



Unraveling a paradox of habitat relationships: scale-dependent drivers of temporal occupancy-abundance relationships in a cooperatively breeding bird

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Abstract

Context Spatial occupancy and local abundance of species often positively covary, but the mechanisms driving this widespread relationship are poorly understood. Resource dynamics and habitat changes have been suggested as potential drivers, but long-term studies relating them to abundance and occupancy are rare. In this 34-year study of acorn woodpeckers (*Melanerpes formicivorus*), a cooperatively breeding species, we observed a paradoxical response to

changes in habitat composition: despite a reduction in the availability of high-quality breeding habitat, the population increased considerably.

Objectives We investigated the role of annual variation in food availability and long-term changes in habitat composition as predictors of population dynamics.

Methods Using model selection, we contrasted competing hypotheses on the effects of changing resource availability on occupancy and social group size across three spatial scales: territory, neighborhood, and landscape.

Results The increase in abundance was largely determined by the formation of new social groups, driven by a landscape-level expansion of canopy cover and its interaction with neighborhood-level acorn abundance, indicative of long-term increases in overall acorn productivity. Group size increased with neighborhood acorn crop two years earlier but groups were smaller in territories with more canopy cover.

Conclusions Our results indicate that scale-dependent processes can result in paradoxical relationships in systems with spatial and temporal resource heterogeneity. Moreover, the findings support the role of resources in driving changes in abundance and occupancy at a landscape scale, suggesting that colonization of marginal habitat drives the positive occupancy-abundance relationship in this cooperatively breeding species.

Natasha D. G. Hagemeyer and Mario B. Pesendorfer have contributed equally.

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Keywords Habitat change · *Melanerpes formicivorus* · Occupancy—abundance relationship · Population dynamics · *Quercus* spp. · Spatial heterogeneity

Introduction

A positive relationship between the abundance and site occupancy of a species is a fundamental pattern in ecology, but the population dynamics underlying this relationship are poorly understood (Andrewartha and Birch 1954; Gaston et al. 2000; Holt et al. 2002; Zuckerberg et al. 2009). 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; Faulks et al. 2015). Species occupancy and abundance are often determined by resource availability both locally and regionally (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 or increase their fecundity (Edworthy et al. 2011). Similarly, landscape-level changes in habitat associated with fragmentation or succession can affect habitat quality, resulting in some patches becoming unsuitable (Vander Haegen et al. 2000; Vallecillo et al. 2008) and thus decreasing local abundance due to emigration or decreased fecundity (Borregaard and Rahbek 2010). Both local and landscape processes may therefore 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 abundance and occupancy (Hanski 1993, Gaston et al. 1997). When resources are consistently available, yet temporally variable, populations of species with high resource tracking remain at high overall abundance with variable occupancy across sites, while species with poor 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 resource peak (Levey 1988, Beehler and Mulia 1995, Schnurr et al. 2002).

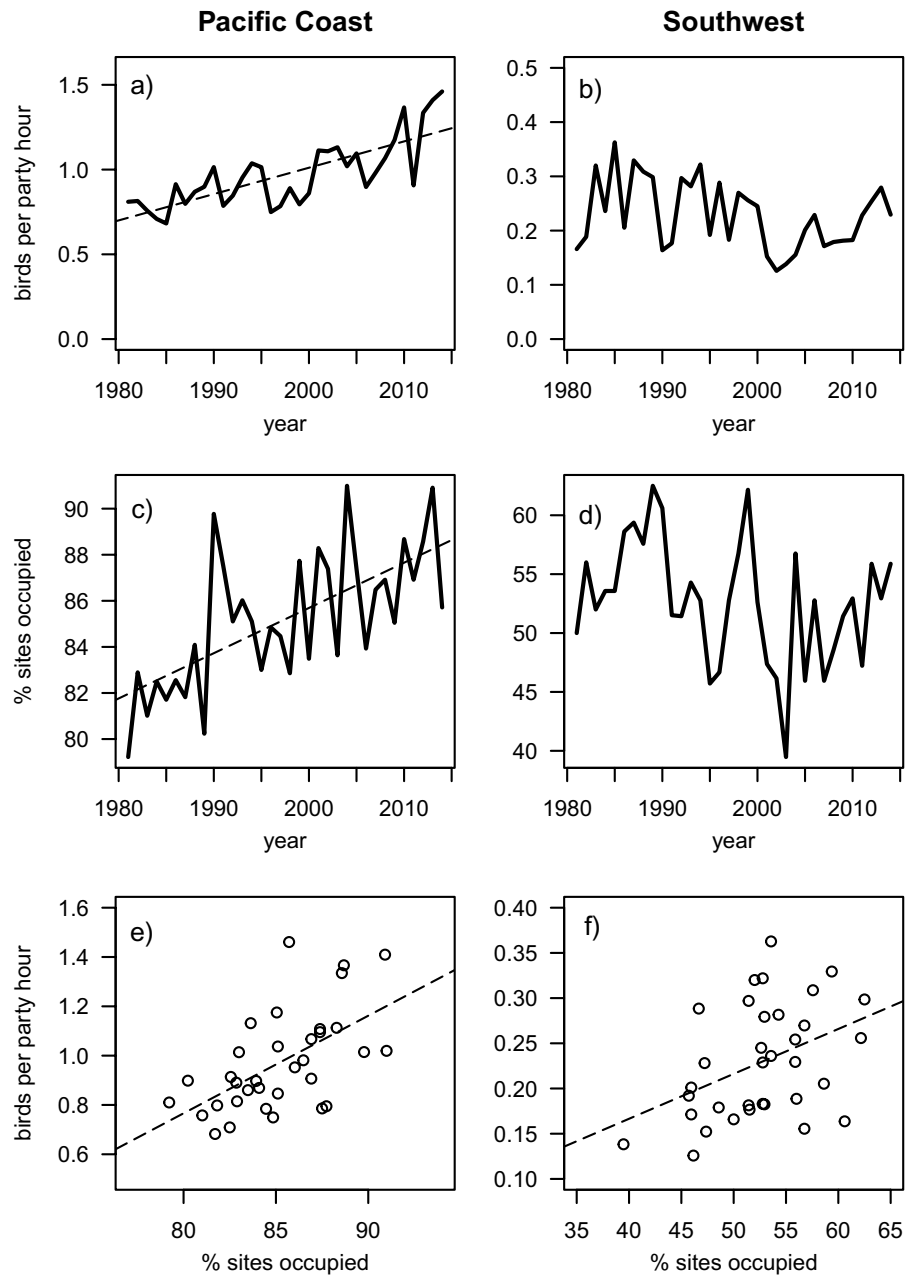
Unfortunately, a historical mismatch in the temporal and spatial scales at which population dynamics and landscape heterogeneity are quantified has often confounded the understanding of population-level processes (Wiens 1989; Lima and Zollner 1996; Wiegand et al. 1999). The relationship between occupancy and abundance can further be complicated in cooperatively breeding taxa, as their local abundance may be determined by changes in mean social group size or the number of social groups.

The cooperatively breeding acorn woodpecker (*Melanerpes formicivorus*) has exhibited an increase in both geographical distribution and local population size throughout the Pacific Coast of continental North America and has a positive intraspecific abundance-occupancy relationship (Fig. 1; Kirk and Kirk 2005). This species lives in variable-sized social groups and specializes on acorns (*Quercus* spp.) as a critical, yet highly variable, winter food source (Koenig et al. 2016). Population fecundity is tied to variation in acorn crop size (Koenig et al. 2011), a dependence illustrated by the extensive acorn hoards this species accumulates in storage trees or ‘granaries’ that provide food when flying insects, a more nutritious resource, are unavailable (MacRoberts 1970; Koenig et al. 2016). Granaries serve as an ecological constraint on independent breeding, and due to their rarity on the landscape and effort required to construct, are often passed down from generation to generation (Koenig and Mumme 1987; Koenig et al. 2020).

Previous work has revealed a paradoxical relationship between acorn woodpeckers and oaks. At the landscape scale, an increase in the acorn woodpecker population size was positively associated with the closing of oak canopy cover (McMahon et al. 2015), while locally, habitat with closed canopy structure was less likely to be occupied than open canopy habitat (MacRoberts and MacRoberts 1976). This paradox—an increase in population size despite a decrease in high-quality habitat—may arise because dispersal and foraging activities occur at different spatial scales (Hooge 1995; Koenig et al. 1996, 2008).

Here we attempt to understand this apparently paradoxical relationship by investigating the drivers of occupancy and abundance in acorn woodpeckers across multiple spatial scales. First, we used citizen science data, results from the annual Audubon Christmas Bird Count (CBC), to investigate range-wide

Fig. 1 Abundance, occupancy, and abundance-occupancy relationship for acorn woodpeckers 1980–2013, Pacific Coast (British Columbia, California, Oregon, Washington) and Southwest (Arizona, Colorado, New Mexico, Nevada, Texas) USA. Data from Audubon Christmas Bird Survey (Sauer and Link 2002)



temporal trends in occupancy and abundance, as well as their relationship, for two subspecies of acorn woodpeckers found in the USA, *Melanerpes formicivorus bairdi*, which ranges from southern Washington to northern Baja California (Mexico), and *M. f. formicivorus*, which ranges from southern Arizona, New Mexico, and western Texas south through Mexico to the Isthmus of Tehuantepec (Koenig et al. 2020). Second, we investigated temporal changes

in occupancy and abundance of the *M. f. bairdi* at our 953-ha study site and explored the relationship with changes in resource availability and habitat composition.

Important resources for this species include acorn availability, tree cover, and access to granary trees (Koenig and Mumme 1987; Stacey and Ligon 1987; Hooge et al. 1999). Increases in acorn availability, for example, lead to increases in population abundance

via enhanced reproductive success and subsequent recruitment of young (Koenig et al. 2011). Increases in abundance may motivate individuals to disperse and colonize formerly marginal habitat, thereby affecting occupancy of sites and increasing group density (Rosenzweig 1991; Gaston et al. 2000). Conversely, increases in resources may lead to recruitment of young into the natal group (Koenig et al. 2011), leading to increased group size (Carvajal et al. 2022). Thus, to determine which aspects of the biotic environment are responsible for the observed increase in abundance of acorn woodpeckers, we investigated whether population increases occurred through changes in the size or density of groups and determined the mechanisms of change in both group size and density across three ecologically relevant spatial scales.

Methods

Data

To determine range-wide population dynamics for the Pacific Coast and Southwestern subspecies of acorn woodpeckers, we used Audubon Christmas Bird Count (CBC) data for the period corresponding to the years of our long-term study covered here (1980–2013). CBC data consist of day-long surveys conducted throughout 24 km diameter circles ('sites') by volunteers between 14 Dec and 5 Jan (Sauer and Link 2002). To standardize the data for effort, the number of bird individuals observed was divided by the number of observer groups, resulting in 'birds per party hour' (bpph), a measure of local abundance. Occupancy was quantified as the percentage of sites each year for which at least one bird was reported. The total number of surveyed sites varied by year, ranging from 101 to 151 sites. Analyses were divided by subspecies; *M. f. bairdi* included counts from California, Oregon, Washington, and British Columbia (76–112 sites), while *M. f. formicivorus* included counts from Arizona, New Mexico, Nevada, Colorado, and Texas (24–39 sites).

For the population-level study, we 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 range of the Pacific Coast

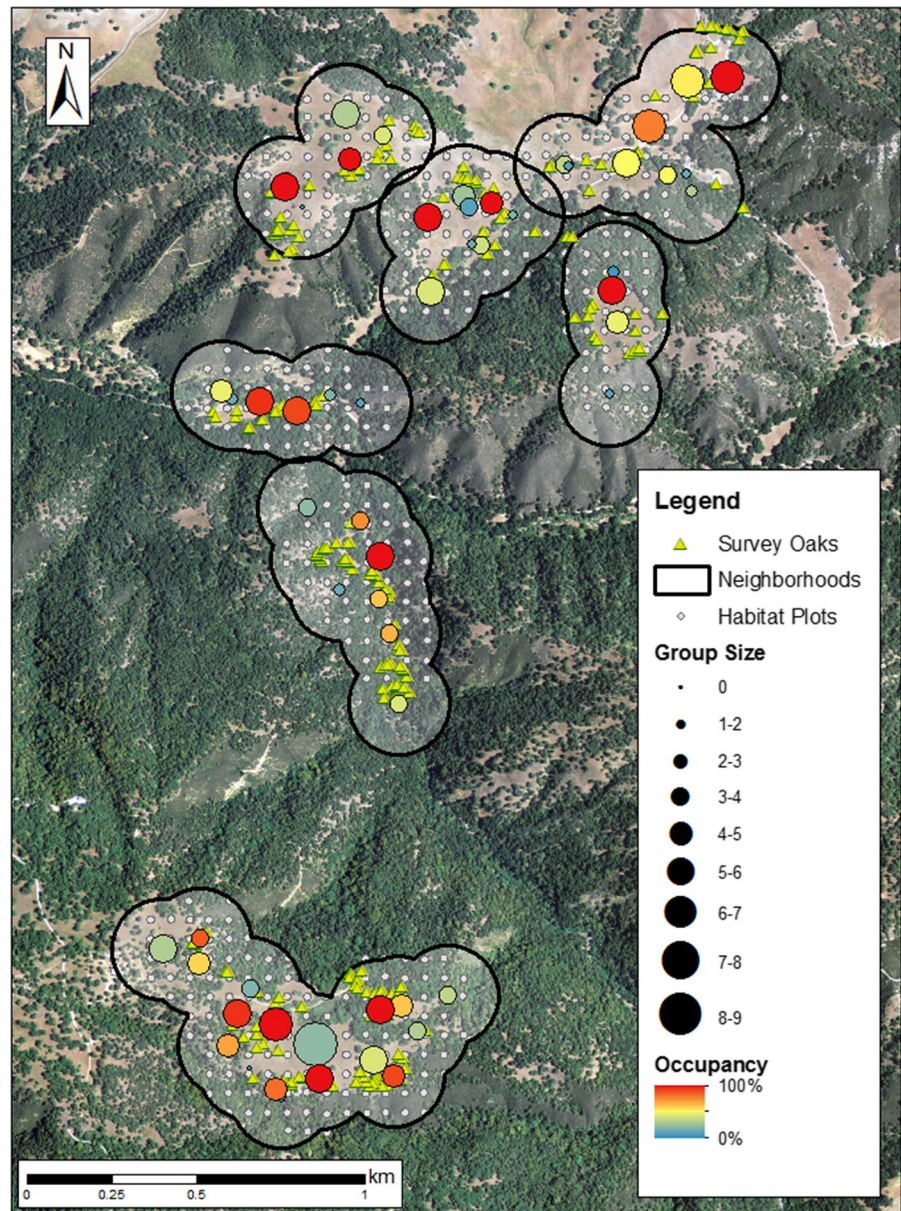
subspecies of acorn woodpeckers, which is a generally continuous and evenly distributed population from southern Washington into northern Baha California (Koenig and Haydock 1999). As the acorn woodpecker is a good colonizer with rapid dispersal into available habitat (Koenig et al. 1996, Koenig et al. 2000), 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, we examined the relationship between changes in habitat composition (canopy and shrub cover), annual variation in acorn production, and population dynamics of acorn woodpeckers. Our analysis used three long-term datasets: i) annual estimates of changes in habitat composition interpolated from vegetation surveys conducted in 1979 and 2013 (see below; 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). We considered three spatial scales: i) the local foraging scale of territories, estimated as a 150 m radius around the granary, which included the area generally defended (MacRoberts 1970) and in which > 95% of foraging occurred (Koenig et al. 2008); ii) the neighborhood scale, consisting of discrete collections of foraging territories where each territory overlapped another by $\geq 10\%$, producing 7 neighborhoods ranging in size from 4 to 18 territories and representing 17.4–50.6 ha (Fig. 2); and iii) the landscape scale, consisting of all habitat surveyed (198 ha; Fig. 2).

Habitat composition

To estimate changes in habitat composition over the study period, we compared two vegetation surveys conducted in 1979 and 2013, respectively. The surveys were laid out in a grid pattern of 613 circular 0.04 ha (11.3 m radius) habitat plots, spaced at 60-m intervals (Fig. 2). 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). We calculated the relative change in habitat composition per plot from 1979 to 2013 for all metrics and interpolated annual estimates of canopy

Fig. 2 Map of the study area, showing the group locations, the associated local foraging territories, the 7 neighborhoods, survey oaks, and the 613 habitat plots. Map is centred on 36° 23'20" N, 121° 33'27" W; imagery is sourced from the National Agriculture Imaging Program 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



cover, shrub cover, and basal area of each species. We assumed a linear trend, an assumption supported by supplemental analyses using National Agricultural Imagery Program aerial photographs from 2005 to 2014 (U.S. Department of Agriculture 2015) showing a linear increase of canopy cover over time at a similar rate to the increase we inferred from the interpolation of the two vegetation surveys (Supplementary material Appendix 1).

To characterize the change of a territory's habitat composition over time, we 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, a procedure that has been shown to have little effect on the error structure of statistical models (Zuckerberg et al. 2012). We assigned habitat plots to neighborhoods in a similar fashion. To capture habitat composition, canopy cover, shrub cover, and basal area of each oak species, we averaged metrics across each territory, neighborhood, and habitat plots.

Acorn production

We used acorn production data provided by the California Acorn Survey (W. D. Koenig and J. Knops, unpublished data) to estimate annual seed production of the five oak species common within the study area. Survey trees were selected in 1980 based on their proximity to existing acorn woodpecker groups. Each autumn, two observers counted as many acorns as they could find on a survey tree within 15 s, which were summed for each tree (N30) and \ln -transformed ($\text{LN30} = \ln(\text{N30} + 1)$) to reduce skew. Averaged together, counts provided an index of annual acorn production for the study site (Koenig et al. 1994a, b). Because woodpecker group size was enumerated on 15 May of each year, we used a one- and two-year lag to investigate the drivers of changes in group size due to demographic changes driven by the acorn crop (the previous years' LN30; Koenig et al. 2011).

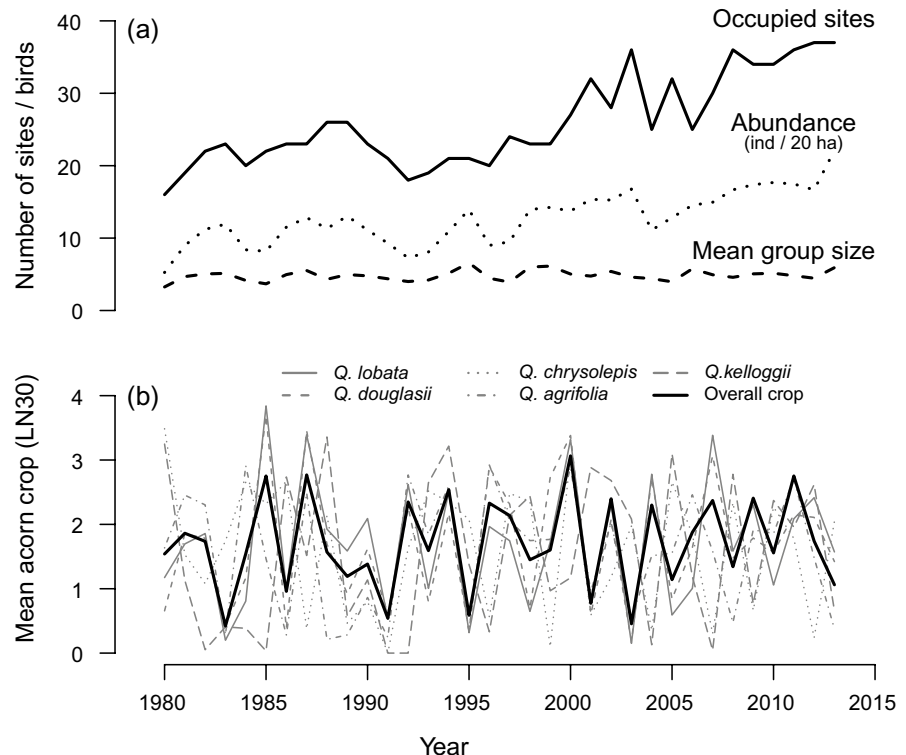
Population dynamics

For the long-term study at the Hastings Reserve, we used the number of granary sites occupied by acorn

woodpeckers as our measure for the spatial distribution of social groups on the landscape (occupancy; Figs. 2, 3a), and the sum of all individuals over all social groups on 15 May as population size (total abundance). We defined group size as the number of adult individuals (i.e. > 5 months post-fledging) present on 15 May during the breeding season (April–July) on an occupied territory. If group size varied over the breeding season due to dispersal or death, we 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 via censuses at each granary site conducted at approximately bimonthly intervals (Koenig and Mumme 1987). Only territories that were occupied at least once between 1980 and 2013 were used, allowing us to include sites that were not inhabited by woodpeckers at the study outset but later occupied. We restricted our analysis to those areas monitored continuously over the duration of the study period. Thus, population increases are due to increases in density of acorn woodpeckers within the study site (local occupancy) rather than an increase in

Fig. 3 Long-term data on **a** acorn woodpecker total abundance, occupancy, and mean group size over 34 years (1980–2013) in the 953-ha study area and **b** mean annual acorn crop size variation in the five common oak species and over all species combined



study site size. Because the survey oaks, habitat plots, and woodpecker territories did not always co-occur in space, we restricted our 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. 2); these territories comprised $>90\%$ of the Hastings Reserve study population.

Statistical Analyses

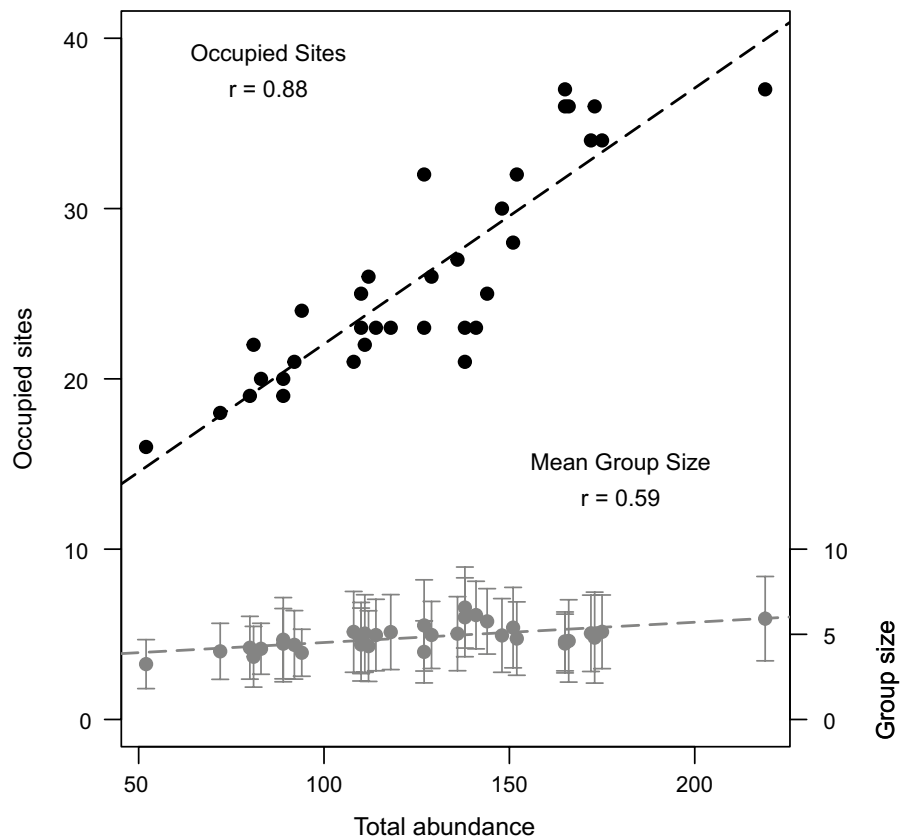
To investigate temporal trends in abundance and occupancy in the CBC data, we used non-parametric Mann–Kendall trend tests and Theil–Sen slope estimators for annual means of *bpph* and *percentage of sites occupied*. Similarly, we determined the temporal abundance-occupancy relationships for the two subspecies by regressing annual *bpph* values against the *percentage of sites occupied* using non-parametric Kendall rank correlations.

To investigate whether changes in acorn woodpecker abundance at the study site were driven by

the number of groups (occupancy) or mean group size, we 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 (Figs. 3, 4).

We 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 2003). To dissociate occupancy from group size, we used a ‘hurdle modelling’ approach which assumes 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, we 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. We then investigated the drivers of variation in group size for occupied sites (for the subset of non-zero values) with GLMMs using zero-truncated Poisson error distributions with a log-link (Zuur et al. 2009). For both occupancy and group size, we assembled

Fig. 4 Relationship between total abundance of acorn woodpeckers at Hastings Reserve 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). Lines indicate linear fit. Analysis of Variance (ANOVA) of the linear correlation of abundance with the number of occupied sites and mean group size per year. Pearson correlation coefficients are presented for illustrative purposes



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 or 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). As dispersal between territories is common, models for occupancy considered drivers at the neighborhood and landscape scale. 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, we included an interaction term between canopy cover and acorn production in the models of occupancy. Because 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, the assumption being that 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 (Figs. 3, 4). Therefore, our models investigated short-term drivers of group size variation. Inclusion of an interaction term between canopy cover and acorn production did not improve the explained variance for these models. We present the model selection results for the top five models in the text and full model selection results in Appendix A2.

Analyses of the effect of species-specific acorn crops and changes in basal area were only conducted 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). We also constructed models where we partitioned oaks into functional groups of 'evergreen' (*Q. agrifolia* and *Q. chrysolepis*) 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 the overall acorn crop as a fixed effect. Acorn production was only considered

at the neighborhood 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, we 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 4.0.2 (R Development Core Team 2020). Non-parametric analyses were conducted using the package 'wq' (Jassby and Cloern 2017). Generalized linear mixed 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 Appendix A2: Tables A1 and A2. Unless noted otherwise, we report mean \pm standard error.

Results

From 1980 to 2013, the Pacific Coast subspecies of acorn woodpecker has increased in abundance (Fig. 1a; slope=0.015, $S=311$, $P<0.001$) and occupancy (Fig. 1c; Theil-Sen slope=0.199, $S=262$, $P<0.001$), while the Southwestern subspecies has fluctuated extensively but not shown a positive or negative overall trend in abundance (Fig. 1b; slope=-0.002, $S=-113$, $P=0.097$) or occupancy (Fig. 1d; slope=-0.002, $S=-96$, $P=0.159$). In both subspecies, we observed a positive correlation between abundance and occupancy (Fig. 1e, f; *M. f. bairdi*: Kendall's $\tau=0.422$, $z=3.50$, $P<0.001$; *M. f. formicivorus*; $\tau=0.298$, $z=2.46$, $P=0.014$).

Reflective of the broader trend in the Pacific Coast subspecies, the acorn woodpecker population in the 953-ha Hastings Reserve increased from 52 individuals in 1980 to 219 in 2013 (Fig. 3a, dotted line), 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. 4) while the association with mean group size was weaker although

Table 1 The variable sets used to build the candidate models for predicting woodpecker occupancy or group size

Variable set	Variables	Spatial Scales
Overall Acorn Crop (OAC)	Summed acorn count (1-year lag) + Summed acorn count (2-year lag)	Neighborhood, Landscape
Species Acorn Crop (SAC)	<i>Q. agrifolia</i> acorn count (1-year lag) + <i>Q. agrifolia</i> acorn count (2-year lag) + <i>Q. douglasii</i> acorn count (1-year lag) + <i>Q. douglasii</i> acorn count (2-year lag) + <i>Q. lobata</i> acorn count (1-year lag) + <i>Q. lobata</i> acorn count (2-year lag)	Neighborhood, Landscape
Habitat Cover (HC)	Percent canopy cover + Percent shrub cover	Territory, Neighborhood, Landscape
Species Basal Area (SBA)	Basal area <i>Q. lobata</i> + Basal area <i>Q. agrifolia</i> + Basal area <i>Q. douglasii</i>	Territory, Neighborhood

Fixed effects included habitat composition and acorn crop; random effect was “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

still statistically significant ($F_{1,32}=17.6$, $P<0.001$, Fig. 4).

Habitat composition at Hastings Reserve changed significantly from 1979 to 2013. Mean canopy cover in habitat plots increased from $21.8\pm 0.9\%$ to $41.5\pm 1.5\%$, while shrub cover increased from $11.5\pm 1.0\%$ to $27.9\pm 1.4\%$ ($n=477$ plots). The number of stems increased from 66.9 ha^{-1} to 78.2 ha^{-1} . Density of *Q. lobata*, the preferred nesting and granary tree species for acorn woodpeckers at the study site, decreased from $21.0\text{ stems ha}^{-1}$ to $14.1\text{ stems ha}^{-1}$. The density of the other oak species remained unchanged. In contrast, acorn production was highly variable among years and exhibited no long-term trend (Fig. 3b).

Occupancy of territories exhibited both spatial and temporal variation (Fig. 2). 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. 3a).

Landscape-level changes in habitat composition and neighborhood acorn production were the most important predictors of woodpecker site occupancy (Table 2a). The top model supported a mechanistic role of overall acorn crop in the previous two years, while the confidence interval for both canopy and

shrubs 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 in the neighborhood, and that this relationship became stronger as the mean proportion of canopy cover on the landscape increased (Fig. 5).

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. 4), mean group size did not increase significantly over the study period (Fig. 3a, 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 (Table 3a) was determined by neighborhood acorn crop and territory-level habitat. Acorn crop sizes in each of the two preceding years were important positive predictors of group size (Table 3b; Fig. 6a, b). Group size was inversely related to mean canopy cover in territories (Fig. 6c).

Discussion

We investigated whether acorn woodpeckers showed a positive occupancy-abundance relationship across multiple spatial scales and to determine which

Table 2 Predictors of acorn woodpecker occupancy of territories

a) Model*	K	AIC	Δ AIC	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
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	

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 S2: Table S1 for full candidate set) where K is the number of parameters, AIC is the Akaike Information Criterion value, Δ AIC 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

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

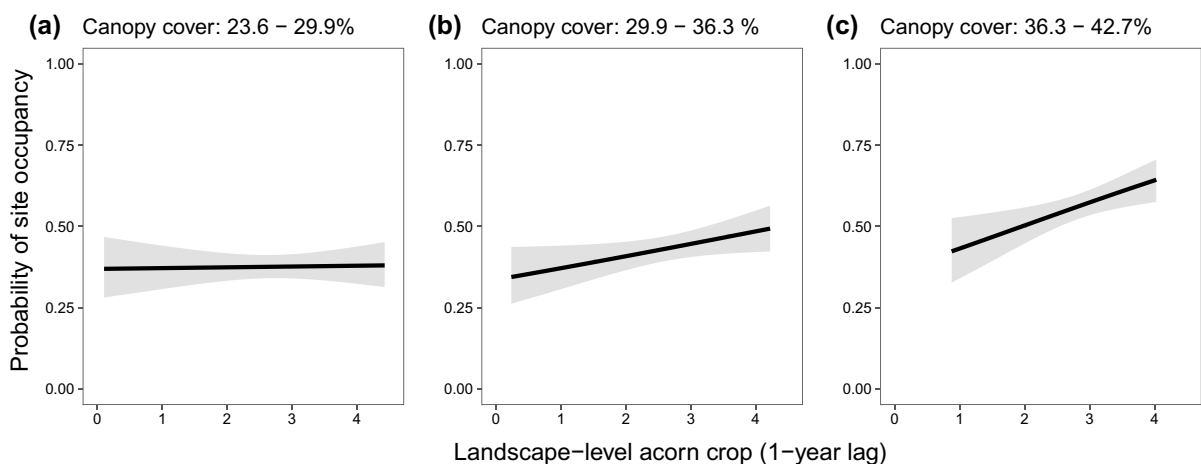


Fig. 5 Predictors of site occupancy. Neighborhood acorn crop in the previous autumn (lag-1) increased the probability of site occupancy, as proportional canopy cover increased on the landscape-level. To illustrate the significant statistical interaction between the two parameters, we partitioned the data into

three subsets (a–c) that represented 33% of the change in canopy cover. Linear regression trendlines are shown with standard error for each subset of the data. See Table 2 for detailed results

changes in the biotic system drove the paradoxical rapid growth in population size despite decreasing habitat quality. More broadly, we sought to understand how changes in resource availability affect

spatial and temporal occupancy-abundance relationship in this cooperatively breeding species. Our findings indicated that the population grew mainly by increasing the number of groups across the landscape

Table 3 Predictors of acorn woodpecker 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
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	

See Table 1 for definitions of model variable sets. a) Model selection table for the top five supported models out of a total of 31 candidate models (see Appendix A2: 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

*All models contain the random effect ‘Territory ID’ (territory identifier) and were modelled with a zero-truncated Poisson error distribution

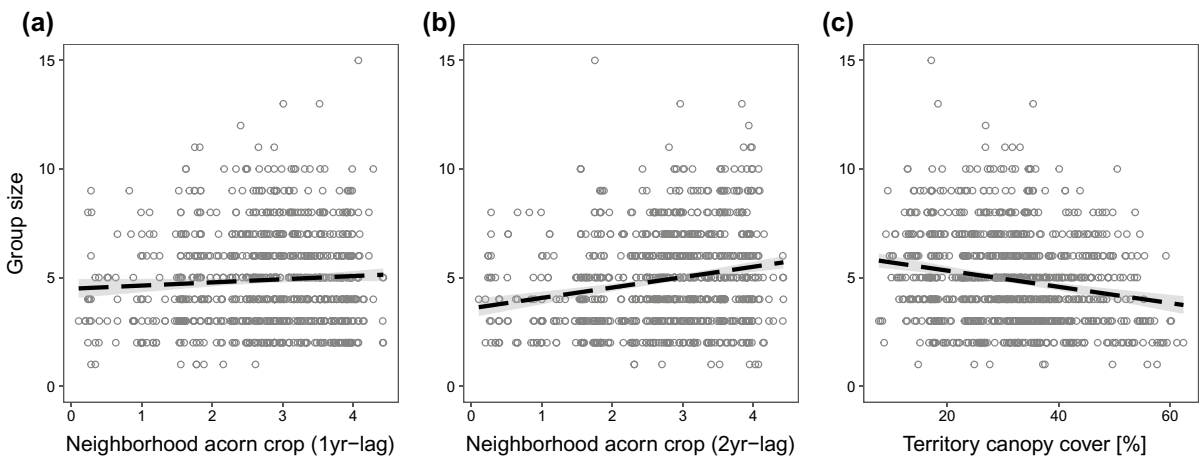


Fig. 6 Predictors of group size in acorn woodpeckers. Group size was **a** positively related to neighborhood-scale acorn production in the previous autumn (lag-1), **b** positively related to neighborhood-scale acorn production two autumns prior (lag-

2), and **c** negatively related to percent territory-level canopy cover. (n=910, site/year combinations for occupied sites). Linear regression trendlines standard error are shown for each plot. See Table 3 for detailed results

(Figs. 3a, 4). We also found a weaker, but significantly positive, relationship between bird abundance and mean group size at the population level (Fig. 4), but these changes took the form of short-term fluctuations and did not result in a significant increase in mean group size over the study period (Fig. 3a).

Occupancy of new sites increased with landscape-scale gains in proportional canopy cover and with the interaction of canopy cover with the previous year’s acorn production within the neighborhood (Table 2b), supporting the hypothesis that increased food availability drove 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 years earlier and, to a lesser extent, the size of the most recent acorn crop within the neighborhood, factors that offset the negative effect of increased canopy cover at the local scale (Table 3b). These results suggest that recruitment is primarily a response to annual fluctuations in food availability (Koenig et al. 2011). Meanwhile, the paradoxical response of the acorn woodpecker population to the decrease in quality of the breeding habitat, achieved by increasing the number of groups, rather than group size, was mediated by increased acorn availability at the landscape scale.

The habitat changes observed at the Hastings Reserve mirrored those found across much of the range of Pacific Coast acorn woodpecker population. Throughout the coastal range and the foothills of the Sierra Nevada, evergreen oaks have been increasing in cover over the last decades (Tyler et al. 2006; McIntyre et al. 2015; Peréa et al. 2017). Similarly, the breeding range of the birds, as well the mean abundance in standardized surveys (Christmas Bird Counts) have increased (Fig. 1). Thus, the landscape-scale pattern in our study appears to be representative of range-wide dynamics for the subspecies of acorn woodpeckers along the Pacific Coast.

Habitat preferences exist at a local scale, with woodpeckers defending a small area around the granary (MacRoberts and MacRoberts 1976). Canopy cover increased at this 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). We also 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 food abundance measured as a function of acorns 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. 3a) and, at one point early in the study (1983–1984), led to abandonment of many territories (Hannon et al. 1987).

Variation in habitat quality, including food resources, can affect both mean abundance within a habitat and the suitability of habitats, which in turn affects both abundance and occupancy (Holt et al. 1997; Gaston et al. 2000; Freckleton et al. 2006; Östman 2011). In species with high dispersal ability, dispersal effects are thought to be limited, and abundance and occupancy are reliant on the quality of the habitat, rather than abundance-based colonization rates or source-sink dynamics (Freckleton et al. 2005). Our results suggest that increased food abundance can lead directly to increases in abundance and in site occupancy, with formerly marginal habitat becoming habitable due to food increases. Indeed, increases in food abundance appears to be sufficient for increases in acorn woodpecker occupancy. Of course, other metrics of habitat quality may play an important role in determining occupancy and abundance in other species (Östman 2011). For example, in Magellanic woodpeckers (*Campephilus magellanicus*), a social species in Patagonia, increased tree senescence was the main driver of increased abundance (Carvajal et al. 2022).

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 year's acorn crop is a critical food source for overwinter survival (Hannon et al. 1987). Our 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. When considering leaving a group and subsequently determining where to settle, individuals are likely to be influenced by the presence of resources (Edworthy et al. 2011), dispersing and occupying locations in years of high acorn availability, and abandoning

marginal territories in years of acorn crop failure (Hannon et al. 1987; Koenig et al. 2011).

Dispersal to new locations is critical for increasing occupancy, and ability to disperse into new locations may help explain abundance-occupancy relationships (Gaston et al. 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 may allow acorn woodpeckers to occupy locations initially lacking granaries through a combination of the persistence of acorns in the canopy (serotiny; Koenig et al. 2014) and storing acorns in cavities and other temporary sites while they begin the construction of more permanent storage facilities (MacRoberts and MacRoberts 1976). As an abundant species with high dispersal ability (Rusk et al. 2013; Barve et al. 2020), acorn woodpeckers have a high likelihood of colonizing new patches or exhibiting rescue effects for groups occupying low quality habitat (Stacey and Taper 1992; Freckleton et al. 2005). 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, factors critical to consider 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. While group size was positively related to abundance (Fig. 3), group size was not important in the long-term increase in abundance (Fig. 2b). The two-year lag effect of the acorn crop may be due to the number of offspring from the previous year's breeding season that remained philopatric, resulting in larger group sizes. However, such short-term changes in group size did not persist. Rather, there may be an optimal group size that 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 have resulted in an increase in group density rather than an increase in group size. This is in contrast to Magellanic woodpeckers, where increased abundance

was driven by increased group size rather than the number of groups (Carvajal et al. 2022).

Our investigation of the intraspecific abundance-occupancy relationship relied on several assumptions. By using the distribution of occupied granary sites as our measure of occupancy, we assumed that territory sizes did not vary 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). We also did not explicitly account for dispersal into and out of the study population, which we assume are comparable given that the study site is part of a much larger continuous population (Koenig et al. 2000). Finally, we interpreted the interaction between changes in canopy cover and relative annual acorn production as changes in overall acorn availability, which assumes that acorn production is proportional to tree crown size (Greenberg 2000).

Conclusion

Our 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, interactions that may occur not only due to mechanistic drivers, but also due to the scale at which the mechanisms act (Pearson 1993, Koper and Schmieglow 2006, Gaillard 2010). Most importantly, the effects of temporal heterogeneity may not be immediately apparent, as patterns may emerge months or years later. 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. 3). 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.

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Author contributions NDGH and MBP contributed equally to this work. All authors conceived the ideas and designed the methodology. NDGH, WDK, and ELW collected the data; NDGH and MBP analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data used in the analysis are available in Data Dryad. Citizen science data from the Audubon Christmas Bird Count can be downloaded at <https://netapp.audubon.org/abcobservation/>.

Declarations

Conflict of interests The authors declare no conflicts of interest.

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