i**
Landscape HC + Neighborhood OAC	8	1469.6		0.913
Neighborhood SBA + Neighborhood OAC	19	1475.6	6.0	0.045
Landscape HC + Neighborhood SAC	16	1475.8	6.2	0.042
Landscape HC + Landscape OAC	8	1488.0	18.4	< 0.001
Landscape HC + Landscape SAC	16	1491.5	25.7	< 0.001

Table 2 continued.

(b) **Parameters for top model**	**β**	**95% C.I.**	
Overall Acorn Crop (1-year lag) (N)	**-1.209**	**-2.146**	**-0.271**
Overall Acorn Crop (2-year lag) (N)	-0.705	-1.674	0.263
Mean Proportional Canopy Cover (L)	14.100	-17.829	46.031
Mean Proportional Shrub Cover (L)	-16.982	-55.266	21.301
Acorn Crop (1-year lag) (N) x Canopy Cover (L)	**0.051**	**0.023**	**0.079**
Acorn Crop (2-year lag) (N) x Canopy Cover (L)	0.027	-0.002	0.056

*All models contain an interaction term between habitat and acorn crop parameters, as well as the random effect ‘Territory ID’ (territory identifier) and are modelled with a binomial error distribution for occupancy.

Table 3.

Predictors of acorn woodpecker group size.

See Table 1 for definitions of model variable sets. (a) Model selection table for the top five supported models out of a total of 9 candidate models (see Appendix Table A2 for full candidate set) where K is the number of parameters, AIC is the Akaike Information Criterion value, ΔAIC is the delta AIC relative to the top model, and *w_i* is the model weight. (b) – Standardized parameter estimates (β) and 95 % confidence intervals for the top model. Predictors with confidence intervals that do not overlap with zero are marked in bold.

Top models of group size

(a) **Model***	**K**	**AIC**	**ΔAIC**	**w_i**
Neighborhood OAC + Territory HC	6	3782.7		0.946
Neighborhood OAC	4	3790.3	7.6	0.021
Landscape SAC + Territory HC	6	3792.0	8.3	0.015
Neighborhood OAC + Neighborhood HC	10	3792.7	10.0	0.006
Neighborhood OAC + Landscape HC	7	3792.9	10.2	0.006

Table 3 continued.

(b) **Parameters for top model**	**β**	**95% C.I.**	
Overall Acorn Crop (1-year lag) (N)	**0.062**	**0.024**	**0.099**
Overall Acorn Crop (2-year lag) (N)	**0.114**	**0.077**	**0.152**
Mean Proportional Canopy Cover (T)	**-0.010**	**-0.016**	**-0.004**
Mean Proportional Shrub Cover (T)	0.005	-0.001	0.010

***** All models contain the random effect ‘Site ID’ and are modelled with a zero-truncated Poisson error distribution.

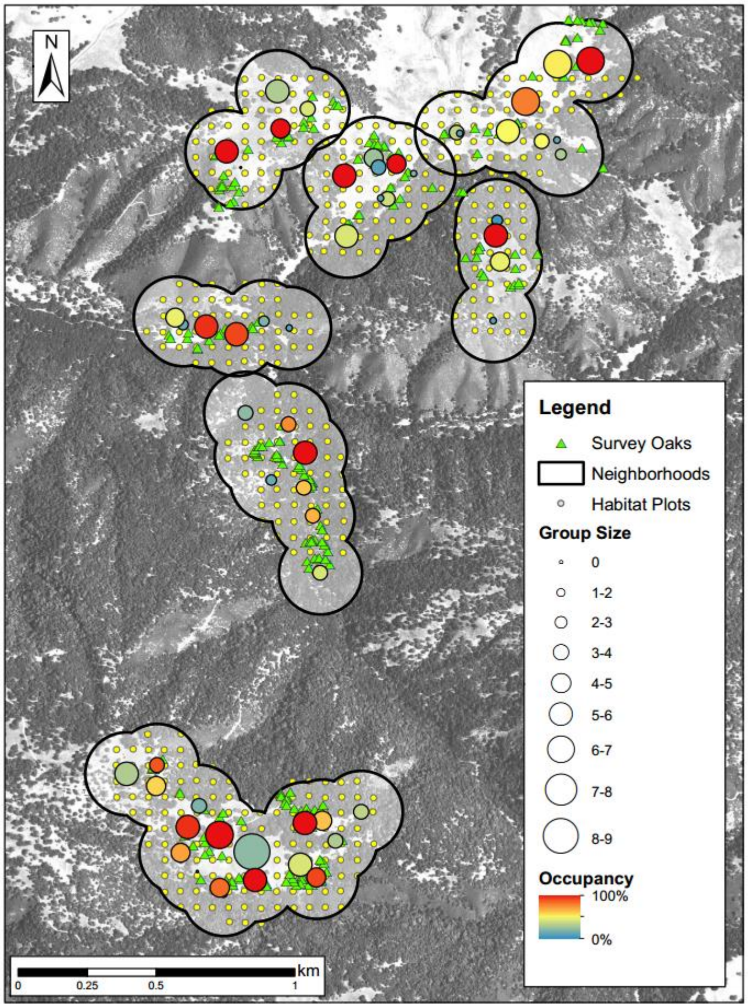

Figure 1.

Map of the study area (Hastings Natural History Reservation, Carmel Valley, CA), showing the acorn woodpecker group locations, the 7 neighborhoods, survey oaks, and the 613 habitat plots.

Map is centered on 36° 23’20” N, 121° 33’27” W; imagery is sourced from the NAIP 2012 dataset (US Department of Agriculture, 2015). Size of the group symbol represents mean group size over occupied periods, and color scale indicates proportional occupancy over the 34-year study period.

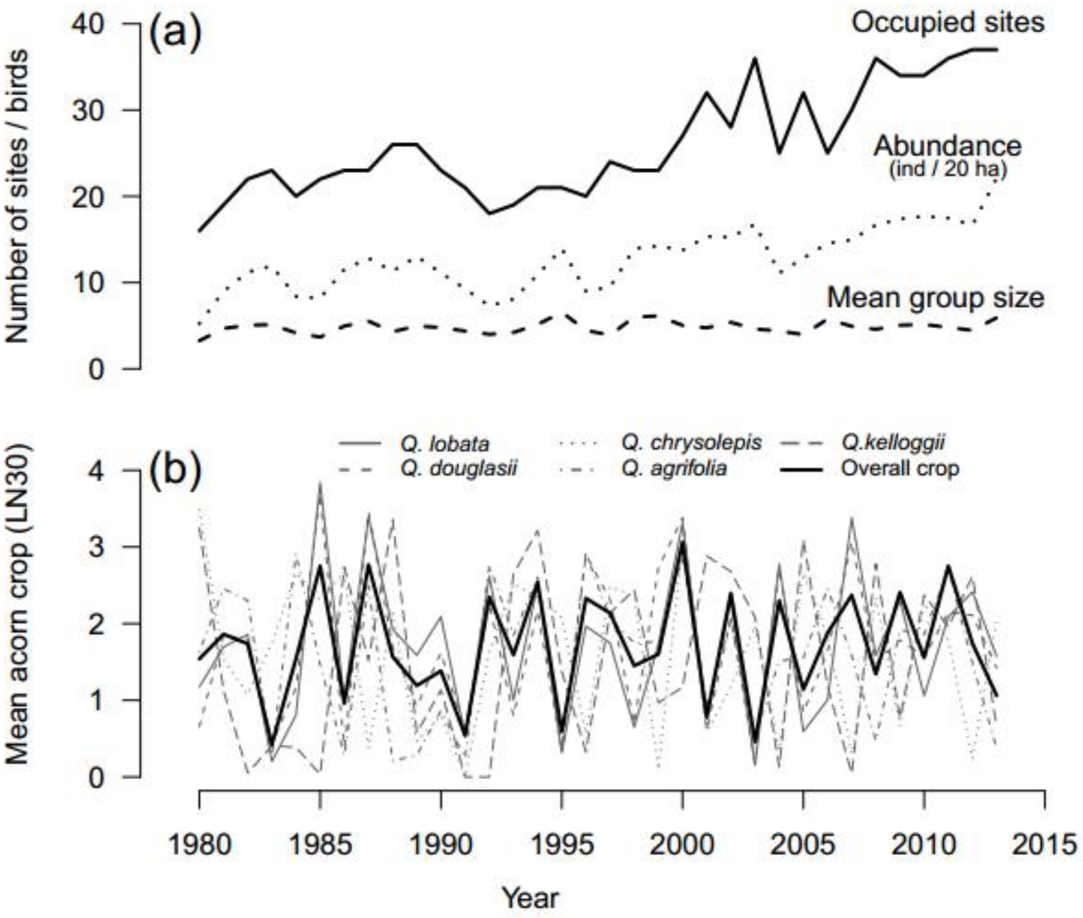

Figure 2.

Long-term data on (a) acorn woodpecker total abundance, occupancy, and mean group size and (b) acorn crop size variation over 34 years (1980–2013) in the 198-ha study area (Hastings Natural History Reservation, Carmel Valley, CA).

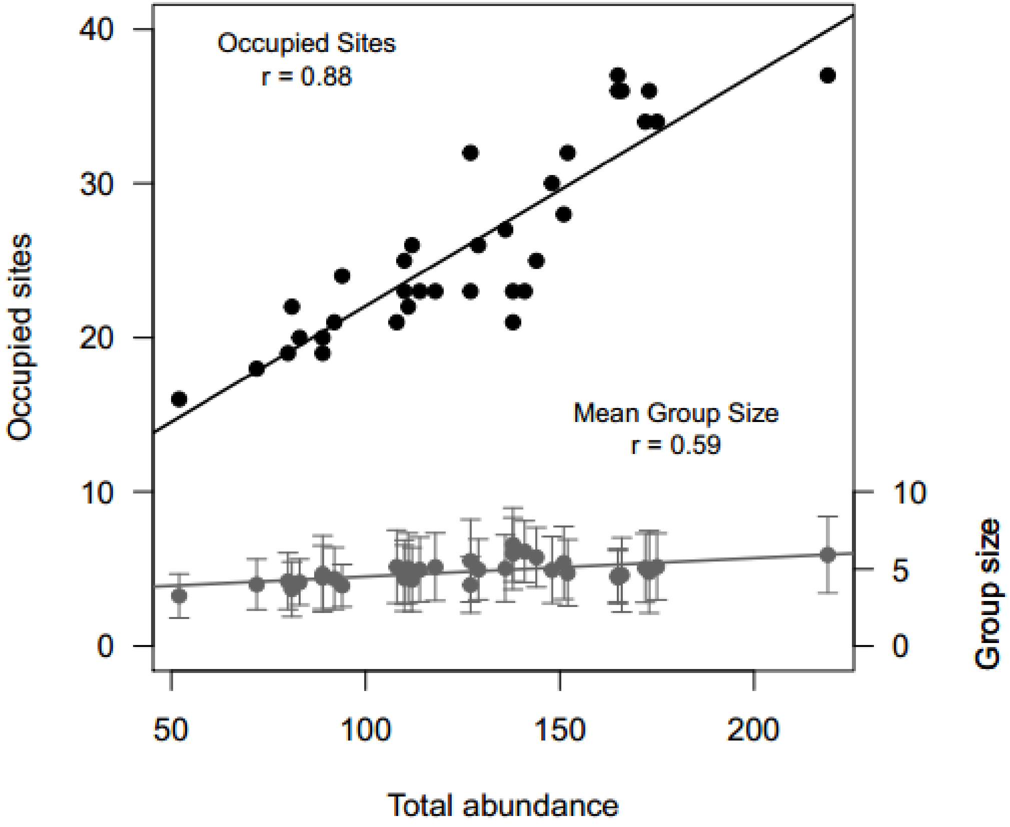

Figure 3.

Relationship between total abundance of acorn woodpeckers at Hastings Natural History Reservation (Carmel Valley, CA) and the number of occupied sites (black; left Y-axis) and the mean group size (grey; right Y-axis) for each study year (1980 – 2013).

Error bars for group size indicate standard deviation. Lines indicate linear fit. Pearson correlation coefficients are presented for illustrative purposes.

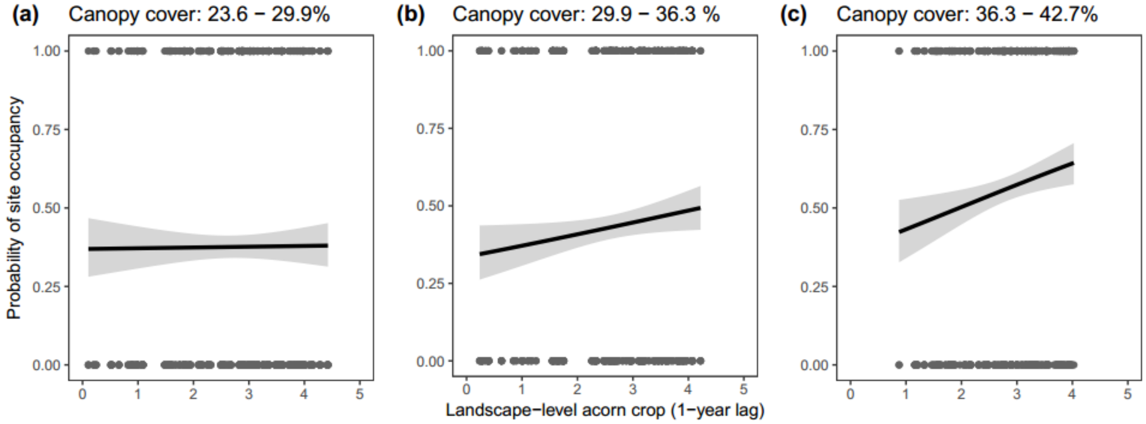

Figure 4.

Predictors of acorn woodpecker site occupancy.

Neighborhood acorn crop in the previous autumn (lag-1) increased the probability of site occupancy, as proportional canopy cover increased at the landscape-level. To illustrate the significant statistical interaction between the two parameters, I partitioned the data into three subsets (a–c) that represented 33% of the change in canopy cover. Linear regression trendlines are shown with 95% confidence intervals for each subset of the data. See Table 5 for detailed results.

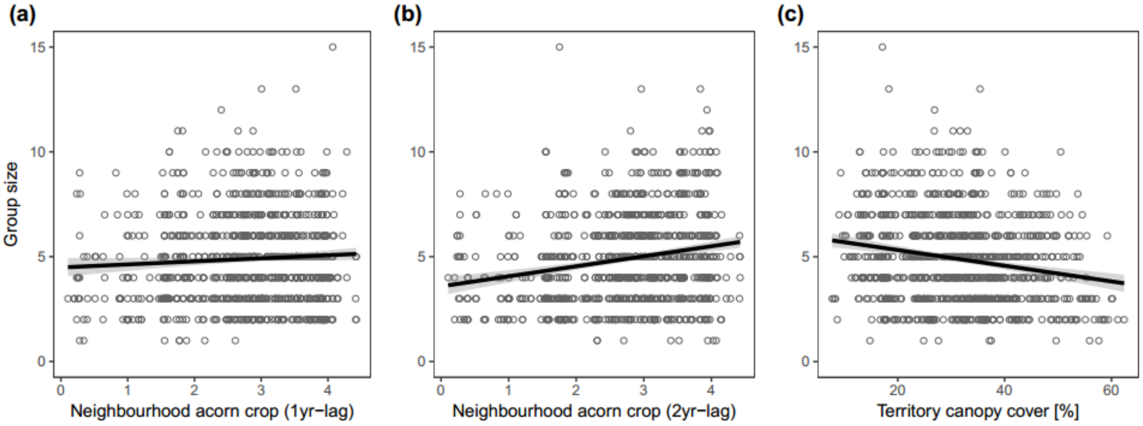

Figure 5.

Predictors of group size in acorn woodpeckers.

Group size was (a) positively related to neighborhood-scale acorn production in the previous autumn (1yr-lag), (b) positively related to neighborhood-scale acorn production two autumns prior (2yr-lag), and (c) negatively related to territory-level canopy cover. (n = 910, site/year combinations for occupied sites). Linear regression trendlines with 95% confidence intervals are shown for each plot. See Table 3 for detailed results.

CONTEXT MATTERS: TERRITORIAL RESPONSE TO PLAYBACKS OF AGONISTIC CALLS AT UNOCCUPIED SITES IN THE COOPERATIVELY BREEDING ACORN WOODPECKER (*MELANERPES FORMICIVORUS*)

Introduction

Agonistic behavior includes all behaviors that cause, threaten to cause, or seek to reduce or evade physical damage, and thus includes threats and aggression as well as conciliatory behaviors during confrontations (McGlone 1986). Many of these interactions are associated with obtaining or defending territories, but also include conflict over resources such as food or reproduction and may involve both individuals or groups of individuals (Lazaro-Perea et al. 2000, Surbeck et al. 2017). In social taxa, agonistic encounters often involve temporary coalitions, allowing for rapid recruitment to conflicts (Widdig et al. 2000).

Temporary coalitions are a common feature of social animals, occurring in social insects (Schwarz et al. 2006), cichlids (Weitekamp and Hofmann 2017), cetaceans (Connor et al. 1998), and terrestrial vertebrates (Loretto et al. 2012). These coalitions range in duration from a single agonistic interaction (Tokuyama and Furuichi 2017) to months or even years (Mosser and Packer 2009) before dissolving. Moreover, relationships among members of coalitions are highly variable and may consist entirely of kin (Mosser and Packer 2009), may be composed of individuals with or without prior affiliative relationships (Perry 1995, Tokuyama and Furuichi 2017), and may even contain formerly agonistic individuals (Lusseau 2007).

Vocal recruitment is an important component for the formation of temporary groups in terrestrial vertebrates and has been associated with a variety of activities including foraging activity (Evans 1982), predator defense (Krama and Krams 2005), extended parental care (recruiting fledglings to a location, Radford and Ridley 2006), group cohesion (Rubow et al.

2017), and agonistic encounters with conspecific individuals (Gouzoules et al. 1984). Calls associated with vocal recruitment may have additional information encoded including the identity of the caller, to whom the call is directed, type of interaction, and the initial level of aggression (Gouzoules and Gouzoules 1990, Engh et al. 2006, Slocombe and Zuberbühler 2007). Such encoded information may be used by a receiver during decision-making, presumably to assess risk vs reward, on whether to join a temporary coalition prior to potential conflict (Goodwin and Podos 2014). Such decisions may have important fitness implications, yet recruitment to agonistic vocalizations has been relatively under-studied (Rubow et al. 2017)

Recruitment to breeding vacancies during conflict is a common behavior in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*). Acorn woodpeckers live in social groups of up to 4 females that nest jointly, up to 8 males that cobreed, and a variable number of non-breeding helpers of both sexes (Koenig et al. 2020). Groups create and maintain specialized storage facilities, known as “granaries”, for the hoarding of acorns as well as cavities for nesting and roosting within defended territories (MacRoberts and MacRoberts 1976). Both granaries and cavities are thought to limit the population, so competition for rare breeding vacancies at occupied territories with granaries and cavities is often fierce, particularly at territories with large granaries (Hannon et al. 1985, Koenig et al. 2000). Dispersal to territories where breeding vacancies have occurred is most common in the early spring before the breeding season begins, with a smaller peak in the autumn when acorns are readily available; dispersal rates are typically lower during the summer after peak breeding season or during the winter (MacRoberts and MacRoberts 1976).

When a breeding vacancy occurs due to the death or disappearance of all breeders of one sex, coalitions of related same-sex helpers from other territories compete against other coalitions to fill the reproductive vacancy (Hannon et al 1985, Koenig et al. 1998). This form of agonistic behavior is similar to that seen in several other social taxa, where achieving breeding status involves winning conflicts among coalitions (Lazaro-Perea et al. 2000, Lusseau 2007, Raihani et al. 2010).

In the acorn woodpecker, conflicts over breeding vacancies, known as “power struggles”, are typified by loud, frequent calls and drumming, behaviors associated with territorial conflicts (Koenig 1981). In contrast, typical group vocalizations when not participating in power struggles contain fewer calls, different call types, and typically lack drumming (Koenig et al. 2020). Recruitment to a power struggle can occur very rapidly—within an hour after the experimental removal of all breeders of one sex—possibly because individuals are alerted to the distinct vocalizations made by individuals during such conflicts. Though the individuals who first recruit to power struggles are typically from neighboring territories (Hannon et al. 1985), individuals from outside of the audible range of a power struggle (>500 m, unpublished data) also recruit rapidly to the conflict. Nonbreeding helpers conduct extensive forays in search of such breeding vacancies, typically ranging from 0.22 to 2.90 km (males) and 0.53 to 9.57 km (females) and averaging one foray per daylight hour, suggesting that forays may provide the route for individuals to detect power struggles outside of audible range from their home territory (Hooge 1995, Koenig et al. 2000, Barve et al. 2020a).

I attempted to determine what factors influence recruitment to power struggles. Participation in a breeding conflict is likely determined by a variety of factors, including the individual’s breeding status and sex, the season, the distance to the conflict, and the quality of the contested territory. Given the importance of granary resources to this species, I predicted that individuals would be more likely to recruit to territories with resources (cavities or granaries) relative to territories without. As helpers are more likely to disperse than breeders (unpublished data), I predicted that helpers would be more likely to attend power struggles than breeders, and that helpers would travel farther than breeders to attend sites with breeding vacancies. In addition, as females are the dispersive sex (Koenig et al. 2000), I predicted that females would be more likely to attend and that females would travel farther distances than males. Finally, I predicted that individuals would recruit more often in the spring than in the summer, and that distances travelled would be higher during spring than summer, as dispersal is more common in the spring (MacRoberts and MacRoberts 1976).

Methods

This study used a population of acorn woodpeckers at Hastings Natural History Reservation (hereafter “Hastings”; Carmel Valley, California, USA) that has been continuously monitored since 1974. Hastings supports approximately 40–50 active groups each year, consisting of about 300 adult individuals in the population at any given time. Nearly all adult woodpeckers at this site have been uniquely marked with color bands (87.7%, N=472 over the course of this study) and monitored year-round, with a continuously maintained database. The social status of each individual, based on genotyping and census data, is known.

To test which factors best predicted vocal recruitment to perceived reproductive vacancies, I used call playbacks of power struggles at suitable, but unoccupied, sites within the study area.

I used ArcGIS 10.1 (ESRI, 2012) to digitize oak savanna and oak woodland habitat, identified by eye using aerial photographs of the study area. I randomly assigned 10 locations >150 m from the centroid of defended acorn woodpecker territories and from each other. This distance was approximately the radius of a defended territory (3.5–9 ha, if circular 106–169 m radius; MacRoberts and MacRoberts 1976) and the distance from within 94% acorns are harvested (Koenig et al. 2008). Locations were ground-truthed prior to experimental playbacks to verify that the random locations were within appropriate habitat and outside occupied woodpecker territories. In addition, I randomly selected a further 10 locations that included a pre-existing granary (> 200 granary holes) and/or cavity that were not currently occupied by acorn woodpeckers. These locations were ≥120 m from occupied territories. To verify that such territories were not occupied, I used a combination of census watches, presence/absence of acorns in the granary, and roost watches at cavities to determine if woodpeckers used the cavity for roosting. Because all high-resource locations (large granaries) were occupied for the duration of the study, any unoccupied locations represented areas of low-quality resources relative to those that were occupied.

Two playback recordings were created using recordings from California, but not from within 50 km of Hastings, to remove possible familiarity with calls and / or individuals. Recordings were sourced from the Cornell Lab of Ornithology Macaulay Library (www.macaulaylibrary.org). One recording was produced using *waka* calls, an individually distinctive, affiliative call typically produced when members of the same group approach one another after a short period of separation (MacRoberts and MacRoberts 1976; hereafter "occupied territory playback"). A second recording was produced using two recordings I deemed to have been at power struggles and included both the vocalizations associated with conflicts (*karrit-kut, urrk,* and *garrik*; Koenig et al. 2020) and drumming (hereafter "power struggle playback"). Recordings were built as a two hour cycle: 1 hour silence followed by 1 hour of intermittent vocalizations (10 min. of spliced recordings with breaks in vocalization of no longer than 30 sec, followed by 10 min. of silence [to prevent habituation] x 3). The first hour of silence allowed the playback to begin without the observer standing or moving to turn the speaker on, to prevent disturbing any individuals in the area. The delivery rate of vocalizations was intended to mimic power struggles, which have a high rate of often-overlapping vocalizations with brief periods of silence (pers. obs.). Playbacks were initiated 5 min. after arrival. A single observer with binoculars and a spotting scope for reading color bands conducted each playback. The observer used a G-Project G-Zip mini portable line-in wired mobile phone speaker paired with an iPod or mobile phone, with a sound pressure level of 100.1 ± 1.3 dB re 20 µPa at 1 m. The speaker was placed several meters from the observer in a clear or raised location to prevent obstruction of the sound by foliage. Marked individuals were identified, and number of unbanded individuals was determined as the maximum number of unbanded individuals present at the same time.

Playbacks were conducted Jun–Jul 2014, Feb–Mar and Jun–Jul 2015, and Feb–Mar 2016, comprising two spring (high dispersal) and two summer (low dispersal; Koenig et al. 2000) playback series. Each playback type (occupied territory and power struggle) was conducted once at each of the 20 sites over the course of each of the four playback series (two spring, two summer). Playbacks were stratified such that no playbacks were conducted at any sites within 300 m of each other in any 48-hour period, to allow for a recovery period and to prevent habituation to the playbacks. Each playback series was completed over the course of 30 days.

Attendance, drumming, and vocalizations were documented for the full duration of the playback. Individuals in attendance were identified when possible. For each playback, a summary was derived for each hour, with min of attendance <50 m from the speaker per individual, min with vocalizations <50 m from the speaker per individual, min drumming <50 m from the speaker per individual, and number of individuals in attendance. For each playback, I calculated the difference of these metrics between the first hour of the playback (silence) and the second hour of intermittent playback to control for the baseline level of activity in the area on that day. For marked individuals, I determined from what territory they came and how far they had traveled using the distance between the playback point and the granary of the territory of origin.

I used paired t-tests to determine if the mean difference between baseline conditions and playback conditions for each measurement (number of individuals responding, time of attendance per woodpecker, time spent vocalizing per woodpecker, and time spent drumming per woodpecker) differed from zero. Differences in sex ratios and in the proportion of unbanded individuals attending playbacks were analyzed using a chi-squared test with Yates correction.

I used linear mixed models for each measurement to predict the number of woodpeckers in attendance, min of attendance per woodpecker, min of vocalization per woodpecker, and min of drumming per woodpecker. Fixed effects included type of playback (occupied territory or power struggle), resources (present or absent), and season (spring or summer). I used a separate mixed model to examine distance travelled from the individual's home group to the playback. Fixed variables included type of playback, resources, season, sex, and social status (breeder or helper) of the individual. Random effects for all models were location of playback, to account for repeated measures at the same location; and year, to account for potential year effects.

All analyses were conducted in R version 3.5.1 (R Core Team 2019). All models were constructed using package *lme4*.

Results

Individuals responded to playbacks, with increases as compared to the control hour in the number of individuals present, the number of minutes attending per woodpecker, and the number of minutes vocalizing per woodpecker; the response in time spent drumming per woodpecker trended positive but was not statistically significant (Table 4). None of the measurements were affected by playback type (occupied territory or power struggle), season (spring or summer), or resources (present or absent) (Table 5). Marked individuals travelled a median of 156 m (120–1523 m); distance travelled to a playback was not affected by playback type, season, resources, sex, or status (breeder or helper) (Table 6).

I identified 34 marked individuals from known territories and 27 unbanded individuals attending playbacks (0.33 and 0.16 per playback, respectively; marked individuals sometimes attended multiple playbacks). Unbanded individuals, non-resident individuals from outside the population, were significantly more likely to respond to playback than marked birds; playbacks saw an average ratio of 0.65 unbanded individuals to 1 banded individual, compared to a ratio of 0.15 unbanded individuals to 1 banded individual in the population over the same time period ($\chi^2 = 366.11$, $p < 0.001$). Males were significantly more likely to respond to playback than females, with a mean sex ratio of 1.54 males to 1 female at playbacks when sex was determined, compared to a sex ratio of 1.09 males to 1 female in the population over the same time period ($\chi^2 = 283.87$, $p < 0.001$).

Discussion

Contrary to my expectations, individuals responded, apparently indiscriminately, to playbacks both of occupied territory vocalizations and of power struggle vocalizations. Similarly, the presence of granary and/or cavity resources did not result in preferential response, nor did season have any effect, as would have been expected if individuals were responding in an attempt to disperse during a particular season. This raises the question: why did individuals respond indiscriminately to playbacks?

The majority (79.4%) of marked individuals that attended playbacks were breeders; when helpers attended, they were generally present with breeders from the same social group. In addition, individuals attending a playback predominantly (93.9%) travelled <300 m (the approximate diameter of a defended territory; Koenig et al. 2008). Taken together, this suggests that individuals were responding not to an auditory signal of a breeding vacancy, but to the presence of vocalizations from unknown acorn woodpeckers at the borders of occupied territories, resulting in a potential territorial incursion. While the area from which acorn woodpeckers harvest acorns is ~ 150-m radius from the granary (Koenig et al. 2008), vocalizations near this edge may encourage territorial breeders to investigate potential intruders, and to assert the territorial boundary as needed.

Given that the playbacks were detectable and elicited an agonistic response from neighboring breeders, why, then, did helpers apparently ignore these vocalizations? There are several possibilities. First, helpers may recruit to power struggles based only on the vocalizations of known individuals, rather than unknown individuals (Pardo et al. 2018). Second, helpers may avoid agonistic interactions at unoccupied or low-quality sites or preferentially engage in fights only at high-quality sites (Barve et al. 2020a, 2020b). Third, vocalizations may not serve as a recruitment aid and helpers may find vacancies in a different fashion. Fourth, helpers may investigate such interactions without being detected (Barve et al. 2020a, 2020b). And fifth, the playbacks were not identified as power struggles, and helpers may not contribute extensively to territorial defense as the breeders have a higher stake in maintaining their territory than helpers.

Acorn woodpeckers can recognize the vocalizations of members of their neighboring social groups and identify when individuals are vocalizing with members outside of their social group (Pardo et al. 2018, 2020). Potentially, then, individuals may be uninterested in investigating vocalizations indicating agonistic interactions composed entirely of strangers. Such investigation would involve crossing territory boundaries, which risks potentially costly agonistic interactions with the territory holders. Thus, when in familiar areas, individuals may use knowledge of who is vocalizing, as well as knowledge of the territory itself, to determine whether to engage in a dispersal conflict. Interestingly, unbanded individuals were significantly more likely than expected to attend playbacks under the assumption that individuals travelled from within the study population; these individuals likely represented both "floaters" as well as individuals on foray with less information about the social groups or the habitat within the 1000-ha study area. Thus, I assume that individuals that are unfamiliar with the environment were more likely to attend the playback, suggesting that familiar individuals (i.e., those that are marked and continuously monitored within the study population) avoided playbacks composed entirely of strangers, or avoided poor-quality habitat.

Previous work on power struggles in the acorn woodpecker found that the onset of power struggles occurs relatively quickly and contains more and larger coalitions of individuals when the granary is larger (i.e. contains more holes; Hannon et al. 1985). Indeed, natural power struggles occur primarily on territories with large granaries, while breeding vacancies on territories without granaries or with small granaries are thought filled without any notable agonistic interactions (Barve et al. 2020b, unpublished data). Given the likely cost of power struggles – which may last for multiple days and involve physical fighting both midair and on the ground (Hannon et al. 1985) – if the playback was perceived as a power struggle conflict, helpers may be reluctant to risk harm for the sake of winning a low quality territory. Indeed, if they were specifically interested in the territory, they could have moved there prior to the playback experiment. As all of my playback sites were at locations with small granaries, a few roosting cavities, or with no granary or cavity resources, it is possible that helpers were uninterested in participating in or even investigating conflicts at sites they knew were low quality (Barve et al. 2020a).

Agonistic vocalizations, however, may not be the method by which helpers find breeding vacancies or recruit to power struggles. Helpers foray widely and multiple times per day (Hooge 1995, Koenig et al. 1996, Barve et al. 2020a); individuals may potentially be monitoring individuals by sight (Barve et al. 2020a) or by the individual vocalizations of breeders (Pardo et al. 2018, 2020), rather than searching for reproductive conflicts. Similarly, helpers sometimes leave a power struggle and return with siblings to rejoin the fray (Hannon et al. 1985), suggesting that the recruitment of coalitions may occur through non-vocal communication rather than through distant vocalizations. Vocalizations used during power struggles, as well as drumming, can be used in other contexts as well, including territorial conflicts or mobbing (MacRoberts and MacRoberts 1976), and thus may not provide an accurate indication of a breeding vacancy.

Conversely, individuals may have been investigating the playbacks more cryptically, and may have left when no agonistic interactions were observed. Despite the high rates of forays, detection of individuals outside their territory is less common than forays identified via radio-tracking, suggesting that helpers on foray are cryptic, and may be difficult to detect (Hooge 1995, Barve et al. 2020a). It seems unlikely, however, that many cryptic helpers were attending the playbacks without being seen by the human observers, especially as on the one occasion on which helpers were detected without breeders from the same social group, the helpers were visible for 26 minutes and vocalized repeatedly.

Rather, it seems more likely that helpers are unwilling to risk injury at low-quality sites, do not use agonistic vocalizations or drumming to detect power struggles, or did not perceive the playbacks of power struggles as reproductive vacancies. Tantalizingly, playback of agonistic vocalizations and drumming can be used to incite territorial responses on high-quality territories, and investigation by neighboring groups along the territory boundaries, but does not appear to cause incursions on the territory (pers. obs.). It is possible that helpers are aware of the membership of groups (Pardo et al. 2018) and are generally unwilling to openly trespass when breeders of both sexes are present.

Though other species show recruitment to agonistic interactions via vocalizations when strangers are calling (Gouzoules et al. 1984, Slocombe and Zuberbühler 2007), acorn woodpeckers do not respond to playbacks of power struggles as they would to an authentic power struggle. Rather, these playbacks seem to incite a territorial response from the less-dispersive breeders and males, rather than the more-dispersive helpers and females. Vocalizations can encode a wide range of information that can be used in decision-making (Goodwin and Podos 2014), but this information is apparently treated differently by acorn woodpeckers when the context of the vocalization is changed. Vocalizations can have different meanings in different contexts (McElligott and Hayden 1999, Vollmer et al. 2015, Hoier et al. 2016), and playbacks of vocalizations associated with high-quality territorial conflicts in low-quality habitat may have changed the context of the vocalization sufficiently to elicit a territorial, rather than a dispersive, response. Acorn woodpeckers demonstrate triadic awareness, and a response to vocalizations played back in an unanticipated context (two individuals from different groups calling together; Pardo et al. 2018); it is therefore unsurprising that context may play a role in determining response to agonistic vocalizations. Equally likely is that since the vocalizations were from woodpeckers outside of the range of my study population, Hastings woodpeckers simply did not recognize the individuals calling from outside the population and, thus, did not act in a predictable manner.

Recruitment to agonistic encounters via vocalizations has been relatively understudied, but recruitment vocalizations may encode information about the agonistic encounter and elicit disparate responses (Gouzoules et al. 1984, Rubow et al. 2017). When played back in a new and socially incongruous context – such as agonistic vocalizations from unknown individuals in known territory – information in the vocalization may be interpreted differently by individuals, leading to the territorial response observed in this study. Thus, it is necessary to maintain social context when conducting playback experiments, lest unanticipated responses occur.

Table 4.

Paired two-tailed t-tests for each measure, to determine if acorn woodpeckers responded to playbacks.

All measures saw an increased response during the playback as compared to the control hour.

Measure	**Value**	**t-value**	**P-value**
No. woodpeckers	0.70 individuals	6.55	< 0.01
Time attending (per woodpecker)	3.55 min	4.88	< 0.01
Time vocalizing (per woodpecker)	0.30 min	2.76	0.01
Time drumming (per woodpecker)	0.06 min	1.94	0.11

Table 5.

Model results for (a) number of woodpeckers in attendance, (b) min in attendance per woodpecker, (c) min vocalizing per woodpecker, and (d) min drumming per woodpecker.

All models included year and site as random variables.

(a)

Variable	**Estimate**	**Std. Error**	**t Value**	**P Value**
Season (spring)	-0.272	0.198	-1.373	0.172
Resources (present)	0.041	0.287	0.142	0.888
Type (power struggle)	0.099	0.198	0.503	0.616

(b)

Variable	**Estimate**	**Std. Error**	**t Value**	**P Value**
Season (spring)	0.005	1.236	0.005	0.996
Resources (present)	-1.290	1.245	-1.036	0.313
Type (power struggle)	0.435	1.235	0.352	0.725

(c)

Variable	**Estimate**	**Std. Error**	**t Value**	**P Value**
Season (spring)	-0.381	0.230	-1.657	0.116
Resources (present)	0.184	0.216	0.852	0.407
Type (power struggle)	0.096	0.215	0.447	0.656

Table 5 continued.

(d)

Variable	**Estimate**	**Std. Error**	**t Value**	**P Value**
Season (spring)	0.010	0.060	0.165	0.869
Resources (present)	0.002	0.060	0.033	0.974
Type (power struggle)	-0.001	0.060	-0.022	0.982

Table 6.

Model results for distance travelled by known individuals. The model included year and site as random variables.

Variable	**Estimate**	**Std. Error**	**T-value**	**P-value**
Season (spring)	-46.2	36.6	-1.262	0.216
Resources (present)	-217.2	141.9	-1.531	0.157
Type (power struggle)	51.1	30.0	1.702	0.098
Sex (male)	-41.9	30.1	-1.393	0.174
Status (helper)	15.8	39.5	0.398	0.693

PARENTAL FACILITATION OF DISPERSAL: BREEDERS HELP THEIR OFFSPRING TO DISPERSE IN THE ACORN WOODPECKER (*MELANERPES FORMICIVORUS*)

Introduction

Dispersal is one of the most important, yet least understood, life history stages (Wiens 2001). By the act of moving from one location to another, dispersal has consequences not only for the fate of the individual, but for population dynamics and even the fate of the species (Bowler and Benton 2005). Though the ramifications of dispersal can be complex, at its core, dispersal is a relatively basic process: a permanent or near-permanent movement of an individual from one location to another, which typically occurs when an individual leaves its natal or breeding site (Greenwood and Harvey 1982).

In group-living species with high dispersal costs, cooperation can be an effective strategy to increase the success of dispersal attempts. Coalition dispersal, where two or more individuals attempt to disperse together, has been observed in a diverse range of taxa where solo dispersers benefit from the addition of coalition members (Sharp et al. 2008, Ridley 2012). More generally, motivation for an individual to seek these cooperative coalitions goes well beyond dispersal and may arise from the benefits of group augmentation (Kokko et al. 2001; Zhang and Hui 2011). Longer term coalitions may facilitate the detection and deterrence of predators (Heg et al. 2004) or acquiring and defending a territory (Williams and Rabenold 2005), beyond reducing costs associated with dispersal (Lee et al. 2010; Ridley 2012).

When dispersing with kin, an individual presumably gains both direct fitness benefits by obtaining a breeding position and indirect fitness from helping relatives gain breeding positions. Coordinated kin dispersal likely helps maintain cooperation, even in the absence of group augmentation effects such as predator deterrence, and thus underscores the potential importance of the implications for increased fitness in such dispersal decisions (Sharp et al. 2008; Cornwallis et al. 2009). Even before the coalition has formed, individuals often participate in pre-dispersal behavior as a precursor to coalition dispersal, underlining the importance of these coalitions (Maklakov 2002; Schoof et al. 2009). Dispersing with kin, as opposed to non-kin, can increase both the likelihood of gaining a breeding territory and the length of breeding tenure via assistance in territorial conflicts (Woodroffe et al. 1995; Doolan and Macdonald 1996). Similarly, reproductive success in a breeding coalition can increase both with relatedness (Pope 2000) and social familiarity (Riehl and Strong 2018), due to increased level of cooperation between coalition members. In addition, coalitions can be dynamic, forming, dissolving, and reforming depending on environmental factors such as food availability or habitat saturation (Konishi and Ray 2003; Barve et al. 2019).

I studied cooperative dispersal in the cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*). Acorn woodpeckers build specialized storage facilities (“granaries”) for the hoarding of acorns (MacRoberts and MacRoberts 1976), a resource that is a limiting factor in the number of social groups in the population (Koenig et al. 1992, 2000). When a breeding vacancy is discovered, potential immigrants unrelated to the remaining opposite-sex breeders may invade the territory, sometimes in large numbers (Koenig 1981). These invasions often result in conflicts, known as “power struggles”, among coalitions of potential immigrants vying for the breeding vacancy (Hannon et al. 1985). Because some individuals compete at power struggles as singletons and not always as part of a coalition, I use the alternative term “dispersal unit” to include one or more related individuals that attempt to compete for breeding vacancies. These conflicts consist of intense, risky, and energetically costly competition among individuals attempting to fill the breeding vacancy (Koenig 1981). Most breeding vacancies are resolved when dispersal units fill the vacancy to the exclusion of any remaining resident same-sex helpers, the latter of which typically leave the group once the dispersal unit is established (Koenig et al. 1998).

In acorn woodpeckers, the likelihood of winning a power struggle and gaining a breeding position increases with increasing coalition size (Hannon et al. 1985). Observed conflict within coalitions attempting to fill a breeding vacancy (Hannon et al. 1985) suggests that not all coalitions persist past initial dispersal, due to within-group conflicts that leave only some members as breeders. Thus, I expected that coalition members would increase their potential to win a power struggle by increasing the number of group members who participated, and thereby enhance the indirect fitness of coalition members that facilitated the successful dispersal event, even though within-group dispersal conflicts may remove direct benefits for some members of the coalition. I therefore predicted that (1) the majority of same-sex helpers at the home territory would participate in the power struggle, (2) not all coalition members would remain at the new territory if the coalition won the power struggle, and (3) historical measures of coalition sizes, based on bimonthly censuses of territories, should underreport the actual coalition size during power struggles, assuming not all coalition members remain at the new territory. In addition, I predicted that same-sex breeders would be more likely to participate in a dispersal coalition if their current breeding coalition was large, reducing their direct fitness benefits within their existing social group.

Methods

This work was conducted at the 953-ha Hastings Natural History Reservation (hereafter “Hastings”) in central coastal California, USA (36° 23’ N, 121° 33’ W). At this site, a population of approximately 40–50 social groups of acorn woodpeckers, representing a population of 200–300 adults, has been continuously monitored since 1971. As nearly all (*N*=6,184 to date) adult woodpeckers at this site are uniquely color banded and monitored year-round, the composition and social status (based on genotyping of demographics) of each individual is known. A database has been maintained continuously and includes 1187 instances of dispersal, along with an assessment of the relative quality of each territory in each year as determined by the size of the granary.

Because each social group is censused, on average, every two months, it was unlikely that an observer would happen to census a territory during a power struggle, an ephemeral event that typically only lasts for a few days (Koenig 1981). Thus, any coalition dissolution would likely have already taken place by the time the group was re-censused. Because power struggles conspicuously occur at groups with moderate to high numbers of granary holes, I excluded all low-quality territories (i.e. those with <1,000 granary holes; Koenig et al. 2019) from my analyses.

Power struggles are relatively obvious and easily detectable at onset because of the large number of intruders and the raucous calls and displays of both intruding and resident individuals (Koenig 1981). If an observer happened to report a power struggle to me, I would conduct three census watches daily until the power struggle concluded. I monitored all such power struggles discovered from Aug 2013 to Aug 2017 to ascertain the identity of the individuals competing in the power struggle by reading uniquely marked color bands on each individual. When unmarked individuals were present at a power struggle, I counted the number of individuals displaying together and used distinguishing features such as facial markings, injuries, or other unique features to estimate the size of the dispersal unit.

To examine the effects of demography on coalition composition, I used bimonthly census data from the groups monitored in the overall population to determine the number of same-sex helpers and breeders within each social group relative to those observed attending the power struggles. Distances among groups were determined by calculating the distances between main granaries at each territory.

Previous work at this study site by Hannon et al. (1985) measured the sizes of dispersal units by removing breeding individuals from groups and documenting the resulting power struggles. I compared differences in dispersal unit sizes between sexes, between the observed power struggles and the Hannon et al. (1985) dataset, and between the historical census dataset and the observed power struggles with t-tests. The participation of helpers and breeders in dispersal units were compared between the historical dataset and observed power struggles using a chi-squared test.

For coalitions observed at power struggles, I examined the following variables as predictors of coalition size and composition : (1) number of same-sex helpers in the home group, (2) number of same-sex breeders in the home group, (3) total number of same-sex individuals (helpers + breeders) in the home group, (4) size of the largest dispersal unit attending, and (5) distance from breeding vacancy to home group. Because (1) same-sex helpers and (2) same-sex breeders were nested within (3) total same-sex individuals; I did not include (1) or (2) in models that contained (3).

I used an information-theoretic approach to compare 10 candidate generalized linear mixed models as predictors of dispersal unit size and number of breeders in a dispersal unit (Table 7) and used model averaging to look at the estimates of each variable (Table 8). Territory ID where the power struggle occurred was included as a random effect in all models to control for which power struggle the dispersal unit was detected. All statistical tests and modelling were conducted in R (R Core Team 2018); models were built using *lmerTest* (Kuznetsova et al. 2017), AIC_c tables were built using *bbmle* (Bolker 2017), and model averaging was performed using *MuMIn* (Barton 2018). All models had variance inflation factors of less than 5.

Results

Historical Census Dataset

The mean size of a dispersal unit in the historical census dataset was 1.50 individuals (range 1–7, *N* = 1187); 11.3% of dispersal units were composed of two or more individuals, with a mean of 2.17 individuals (*N* = 135), and the remaining 88.7% of dispersal units were lone individuals. The mean size of male dispersal units in the historical census dataset was 1.65 individuals (range 1–7, *N* = 574), and was significantly larger than the mean size of female dispersal units, which was 1.36 individuals (range 1–6, *N* = 613; $t = -5.80$, $p < 0.001$, *N* = 1187).

Observed Power Struggles

Dispersal unit sizes from Hannon et al. (1985) did not differ significantly from those measured during my study ($t = 0.39$, $p = 0.70$; $\bar{x} = 1.84$ [Hannon et al. 1985] and 1.94 [observed power struggles in current study]); thus, to increase power, I combined my measures of dispersal unit size with those from Hannon et al. (1985).

I observed 50 dispersal units ranging from 1 to 6 individuals, at 18 power struggles. Of these observed dispersal units, 21 were coalitions comprising two or more individuals. When combined with the observations from Hannon et al. (1985), this led to observations of 106 dispersal units. At power struggles, dispersal units had a mean of 1.89 individuals. Coalitions of two or more individuals comprised 45.3% of dispersal units, with a mean of 2.96 individuals (*N* = 106).

There was no significant difference in size between male ($\bar{x} = 2.08$) and female ($\bar{x} = 1.89$) dispersal units at observed power struggles ($t = -0.31$, $p = 0.76$, $N = 50$). Solo invaders never won a breeding vacancy at power struggles where a coalition of 2 or more individuals was also competing ($N = 17$ power struggles with both a solo invader and a coalition). Dispersal units were composed of a majority of the same-sex individuals available at the home territory ($\bar{x} =$ 60.2%, median = 50%, range 11.1–100%). Coalitions that successfully dispersed often partially or completely dissolved before breeding occurred at the new location, with as few as 20% of individuals remaining at a territory after winning a vacancy; when power struggles involved coalitions that contained breeders, the majority of these breeders returned to their home territory after winning the power struggle ($\bar{x} =$ 66.7% returned, $N = 9$ breeders).

Comparison Between Historical and Observed

Historical measurements of dispersed coalitions were significantly smaller than coalitions observed during power struggles (historical: 1.45, power struggles: 1.89, $t = 6.30$, $p < 0.001$). In further contrast to the historical data, most coalitions observed during power struggles included breeders (83.3%, $N = 21$ coalitions), and breeders were more likely to be present in coalitions at observed power struggles than to be present in coalitions from the historical data (20.6%, $\chi 2 = 80.7$, $p < 0.001$).

Home group composition had major effects on the size and composition of power struggle coalitions. All top models ($\Delta AIC_c <5$) for both coalition size and the number of breeders present included a measure of home group composition as a variable (Table 6). Coalition size was positively influenced by the number of same-sex helpers in the group and the total number of same-sex individuals in the group, and negatively related to the size of the largest opposing coalition and the distance from the home group to the power struggle; number of same-sex breeders did not have an effect (Table 8a). The number of breeders present was positively influenced by the number of same-sex breeders in the group, and negatively influenced by the number of same-sex helpers in the group, and the total number of same-sex individuals in the group (Table 8b). Neither the size of the largest opposing coalition nor the distance from the home group to the power struggle had an effect on the number of breeders present.

Discussion

When acorn woodpeckers disperse to a medium- or high-quality territory, coalition dispersal was the rule, and not the exception, and the prevalence of lone breeders at high-quality territories after territory changeovers reflected coalition dissolution, rather than solo dispersal. Vacancies at high- and moderate-quality territories were filled during power struggles, where solo invaders were clearly at a disadvantage compared to coalitions (Koenig 1981; Hannon et al. 1985). Low-quality territories, which may remain vacant for many years, appeared to be settled without conflict, and, unlike territories with the granary resources to support individuals through food-poor winters, low-quality territories were readily available. Power struggles thus represented contention for the critical granary resources present on the landscape, and by and large, the largest dispersal unit wins (Hannon et al. 1985). This pattern is similar to those seen in other species, and can lead to source-sink dynamics in the population, where high-quality territories produce large coalitions that dominate the next generation's reproduction, while low-quality territories produce small coalitions that cannot compete successfully for reproduction (Marjamäki et al. 2019). This pattern may also lead to site-dependent regulation, where population size is regulated due to decreased survival and reproduction at lower-quality territories and preferential dispersal to high-quality habitat (Rodenhouse et al. 1977.)

Under these circumstances, it is perhaps unsurprising that related acorn woodpeckers cooperate extensively to win these limited resources. I predicted that (1) the majority of available same-sex relatives would participate in the power struggle, and that (2) not all coalition members would remain at the new territory if a coalition won the power struggle. Indeed, on average, the majority of same-sex relatives participated in power struggles, including individuals with breeding positions. Coalition dissolution appeared to be the norm after dispersal, with single individuals sometimes remaining and breeding alone, potentially after driving off former coalition members. In this case, “coalition-mediated dispersal” may serve as a better term for describing the process of cooperative dispersal, rather than simple coalition dispersal. Moreover, I predicted that (3) historical measures of coalition sizes, based on bimonthly censuses of territories, would underreport the actual coalition size post-power struggle. As predicted, historical measures of both dispersal units and coalitions were significantly smaller than those documented at power struggles, indicating a historical underestimate of the extent and scope of coalition-mediated dispersal. Such underestimation of dispersal unit sizes is likely in other taxa where coalition dissolution after dispersal occurs.

When coalition size is a critical factor in winning reproductive vacancies, related individuals gain fitness benefits from helping their descendant offspring secure a breeding position, providing selection pressure for cooperation during dispersal when direct fitness benefits from securing a high-quality breeding position themselves are not available because of environmental or demographic constraints (Emlen 1982; Heinsohn et al. 2000; Sharp et al. 2008). In addition to the direct benefits gained from assisting offspring gain breeding positions, such cooperation may have delayed direct fitness benefit payoffs (Kern and Radford 2018). In the acorn woodpecker, these direct benefits may include later dispersal to the territory when conditions change (for example, if there is a breeder turnover on the home territory that forces the individual to emigrate), suggesting a bet-hedging mechanism where individuals may attempt to inherit the home territory, but maintain the ability to disperse to a relative's territory as a breeder (Rubenstein 2011; Koenig and Walters 2015). Acorn woodpeckers may also receive assistance in later power struggles from coalition members who previously gained a breeding position, which may serve a form of reciprocity (pers. obs.). These indirect or delayed fitness benefits, in conjunction with the direct fitness benefits of those that remain as breeders, may explain coalition-mediated dispersal in acorn woodpeckers, particularly given that dispersal success is directly linked to the size of the dispersal unit (Hannon et al. 1985).

In other taxa, kin cooperation during dispersal improves dispersal outcomes and may reduce costs of dispersal via mechanisms such as cost-sharing (Maag et al. 2018, Romano et al. 2019); similar factors may also be at play in this species. Indeed, the strongest predictor of dispersal unit size was the number of available same-sex individuals that could potentially participate in the coalition (Fig. 6), with these groups fielding larger coalitions, suggesting that the upper bound of coalition size is determined primarily by demographic composition of the originating group. There is therefore a high level of kin cooperation during dispersal in the acorn woodpecker – particularly sibling cooperation, a process that has been neglected in the study of kin interactions (Kramer and Meunier 2018). Kin cooperation, however, cannot be the only driver in coalition-mediated dispersal in the acorn woodpecker, as opposite-sex individuals do not participate in power struggles to aid their kin. Thus, the lure of potential direct fitness benefits is likely an important driver in the participation of individuals in the dispersal coalition.

Nevertheless, there are costs to participating in dispersal coalitions. Power struggles are violent and energy-intensive, and neighboring groups may take advantage of the disturbance to annex part of a group’s territory or steal stored acorns (unpublished data). Territory defense is likely an important factor mediating participation in the power struggle, with some individuals remaining behind to defend the home territory while others attempt to secure the breeding vacancy. Additionally, individuals may gain a competitive advantage from proximity to the territory of the power struggle, and thus be more likely to compete (Zack 1990). This tradeoff appears to be especially true for breeders, which are less likely to participate when more individuals are available in the group to participate (Fig. 2a), suggesting that breeders facultatively participate in power struggles, perhaps by assessing the size of the competing coalitions and the available coalition members. In addition, breeders are more likely to participate when there are multiple same-sex breeders available on the home territory (Fig. 2b), potentially due both to the ability of the remaining same-sex breeders to defend the home territory, and to the costs of co-breeding increasing the benefits of attempting to disperse and potentially secure a solo breeding position after coalition dissolution (Barve et al. 2019).

The evolution of breeder participation in coalition-mediated dispersal of their offspring is likely due to the fitness gained from increasing the reproductive success of their relatives and offspring. Fitness gains from reproductive offspring may provide selective pressure for parents to assist their offspring after independence (Brown and Brown 1984). This form of assistance by parents, known as parental facilitation, typically refers to parents promoting the survival and reproduction of their offspring by conceding resources such as food or part of a territory (Ekman et al 2000). In species with helpers, parental facilitation may also be a form of delayed reciprocity, where parents assist their offspring in dispersal to pay back helping at the parent’s nest. Previous research has shown that offspring with access to parental resources have higher survivorship and are more likely to acquire breeding positions, suggesting that parental facilitation is a powerful method for ensuring that offspring survive and reproduce (Ekman et al. 2004, Eikenaar et al. 2007).

This raises a compelling question: given that parental participation in a dispersal coalition increases dispersal success, why is parental-assisted dispersal not commonly documented? Parental facilitation appears to be typically passive: parents will tolerate offspring, allowing them access to resources denied to unrelated individuals, such as food or breeding opportunities (Ekman et al. 2001; Dickinson and McGowan 2005). Such nepotism can confer fitness advantages to the offspring, both by enhancing the survival of offspring and improving their chances of acquiring a high-quality breeding territory (Ekman et al. 2000, 2008; Eikenaar et al. 2007). Some forms of parental facilitation are more active; for example, parents may provide behavioral support in social groups, thus transferring social status within the group (e.g. a high-ranked female spotted hyena [*Crocuta crocuta*] will help her daughters attain high rank; Hofer and East 2003, East et al. 2009). In addition, parents and offspring may disperse together in kin coalitions, but by doing so, parents gain a direct fitness benefit by dispersing as well as aiding their direct offspring (Wang and Lu 2014).

Most similar to the parental-assisted dispersal observed in acorn woodpeckers is the behavior of territory bequeathal. In red squirrels (*Tamiasciurus hudsonicus*), females with offspring will disperse to allow their offspring to remain on the natal territory, increasing the offspring survival (Boutin et al. 1993; Price and Boutin 1993). Females may even acquire food caches prior to mating to bequeath to offspring (Boutin et al. 2000). Evidence for bequeathal is seen only in species that possess semi-permanent resources such as middens, food caches, or burrows (Lambin 1997). Potentially, such territorial resources are necessary for selection favoring parental facilitation of territory acquisition.

In addition, costs for parental facilitation in a dispersal context may simply be too high in most species for selection for coalition mediation. In other taxa with coalition dispersal, the dispersal process may require extensive travel and occur over extended time periods (Doolan and Macdonald 1996; Roper et al. 2003; Maag et al. 2018), preventing assistance from breeders without a heightened risk of the breeder losing control over their territory. Indeed, acorn woodpecker breeders from high-quality territories foray closer to their territories than breeders from low-quality territories, suggesting that there is indeed a trade-off between territory defense and dispersal (Barve et al. 2020a). Given the rapid time frame of power struggles, parents may potentially be able to facilitate dispersal by participating in dispersal coalitions over only short periods, before returning to their home territory and continuing as a breeder. Furthermore, acorn woodpeckers may return repeatedly to their territory during power struggles to forage and display, and often are able to travel between the power struggle and their territory in a single, sustained flight of under 30 seconds (pers. obs.). Thus, participating in a power struggle may represent only a low risk of territory incursion for a breeder.

Given the difficulty of tracking dispersal, it is possible that parental-assisted dispersal is more common than documented. In the heavily monitored population reported on here, the prevalence of coalition-mediated dispersal and the sizes of dispersal units were significantly underestimated, because of the difficulty of observing dispersal events. Parental-assisted dispersal may exist in other cooperatively dispersing taxa, and targeted documentation of dispersal events may uncover this phenomenon in other species.

In family-based cooperatively breeding species, helping is typically thought to be directed from non-breeding “helpers” to their breeding kin, such that helpers gain indirect fitness benefits through improving the reproductive success of breeders (Brown 1987; Clutton-Brock

2002). Indeed, enhancement of breeder reproductive success via helpers is central to an understanding of the evolution of cooperative breeding (Cockburn 1998; Hodge 2005). Parental-assisted dispersal flips this paradigm: helping is directed from the breeders to their non-breeding kin, such that the breeders gain indirect fitness benefits through improving the reproductive success of “helpers”. Indirect fitness benefits from parental facilitation may help to explain why in some systems, including the acorn woodpecker, studies fail to detect benefits from the presence of “helpers” on breeder survival or reproductive success, or find negative effects of “helpers” (Gilchrist 2007; Koenig et al. 2011). In such cases, breeders may be serving as the “helpers,” while non-breeders are the recipients of assistance, as is true in species with prolonged parental investment (Ekman et al. 2000). When examining the evolution and maintenance of cooperative and communal breeding, it is therefore critical to include the indirect fitness benefits accrued by breeders tolerating or assisting non-breeding kin.

Table 7.

AIC_c table ranking the models predicting (a) the size of power struggle dispersal units and (b) the number of breeders present in the dispersal unit.

All models included territory of the power struggle as a random effect.

(a)

Model	**ΔLog-Likelihood**	**ΔAIC$_c$**	***k***	***w*$_i$**
No. same-sex helpers	17.0	0.0	2	0.486
No. same-sex individuals	16.4	1.4	2	0.246
No. same-sex individuals + largest opposing coalition	16.9	2.6	3	0.133
No. same-sex helpers + largest opposing coalition	16.9	2.6	3	0.133
No. same-sex helpers + distance to home group	11.9	12.3	3	0.001
No. same-sex individuals + distance to home group	11.0	14.0	3	<0.001
Largest opposing coalition	6.6	20.9	2	<0.001
Intercept	5.3	21.4	1	<0.001
No. same-sex breeders	4.8	24.4	2	<0.001
Distance to home group	0.0	34.1	2	<0.001

Table 7 continued.

(b)

Model	**ΔLog-likelihood**	**ΔAIC**	***k***	***w_i***
No. same-sex helpers	8.8	0.0	2	0.539
Intercept	7.0	1.7	1	0.225
No. same-sex breeders	7.7	2.4	2	0.165
No. same-sex individuals	6.5	4.6	2	0.055
Largest opposing coalition	4.9	7.9	2	0.010
No. same-sex individuals + largest opposing coalition	4.6	10.4	3	0.003
No. same-sex helpers + largest opposing coalition	4.6	10.4	3	0.003
No. same-sex helpers + distance to home group	2.4	14.8	3	<0.001
Distance to home group	0.1	17.6	2	<0.001
No. same-sex individuals + distance to home group	0.0	19.7	3	<0.001

Table 8.

Model averaging results for models predicting (a) the size of power struggle dispersal units and (b) the number of breeders present in the dispersal unit.

Estimates where the 95% confidence interval does not include 0 are bolded. SE: Standard Error

(a)

	Estimate	95% Conf. Int.	SE	Z-value
Same-sex helpers	0.309	0.207, 0.411	0.050	6.03
Total same-sex individuals	0.276	0.175, 0.372	0.047	5.70
Largest opposing coalition	-0.160	-0.339, -0.010	0.079	2.00
Distance to home group	-0.0006	-0.001, -0.000	0.0003	1.98
Same-sex breeders	0.161	-0.267, 0.527	0.194	0.81

(b)

	Estimate	95% Conf. Int.	SE	Z-value
Same-sex helpers	-0.085	-0.146, -0.033	0.028	2.96
Total same-sex individuals	-0.054	-0.113, -0.004	0.027	1.94
Largest opposing coalition	-0.004	-0.113, 0.077	0.046	0.08
Distance to home group	-0.0003	-0.001, 0.000	0.0002	1.50
Same-sex breeders	0.202	0.010, 0.370	0.087	2.27

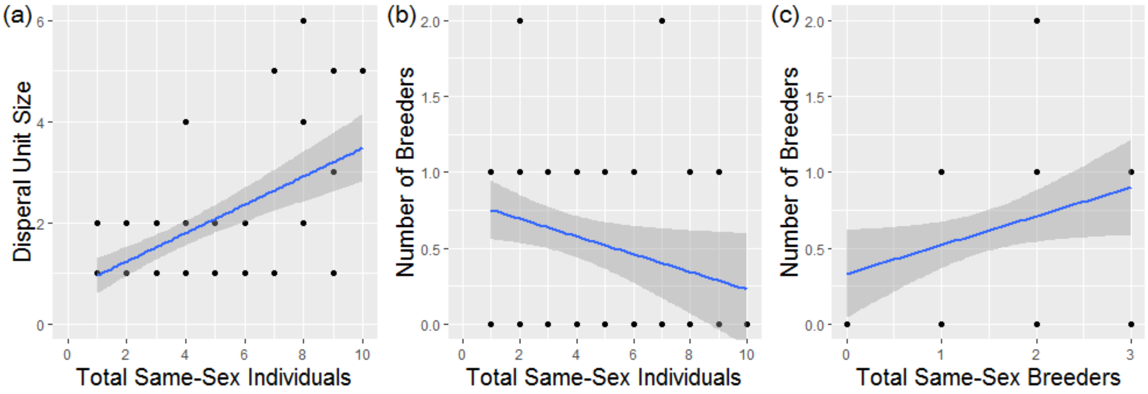

Figure 6.

(a) Size of the dispersal unit in relation to the total number of same-sex individuals at the home group; (b) Number of breeders participating in the dispersal unit in relation to the total number of same-sex individuals in the home group; and (c) the total number of same-sex breeders in the home group.

Linear model with standard error (shaded region) indicated for each.

CONCLUSION

At a landscape level, resources are increasing at Hastings Natural History Reservation (Carmel Valley, CA, USA), caused largely by the maturation of oaks and a concomitant increase in acorn production. As these food resources have increased over the 34-year period examined, the population of acorn woodpeckers at my study site has similarly increased. My research shows that the increase in population led to an increase in colonization of previously marginal habitat, driven by the dispersal of single individuals into this habitat and the formation of new social groups.

I found that occupancy of new sites increased with landscape-scale increases in food availability as measured indirectly by the interaction between canopy size and acorn crop. This led to a paradoxical response where population abundance increased despite a landscape decrease in preferred habitat caused by closing canopy. These habitat preferences were apparent in local dynamics, where territories with closing canopy had decreased group sizes; this loss of habitat was offset by a landscape increase in acorn availability. Acorn crops at a more local scale affected short-term fluctuations in group size, upholding previous findings that annual fluctuations in acorn crop determine the recruitment of helpers to a group (Koenig et al. 2011).

Although acorn woodpeckers rely on the storage of acorns in granaries for survival through the winter, smaller groups (such as pairs) may be able to persist through the winter via a combination of acorn persistence in the canopy (i.e. serotiny; Koenig et al. 2014) and storing of acorns in temporary sites, such as cavities (MacRoberts and MacRoberts 1976). The high dispersal capabilities of acorn woodpeckers allows them to take advantage of previously marginal habitat as food resources increase.

I also established that this marginal habitat (both with and without low amounts of non-food resources, such as granaries or cavities) is not attractive to dispersal coalitions, even when recordings of dispersal conflict vocalizations are played. I found that playbacks of dispersal conflict ("power struggle") vocalizations in this habitat led to apparent territorial responses, primarily by individuals with breeding status. While vacancies at low-quality territories (as measured by the number of granary holes) are typically filled without power struggles, vacancies at high- and moderate-quality territories most often lead to power struggles, where solo invaders are at a clear disadvantage to coalitions (Koenig 1981; Hannon et al. 1985; Barve et al. 2020b). Thus, I conclude that this apparently marginal habitat is likely only of interest to individuals dispersing alone, and power struggle vocalizations are not sufficient to convince individuals to recruit to a conflict.

Individual acorn woodpeckers foray extensively and have more interest in high-quality than low-quality habitat (Barve et al. 2020a). In addition, acorn woodpeckers have the ability to recognize individuals and to what social group individuals belong (Pardo et al. 2018). Thus, when in familiar areas, acorn woodpeckers likely use both information about the vocalizer as well as the habitat to make decisions as to whether to engage in a conflict. As all vocalizations used in playbacks were from outside of the study area, individuals may have been avoiding conflicts composed entirely of strangers, or avoiding marginal habitat, or both.

Acorn woodpeckers do cooperate extensively to win the limited resource of high-quality territories. Power struggles represent contention for the critical granary resources present on the landscape, and are battles in which the largest coalition wins (Hannon et al. 1985). I found that, on average, the majority of same-sex relatives participated in power struggles, including individuals who already possessed a breeding position. I also documented that coalition dissolution was the norm after dispersal, to the point where single individuals of large coalitions sometimes remained and bred alone after the conclusion of the power struggle.

Given the coalition size is a critical factor in successfully winning a breeding vacancy, there are indirect fitness benefits available to individuals who help their relatives secure a high-quality breeding position (Heinsohn et al. 2000; Sharp et al. 2008). This is especially striking in the behavior of breeding individuals who participate in power struggles with their offspring or non-breeding kin. I found that breeders appear to facultatively participate in power struggles, participating when there are fewer available non-breeding coalition members and when there are multiple same-sex breeders on the home territory to defend the territory.

Such behavior — where breeders assist their offspring in gaining a breeding opportunity — is incredibly rare. In cooperatively breeding species with kin coalitions, helping is typically directed from non-breeding "helpers" to their breeding kin, with helpers gaining indirect fitness benefits through improving the reproductive success of breeders (Clutton-Brock 2002). Parental-assisted dispersal flips this paradigm, with helping directed from the breeders to their non-breeding kin, with breeders gaining indirect fitness benefits from improving the reproductive success of individuals commonly labeled "helpers."

I propose that indirect fitness benefits from parental facilitation presents a possible explanation for systems, including the acorn woodpecker, where "helpers" often do not benefit and may even harm breeder survival or reproductive success (Gilchrist 2007; Koenig et al. 2011). It is possible that in these systems, breeders may be serving as the "helpers" to their non-breeding kin, as is the case in species with prolonged parental care (Ekman et al. 2000). This paradigm shift may be necessary to understand the dynamics and maintenance of cooperation in these species.

Cooperative dispersal is a complex system which can have unexpected outcomes. In the cooperatively breeding acorn woodpecker, I found that non-cooperative dispersal is the driver of occupancy growth, which mirrors increases in abundance. Individuals do not recruit to coalitions at playbacks of vocalizations in low-quality habitat, which is primarily colonized by solo dispersers. Rather, coalitions focus their attention on high-quality habitat, where they may gain both direct and indirect fitness benefits for winning a large granary with their kin.

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APPENDIX

VEGETATION DATA VALIDATION

To test my assumption of linear changes in habitat cover, based on McMahon et al. (2015) data for 1979 and 2013, I used National Agricultural Imagery Program (NAIP) imagery, which was available for this geographical region for 2005, 2006, 2012, and 2014 (U.S. Department of Agriculture 2015) to estimate the temporal pattern of changes in habitat composition. NAIP imagery is leaf-on imagery collected at the 1–2 m scale to assess agricultural yields (Davies et al. 2010). Unlike satellite imagery, NAIP imagery captures the presence of discrete trees outside of forest patches; these trees are an essential structural resource in the landscape for many organisms (Meneguzzo et al. 2013). I classified each aerial photograph into four land cover categories (open field, chaparral, evergreen canopy, deciduous canopy) using supervised maximum-likelihood classification in ArcGIS 10.1 (ESRI, Redlands, CA). Initially, 20 sample land cover classification sites (“training sites”, >100 m^2 area each) were haphazardly selected by eye for each land cover type for each image. Up to 50 additional training sites were added to each land cover type until resulting land-cover maps were negligibly different to the naked eye between supervised classification iterations of the NAIP imagery (Davies et al. 2010; Meneguzzo et al. 2013).

For each habitat plot used in my analysis, I created a buffer around the GPS point of the center of each surveyed habitat plot with the same radius as the habitat plot (11.3-m radius) and overlaid it with the classified NAIP imagery. I extracted the land cover composition of each buffer using the zonal composition tools in Geospatial Modelling Environment (Beyer 2012), and compared the mean of 2012 and 2014 NAIP imagery composition (evergreen canopy + deciduous canopy) of the buffer to the canopy cover percentage measured in the habitat plot in 2013. The data were significantly positively related ($r = 0.76$, $p < 0.0001$). The habitat plot data tended to underestimate canopy in comparison to the NAIP imagery, likely due to the fact patches of open canopy < 1 m in size are not detected by NAIP imagery due to the resolution of the imagery, leading to areas of canopy with small open patches detected as closed canopy.

To test for linear habitat change over time, I compared the trends in canopy changes across the four years of NAIP data to the interpolated values from the McMahon et al. (2015) data for the same years. Canopy cover in the NAIP data were positively linearly correlated (Pearson's correlation, $r = 0.96$) and areas of open field (areas not covered by trees or shrubs) were negatively linearly correlated ($r = -0.92$); I assumed that this linear trend continued across the 34 years of the McMahon et al. (2015) data and used a linear interpolation between the two survey years of the habitat plots to produce annual estimates of canopy cover, shrub cover, and basal areas. The NAIP and McMahon et al. (2015) slopes for the canopy and open field measures were significantly different (respectively: $F_{1,4} = 9.9$, $p = 0.035$ and $F_{1,4} = 7.6$ $p=0.051$); thus, even though the McMahon et al. (2015) data tended to underestimate canopy in comparison to the NAIP imagery, I considered the differences in slope of these measures acceptable for the purpose of my analysis.

FULL MODEL SELECTION RESULTS

Table A1.

Model selection results for site occupancy models.

Fixed effects, their scale T – territory, N – Neighborhood, L – landscape), number of parameters K), ΔAIC, and model weight w_i). All models contained the random effect “SITE ID”, the interaction between canopy cover or basal area with acorn crop, and binomial error distribution. Total number of site/year combinations n = 2006. OAC – overall acorn crop; SAC – species-level acorn crop; HC – habitat cover; SBA – species-level basal area; *Ql – Quercus lobata*, *Qa – Q. agrifolia*, *Qd – Q. douglasiii*.

Table A1 continued.

Model	**Parameters**									**Model Selection Parameters**		
	Acorn Crop*				**Habitat**							
					Cover		**Basal Area#**					
	OAC	***Ql***	***Qa***	***Qd***	**Canopy**	**Shrub**	***Ql***	***Qa***	***Qd***	**K**	**ΔAIC**	w_i
N OAC + L HC	N				L	L				8		0.913
N OAC + N SBA	N						N	N	N	19	6.0	0.045
N SAC + L HC		N	N	N	L	L				16	6.2	0.042
L OAC + L HC	L				L	L				8	18.4	< 0.001
L SAC + L HC		L	L	L	L	L				16	25.7	< 0.001

Table A1 continued.

Model	**Parameters**									**Model Selection Parameters**		
	Acorn Crop*				**Habitat**							
					Cover		**Basal Area$^{\#}$**					
	OAC	***Ql***	***Qa***	***Qd***	**Canopy**	**Shrub**	***Ql***	***Qa***	***Qd***	**K**	**ΔAIC**	w_i
L HC					L	L				4	31.1	< 0.001
L OAC + N SBA	L						N	N	N	13	39.4	< 0.001
L SAC + N SBA		L	L	L			N	N	N	17	46.8	< 0.001
N OAC + N HC	N				N	N				8	54.0	< 0.001
L OAC + N HC	L				N	N				8	61.5	< 0.001

Table A1 continued.

Model	**Parameters**									**Model Selection Parameters**		
	Acorn Crop*				**Habitat**							
					Cover		**Basal Area**$^{\#}$					
	OAC	***Ql***	***Qa***	***Qd***	**Canopy**	**Shrub**	***Ql***	***Qa***	***Qd***	**K**	**ΔAIC**	w_i
L SAC + N HC		L	L	L	N	N				16	70.3	< 0.001
N HC					N	N				4	77.1	< 0.001
N SAC + N HC		N	N	N	N	N				16	84.4	< 0.001
N OAC	N									4	119.4	< 0.001
L OAC	L									4	129.4	< 0.001
NULL MODEL										2	171.2	< 0.001

Table A1 continued.

* Acorn crop of the previous two autumns lag-1 and lag-2)

[#] Due to my linear interpolation method for habitat changes, landscape-level changes in basal area are perfectly correlated among species. Therefore, only one species' metric was used.

Table A2.

Model selection results for group size models.

Fixed effects, their scale T – territory, N – Neighborhood, L – landscape), number of parameters K), ΔAIC, and model weight wi). All models contained the random effect "SITE ID" and a truncated poisson error distribution. Total number of site/year combinations for occupied sites n = 910. OAC – overall acorn crop; SAC – species-level acorn crop; HC – habitat cover; SBA – species-level basal area; *Ql – Quercus lobata*, *Qa – Q. agrifolia*, *Qd – Q. douglasiii*.

Table A2 continued.

Model	**Parameters**									**Model Selection Parameters**		
	Acorn Crop*				**Habitat**							
					Cover		**Basal Area**					
	OAC	***Ql***	***Qa***	***Qd***	**Canopy**	**Shrub**	***Ql***	***Qa***	***Qd***	**K**	**ΔAIC**	w_i
N OAC + T HC	**N**				**T**	**T**				**6**		**0.940**
N OAC	N									4	7.6	0.021
N OAC + N HC	N				N	N				6	8.3	0.015
N SAC + T HC		N	N	N	T	T				10	10.0	0.006
N OAC + N SBA	N						N	N	N	7	10.2	0.006

Table A2 continued.

Model	**Parameters**									**Model Selection Parameters**		
	Acorn Crop*				**Habitat**							
					Cover		**Basal Area**					
	OAC	***Ql***	***Qa***	***Qd***	**Canopy**	**Shrub**	***Ql***	***Qa***	***Qd***	**K**	**ΔAIC**	w_i
N OAC + T SBA	N						T	T	T	7	10.4	0.005
N SAC + N HC		N	N	N	N	N				14	16.8	< 0.001
N SAC + T SBA		N	N	N			T	T	T	16	16.9	< 0.001
N SAC + N SBA		N	N	N			N	N	N	11	16.9	< 0.001
NULL MODEL										2	40.9	< 0.001

Table A2 continued

* Acorn crop of the previous two autumns lag-1 and lag-2)

[#] Due to my linear interpolation method for habitat changes, landscape-level changes in basal area are perfectly correlated among species. Therefore, only one species' metric was used.

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SELECTED PUBLICATIONS

Pardo, M. A., E. A. Sparks, T. S. Kuray, N. D. G. 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

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