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SYNTHESIS

Territory Sizes and Patterns of Habitat Use by Forest Birds Over Five Decades: Ideal Free or Ideal Despotic?

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ABSTRACT

Relations among territoriality, abundance and habitat suitability are fundamental to the ecology of many animal populations. Theory suggests two classes of possible responses to increasing abundance in territorial species: (1) the ideal free distribution (IFD), which predicts smaller territory sizes and decreased fitness as individuals adaptively pack into suitable habitats, and (2) the ideal despotic distribution (IDD), which predicts stable territory sizes and fitness in preferred habitats for dominant individuals and increased use of marginal habitats, reduced fitness and changes in territory sizes for subordinate individuals. We analysed the territory sizes and locations of seven migratory songbird species occupying a 10-ha plot in the Hubbard Brook Experimental Forest, New Hampshire, USA over a 52-year period. Species varied in abundance over years from twofold to 22-fold, and all species displayed clear patterns of habitat preference within the study plot. Consistent with IFD, and contrary to IDD, territory sizes decreased with local abundance for all species, irrespective of habitat preferences. There was at least a twofold variation in territory size within years. Conformity of territory size to predictions of the IFD argues for the efficacy of territorial defence in songbirds and has general consequences for population dynamics.

1 | Introduction

Habitat selection is a frequent determinant of fitness in biological populations (Rosenzweig 1991). The manner in which individuals distribute themselves across habitats of variable quality and across years with variable densities has emergent consequences for populations that influence dispersion, abundance and dynamics (Fretwell and Lucas 1970; McPeek et al. 2001; Pulliam and Danielson 1991). A knowledge of the relations between habitat quality and population density is necessary to understand how habitat selection influences individual fitness and population growth. One form of habitat selection involves the establishment of territories, which is thought to confer benefits that include greater access to resources and mating opportunities. However, defending territories against conspecifics entails costs in time, energy and exposure to predators (Brown 1964; Sells and Mitchell 2020). Apparently, it is common for the benefits of territorial defence to exceed the costs, as many animals from diverse taxa exhibit territoriality (e.g., Adams 2016; Bee and Gerhardt 2002; Brown 1964; Burt 1943; Calsbeek and Sinervo 2002; Hinde 1956; Hixon and Brostoff 1996; Imre, Grant, and Keeley 2004; Lindeman, Grant,

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and Desjardins 2015; Luría-Manzano et al. 2023; Ostfeld 1990; Pröhl 2005; Waage 1973).

Territory size can impact the fitness of territory holders (Both and Visser 2000; Maynard Smith 1982). For instance, experiments with *Parus major* (Great Tits) and *Setophaga caerulescens* (Black-throated Blue Warblers) showed that the removal of some individuals resulted in larger territories and higher reproductive success for those remaining (Both and Visser 2000; Sillett, Rodenhouse, and Holmes 2004). While larger territories presumably provide more resources given comparable habitat quality (Atuo and Manu 2013; Stenger 1958; Village 1982), theory suggests that the optimal territory size is not necessarily the largest that might be attainable (Davies and Houston 1984; Krebs, Davies, and Parr 1993; Rosenzweig 1985; Schoener 1983). Although relationships between habitat quality and territory size have been studied (Grant, Weir, and Steingrímsson 2017; Kittle et al. 2015; Smith and Shugart 1987), less is known about how local abundance influences territory size. It can be expected that the pattern of territory sizes in a habitat will be influenced by temporal changes in the abundance of conspecifics and spatial variation in habitat quality (Fretwell 1972; Fretwell and Lucas 1970).

The ideal free distribution is a well-known model of how habitat quality and the abundance of individuals can interact to influence habitat selection and territory size. Under this model, individuals distribute themselves across habitats of different quality such that some individuals hold larger territories in lower quality habitat while others hold smaller territories in higher quality habitat, but all experience equal fitness (Fretwell and Lucas 1970). An alternative model is the ideal despotic distribution (Fretwell 1972). Like the ideal free distribution, the ideal despotic distribution predicts that birds in lower quality habitats will have larger territories, but it differs in postulating that some individuals are socially dominant (despots) and hold territories in the best habitats that resist reductions in territory size even as the landscape abundance of individuals increases (Fretwell 1972). Consequently, high abundance causes subordinate individuals either to compress their territory sizes in suboptimal habitat or to move into even poorer, otherwise unused, habitats where extra-large territories are expected. Under this model, socially dominant individuals consistently hold better territories that confer higher fitness than is possible for subordinate individuals that are restricted to less suitable habitat (Fretwell 1972).

Other variations of the ideal free distribution and the ideal despotic distribution are possible in systems with nonterritorial males (floaters in the sense of Smith 1978). If floaters are present, they might be restricted to poor habitat because they are excluded from high-quality sites by socially dominant individuals, or they might maintain some presence in good habitats by being discreet and avoiding competition (Brown and Long 2007). Being a nonterritorial floater, therefore, may be the optimal strategy for some individuals in some situations (Brown and Long 2007; Petit and Petit 1996).

It is not known if the ideal free distribution or the ideal despotic distribution better describes interannual patterns of habitat use over decades under natural fluctuations in abundance. Some studies have yielded evidence of populations conforming to the ideal free distribution (Haché, Villard, and Bayne 2013; Pagán, Martínez, and Calvo 2009; Petit and Petit 1996; Whitham 1980), while others have found evidence of ideal despotic distribution (Niederhauser et al. 2021; Zimmerman, LaHaye, and Gutiérrez 2003). Boyce et al. (2016) suggested that birds and mammals do not usually follow an ideal free distribution. Most of the available information for birds and mammals comes from observational or manipulative studies of single species over a few years (e.g., Both and Visser 2000; Martins, Cunha, and Lopes 2021; Marshall and Cooper 2004; Verheijen et al. 2019). Short-term manipulative studies may not match the natural magnitude of multi-year variation in abundance and patterns of response in territoriality. By comparison, patterns of territory size with natural fluctuations in abundance across decades have rarely been documented. This is at least partly because territories are challenging to measure. Here we address this knowledge gap by using a long-term dataset of mapped bird territories to assess how abundance and habitat quality influence territory size in co-occurring species of migratory passerine birds breeding in a temperate zone forest. We examined spatiotemporal patterns in the size and location of defended territories during the peak breeding season (late May—late June) by the seven most abundant bird species occupying the same 10-ha forest plot over a 52-year period.

All seven study species varied among years in the number of individuals that occupied the 10-ha plot. This allowed us to quantify the extent to which defended territory size changed with changes in local abundance. Furthermore, all species displayed preferences for some parts of the plot over others. The combination of variation in local abundance and relatively stable habitat preference allowed us to fit a statistical model for each bird species of territory size as a function of the numbers of conspecific individuals, habitat preferences and their interaction. The model of an ideal free distribution predicts that territory size will decrease with increasing abundance and that territories will be smaller in the most preferred habitats. Alternatively, the ideal despotic distribution predicts that territory size in the most preferred habitats would fluctuate less because the most preferred habitats tend to be occupied by socially dominant individuals (despots). They are less yielding at territory boundaries to neighbouring conspecifics. In the presence of despots, changes in territory size are predicted to be chiefly expressed in subordinate individuals. Subordinate individuals may increase their territory size to obtain necessary resources in lower quality habitat or decrease their territory size due to spatial limitations. These predictions of the ideal despotic distribution corresponded to the statistical interaction between conspecific abundance and habitat preference (territory size predicted to vary least in the most preferred habitats). Alternatively, birds could select sites randomly (McPeek et al. 2001), in which case, there would be no relationship among abundance, habitat preference and territory size. By assessing the modelling results for seven species that have been studied in the same way over the same decades in the same forest plot, we were able to compare bird species with respect to how well they conformed to predictions of the ideal free distribution versus the ideal despotic distribution. Improved knowledge of territorial patterns has relevance to habitat selection, the proximate and ultimate causes of variation in territory size and population dynamics.

2 | Methods

2.1 | Study Area

This study was conducted on a 10-ha plot (200 × 500 m) located near the centre of the Hubbard Brook Experimental Forest in Woodstock, New Hampshire, USA. The experimental forest occupies a 3037-ha valley within the White Mountain National Forest, which was logged in the late 1800s and early 1900s and has remained relatively undisturbed since about 1915 (Bormann and Likens 1979; Holmes 2011). At the start of the study, in 1969, the forest was about 60 years postharvest and was considered a mixed-age forest in the mid to late stage of succession (Bormann and Likens 1979; Holmes, Sherry, and Sturges 1986). The forest trees continued to accumulate biomass until the early to mid-1980s after which it was characterised as a mature second-growth northern hardwood forest (Battles et al. 2014; Siccama et al. 2007).

Since the study began, the species composition of forest vegetation has been relatively stable, consisting mainly of *Fagus grandifolia* (American beech), *Acer saccharum* (sugar maple) and *Betula alleghaniensis* (yellow birch) with some *Fraxinus americana* (white ash) and *Picea rubens* (red spruce). Changes in forest structure during the study period occurred due mostly to the deaths of large, older *F. grandifolia* caused by beech bark disease (Rhoads et al. 2002) and *A. saccharum* decline (Cleavitt et al. 2018; Juice et al. 2006). Other natural disturbances, such as ice storms (Rhoads et al. 2002) and strong wind events have caused some structural damage to canopy trees (Battles et al. 2017). The canopy gaps created by these disturbances tended to be occupied by dense patches of *Viburnum lantanoides* (hobblebush), an understory shrub, and saplings of *F. grandifolia*.

2.2 | Territory Mapping

The territories of all birds occupying the plot were mapped each year from 1969 through 2021 (except in 2020) as part of a study of bird community dynamics in this forest ecosystem (Holmes 2011; Holmes, Sherry, and Sturges 1986; Holmes and Sturges 1975). Territories were operationally defined, following Mayr (1935) and Tinbergen (1936, 1957), as areas defended against intrusion by conspecifics. In our system, territorial defence is mainly through singing, so we mapped territory boundaries primarily through recording countersinging by adjacent males (Nice 1941), augmented with opportunistic discoveries of nest locations and observations of physical altercations between conspecifics. Like many forest-nesting passerines, our study species were socially monogamous and exhibited resource-defence territoriality where resources include food as well as mates (see Luepold et al. 2024).

Measurements of bird abundance were conducted during the peak breeding season from late May to about the end of June using two techniques: spot mapping and timed censuses (Holmes, Sherry, and Sturges 1986; Holmes and Sherry 2001; Holmes and Sturges 1975). In brief, spot mapping was conducted for about 16 h per week. In each bout, an observer moved opportunistically throughout the 10-ha plot, frequently moving from one singing male to the next, and for each, recording the bird's location and species identity on a spatially referenced 50 × 50 m grid sheet. Special care was taken to map the locations of countersinging by conspecific males, which gave the best indications of territorial boundaries. All females that were detected were also mapped and identified. All parts of the 10-ha plot received approximately equal observation time each year. As each day's maps were overlaid onto each other through the season, territory dimensions and boundaries became evident, as was the presence of female mates.

The timed census method was similar to spot mapping but occurred during a more narrowly defined 1-h time period. Twice a week from late May to late June, starting shortly after dawn, two observers simultaneously walked slowly but steadily (about 50 m per 6 min) on parallel transect lines along the long axis of the 10-ha plot and recorded the species, sex and locations of each bird encountered visually or audibly within 50 m of the transect line. This resulted in a 1-hr snapshot of the numbers and locations of all birds within the study area, which aided in the final determinations of population sizes.

At the end of each field season, all records from the 5 weeks of spot mapping and timed censuses were compiled into a composite map for each species from which the territories could be determined. Boundaries were drawn under the assumption that territories did not overlap, which was consistent with our observations. We interpreted these drawn boundaries as centres of activity and food acquisition during the nesting season for individual males and their social mate but acknowledge that some individuals might sometimes make forays outside of their singing territory, either seeking mating opportunities (Webster, Chuang-Dobbs, and Holmes 2001) or in some cases foraging (Zach and Falls 1979). Although many birds on the plot were banded for measuring return rates and survivorship in the early years of the study, only two species were given colour bands for intensive study of local movements and reproductive success: *Setophaga caerulescens* (Black-throated Blue Warbler; 1981—present) and *Setophaga ruticilla* (American Redstart; 1980—about 1995). Observations of these colour-banded individuals indicated they fed almost exclusively within their defended area. Nonterritorial males (floaters) may be present in some of our study species (see Marra and Holmes 1997), but even if such males were present, we do not believe they would have influenced our maps of singing territorial males. Estimated territory boundaries were drawn by the same person in each of the 52 years (R.T.H.), usually in collaboration with colleagues who helped conduct the field censuses, ensuring that boundaries were consistently defined across years. Each year, the abundance was estimated for each species as individuals per 10-ha (males and females), with corrections for territories that fell partly outside of the plot (Holmes, Sherry, and Sturges 1986). Males were assumed to have one female mate unless otherwise observed. The product for each year was one final summary map for each species showing the territories for that season.

Summary maps were digitised using a KIC Bookeye 4 flatbed scanner and saved as high-resolution JPEGs (Zammarelli, Holmes, and R.T. 2023). Across the 52 years of study, the total number of adult birds of all species ranged from 71 to 214, representing 18–28 bird species. The seven species with the highest average abundance over the time series were chosen for analysis of territory size. In descending order of average annual abundance (with number of years for which we had usable maps), the species included *Vireo olivaceus* (Red-eyed Vireo, 50), *Setophaga ruticilla* (American Redstart, 28), *Setophaga virens* (Black-throated Green Warbler, 47), *Seiurus aurocapilla* (Ovenbird, 48), *Setophaga caerulescens* (Black-throated Blue Warbler, 30), *Empidonax minimus* (Least Flycatcher, 13) and *Catharus guttatus* (Hermit Thrush, 42). These species represented four families of birds and presented considerable variability in size, foraging habits, nesting locations, life history and temporal population dynamics over the study period (Table 1). Maps were not available for all species in all years because two species stopped breeding on the plot as the forest matured (*S. ruticilla* and *E. minimus*; Holmes and Sherry 2001) and because some maps were missing. A few *S. caerulescens* maps were excluded from analysis as they were created following a different protocol.

To calculate apparent territory size, we traced the hand-drawn territory boundaries from JPEG images of the territory maps for each species using a fifth Generation iPad Pro and a second Generation iPad Pencil in Adobe Illustrator: Graphic Art. Six points were added to each summary map for georeferencing in ArcGIS Pro version 3.1.0. Four of the six points aligned with the four corners of the 10-ha plot and two with the centre of the long edges. Georeferencing reports were produced to calculate root mean square (RMS) errors when aligning the images to the 10-ha plot coordinates. Two maps, one for *E. minimus* in 1981 and one for *S. aurocapilla* in 2000, were removed because the RMS errors were > 20 m. Once the images were georeferenced, territories were converted to unique polygons. All polygons were smoothed (Smooth Tolerance $= 25$ m) to remove jagged edges and corners that were artefacts of pixel size (Zammarelli, Holmes, and R.T. 2023). We removed edge territories that were $< 75\%$ within the 10-ha plot boundary. This process reduced the usable maps for *C. guttatus* from 42 to 37. After geoprocessing, the final number of territories available for analysis was 239 for *S. ruticilla*, 119 for *S. caerulescens*, 260 for *S. virens*, 72 for *C. guttatus*, 189 for *E. minimus*, 254 for *S. aurocapilla* and 479 for *V. olivaceus*. For all species, territory sizes (in ha) tended to follow a log-normal distribution (Figure S1) and were transformed prior to statistical analyses as log10 (ha).

We assessed spatial autocorrelation of territory size for each species to evaluate if territories of similar sizes were grouped together. Using the Merge tool (ArcGIS Pro, Data Management), we combined all years per species into a single layer. We standardised abundance data (individuals per 10-ha) and territory size (log10 ha) for each species to a mean of 0 and SD of 1 to facilitate comparisons among species. For the purposes of testing for spatial autocorrelations in territory size, we needed to account for interannual variation in territory size as a covariate. We then fitted a linear model of territory size versus individuals per 10-ha and used the residuals to calculate a Global Moran's I (Cliff and Ord 1973; Moran 1948) across five distance classes (Valcu and Kempenaers 2010a; Valcu and Kempenaers 2010b; ArcGIS Pro, Spatial Statistics, Incremental Spatial Autocorrelation). Moran's I was calculated as follows:

$$I = \frac{n}{W}\left[\sum_{i=1}^{n}\left(y_i - \bar{y}\right)^2\right] \qquad (1)$$

in which n is the number of observations, y is the value of the residual at each location and W is the spatial weights matrix. The first distance class was selected using the default search threshold from the centre of territories to ensure every territory had at least one neighbour. The first distance classes were 51 m for *S. ruticilla* and *S. virens*, 73 m for *S. caerulescens*, 43 m for *C. guttatus*, 57 m for *E. minimus*, 44 m for *S. aurocapilla* and 32 m for *V. olivaceus*. The four subsequent distance classes increased by increments of 100 m for six species and 50 m for *C. guttatus*.

2.3 | Habitat Preferences

Habitat can be defined as the places in space used by a species (Krebs 2009). In our study system, the arriving birds establish territories in the habitat each spring, many of which are yearling individuals choosing territories for the first time. Repeatable patterns of habitat occupancy by a species across years can be used as a measure of preference and can provide an index of habitat quality (Betts et al. 2008; Doran and Holmes 2005; Sergio and Newton 2003). Thus, we used occupancy patterns across seasons to quantify habitat preference (and apparent habitat quality) for each species. To calculate habitat preference for a territory we created a 2×2 m grid, adding each territory map per year per species to the grid using the Spatial Join tool (ArcGIS Pro, Analysis). Using the Merge tool (ArcGIS Pro, Data Management), we combined all years and the grid into a single data table for each species. We divided the number of times each grid square fell within a territory by the number of years to calculate the probability of a grid square being occupied by that species in any 1 year. For subsequent analyses, we averaged the probability of occupancy for all grid squares within each territory in each year to yield a single value, P, representing habitat preference for that area of the study plot (Zammarelli et al. 2024). Low and high habitat preferences for each species were operationally defined as the 10th and 90th percentiles, respectively, of the distribution of habitat preferences for the species.

We tested for nonrandom spatial patterns in the probability of occupancy by overlaying all years of territory maps for each species. Areas with a high probability of occupancy were considered preferred habitats (hot spots) compared to those with a low probability of occupancy (cold spots). We tested for statistically significant spatial variability in the probability of occupancy using the Getis-Ord Gi* statistic (ArcGIS Pro, Spatial Statistics, Hot Spot Analysis, Getis-Ord Gi*; Ord and Getis 1995). The Gi* statistic compared the weighted average of pixels in a map j surrounding a pixel i and the sum of all values in pixels j utilising queen's adjacency criterion. The Gi* statistic is a z-score where positive values indicate hot spots and negative values indicate cold spots: z-scores of ± 1.65, ± 1.96 and ± 2.58 in these analyses correspond to confidence intervals of 90%, 95% and 99% respectively.

Changes in environmental variables, and potentially habitat preference, due to forest maturation or other processes could result in changes in bird habitat preference. To test for such changes, we calculated Gi* statistics (with same algorithm as described above) for each of five 10-year time intervals (1969–1979, 1980–1989, 1990–1999, 2000–2009, 2010–2021) and compared the results across these intervals (ArcGIS Pro, Spatial Statistics, Hot Spot

TABLE 1 | Comparison of seven bird species studied in the Hubbard Brook Experimental Forest, 1969–2021.

Species	Nesting location (metres above the ground)[c]	Average foraging height (males; metres)[c,d]	Family	Years present on 10-ha plot	Mass (g)[d]	Foraging movements[a,d,e]	Basal metabolic rate (W)[d]
Vireo olivaceus (Red-eyed Vireo)[a]	10.7	11.8	Vireonidae	1969 to present	17.3	Hover	0.304
Setophaga ruticilla (American Restart)[b]	7.4	10.9	Parulidae	1969 with only a pair or two from 2008 onwards	8.6	Hover	0.142
Setophaga virens (Black-throated Green Warbler)[c]	11.3	13.1	Parulidae	1969 to present	9.2	Glean	0.147
Seiurus aurocapilla (Ovenbird)[d]	On the ground	Ground	Parulidae	1969 to present	22.5	Glean	0.246
Setophaga caerulescens (Black-throated Blue Warbler)[e]	0.5	5.9	Parulidae	1969 to present	10.0	Glean	0.189
Empidonax minimus (Least Flycatcher)[a]	11.8	10.5	Tyrannidae	1969 to 1994	10.3	Hover	0.238
Catharus guttatus (Hermit Thrush)[b]	On the ground	2.5	Turdidae	1969 to present	31.2	Glean	0.337

Note: Listed in order of average annual abundance from highest to lowest.

[a] Cimprich, Moore, and Guilfoyle (2020), Tarof and Briskie (2020), Holmes and Robinson (1988).

[b] Sherry et al. (2020), Dellinger et al. (2020), Basal metabolic rates from direct measurements (*V. olivaceus*, *S. caerulescens*, *E. minimus*; Holmes, Bonney Jr., and Pacala 1979) or estimated from the interspecies relationship (McKechnie and Wolf 2004).

[c] Morse and Poole (2020), Holmes (1986).

[d] Porneluzi, Van Horn, and Donovan (2020), Holmes, Bonney Jr., and Pacala (1979).

[e] Holmes et al. (2020), Robinson and Holmes (1982).

Analysis Comparison). Comparisons were made only if data from five or more years were available within a decade. This excluded *E. minimus* from analysis since it was only present for 13 years.

2.4 | Statistical Analysis

For each species, we fit the same multiple linear regression model comparing the sensitivity of territory size to abundance, habitat preference and their interaction:

$$S = \beta_0 + \beta_1 N + \beta_2 P + \beta_3 NP + \varepsilon \tag{2}$$

where S is log10(territory size), N is abundance of the species in that year (individual adults in the 10-ha), P is the calculated preference for the territory by the species, NP is the interaction between abundance and preference and ε represents lack of fit. In this model, β_1 represents the change in territory size in response to interannual variation in local abundance, β_2 represents the effect of habitat preference on territory size and β_3 represents the effect of habitat preference on the elasticity of territory size (i.e., responsiveness of territory size to change in abundance). Reduced elasticity in territory size in the most preferred habitats was the expectation if socially dominant individuals (despots) tend to hold territories in the best habitats that remain similarly sized regardless of local abundance. For the analyses, each territory in each year was an observation. For any one species, values for N were the same for each territory in a year but varied across years, while values of P varied spatially across the plot but were the same across years for any specified location within the plot. To facilitate comparisons of model coefficients among species, we standardised S, N and P for each species to a mean of 0 and SD of 1. N and P were approximately normally distributed and were not transformed. We compared model coefficients among species following Zar and H. (1996) with ANOVAs that tested for reductions in the pooled residual error of the species-specific models. This was compared to residual error of the reduced model that did not include species identity. Because most birds were not individually identifiable, we could not test for random effects of individuals, that is, do some birds consistently tend to establish smaller or larger territories? However, with 50+ years of data and the short lifespan of adult birds in this system being no more than 2 or 3 years (Donovan et al. 1995; Sillett and Holmes 2002) each species was represented in the time series by many different individuals.

3 | Results

3.1 | Territory Size

Among our seven study species, *C. guttatus* maintained the largest territories (median = 2.56 ha) and *E. minimus* the smallest (median = 0.32 ha); median territory sizes for the other species ranged from 0.65 ha (*S. ruticilla*) to 1.71 ha (*S. caerulescens*; Figure 1a, Figure S1). Territory sizes showed striking variation both within and across years (Figure 2; Table S1). For most species, in most years, territory size ranged by at least twofold across the 10-ha plot within years, and median territory sizes ranged from 3.3- to 14-fold across years (*S. ruticilla* > *S. virens* and *C. guttatus* > others; Figure 2).

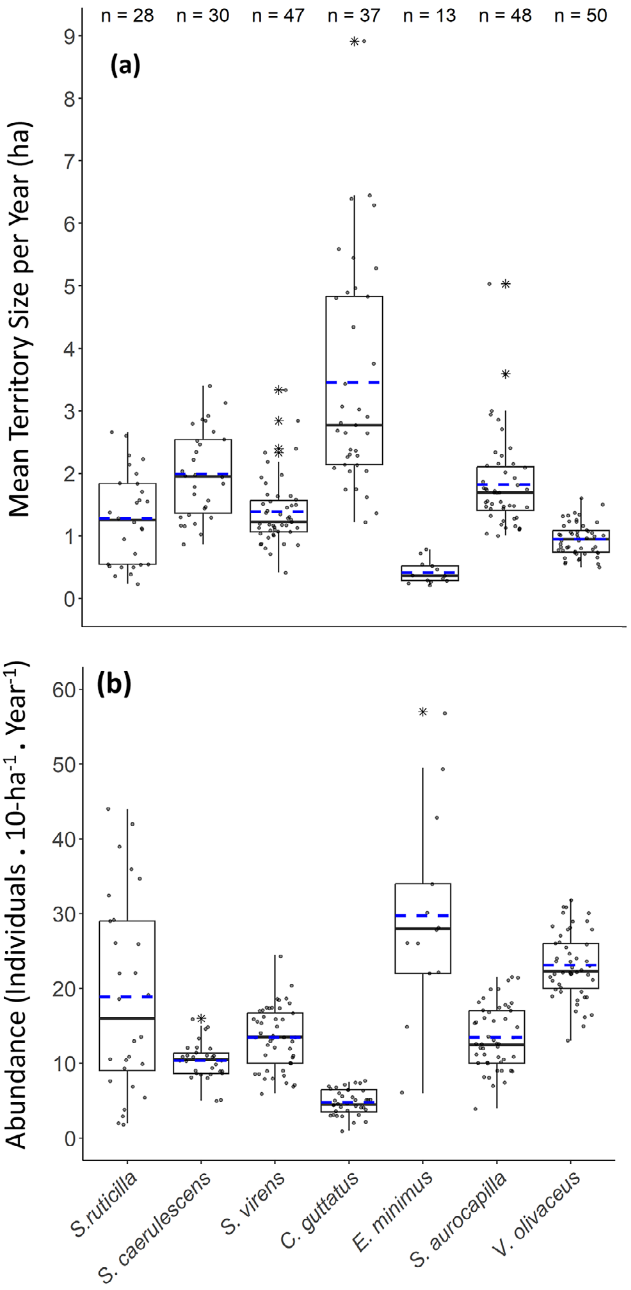

FIGURE 1 | (a) Distributions of mean annual territory size and (b) abundances (individuals per 10-ha) of seven bird species breeding at Hubbard Brook, 1969–2021, n = number of available years. Box plots show the 1st, 2nd and 3rd quartiles. Whiskers show 1.5 times the interquartile range. Mean is indicated in blue. Mean territory size was calculated from log-transformed territory sizes and then back-transformed for this graphic. *Empidonax minimus* and *S. ruticilla*, which disappeared from the plot during the study, were only considered for years (n = 13 and n = 28 respectively) when they were nesting on the plot.

Given the high variation in territory size, there was surprisingly little spatial structure, that is, very limited evidence for territories of similar sizes being grouped together (Figure 3). Even with robust estimates of Moran's I, four of seven species showed no evidence of spatial autocorrelation in territory size (Figure S2). *Catharus guttatus* showed the strongest spatial structure in territory size (Moran's I ± SD = 0.36 ± 0.10 at ≤ 43 m, Figure S2; in Figure 3, note

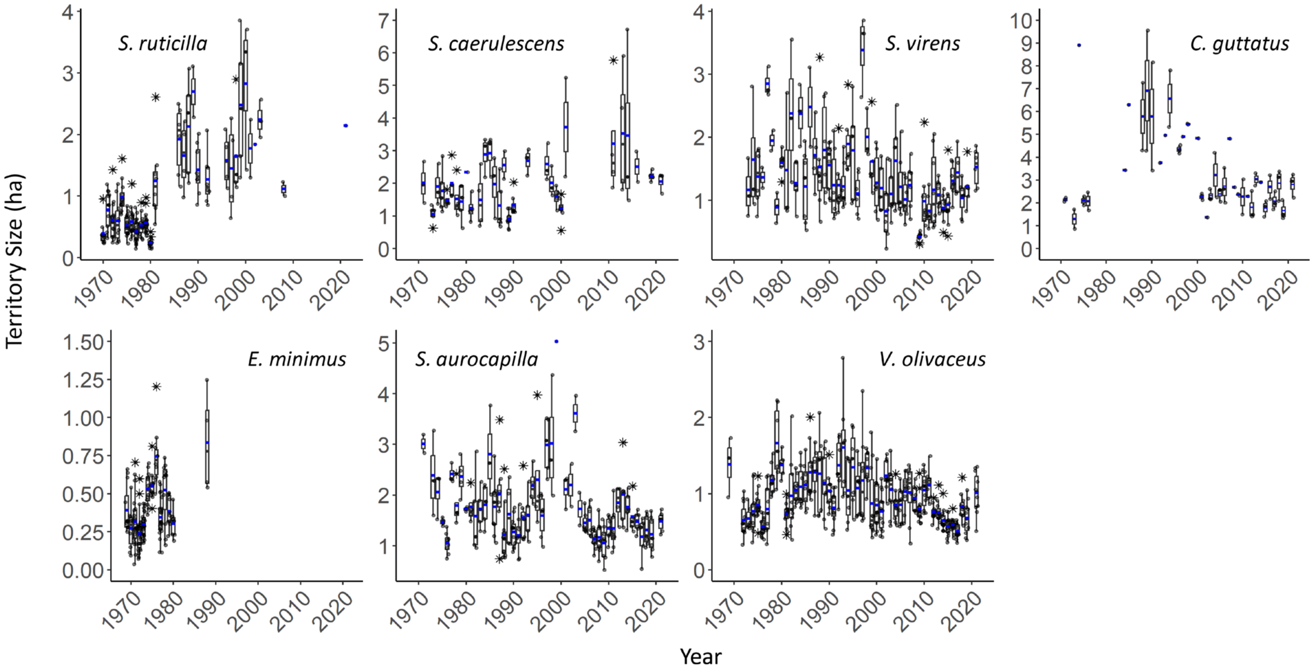

FIGURE 2 | Distributions of territory sizes from 1969 to 2021 for the seven most common bird species at Hubbard Brook, where n = number of available years. Box plots show the 1st, 2nd and 3rd quartiles. Whiskers show 1.5 times the interquartile range.

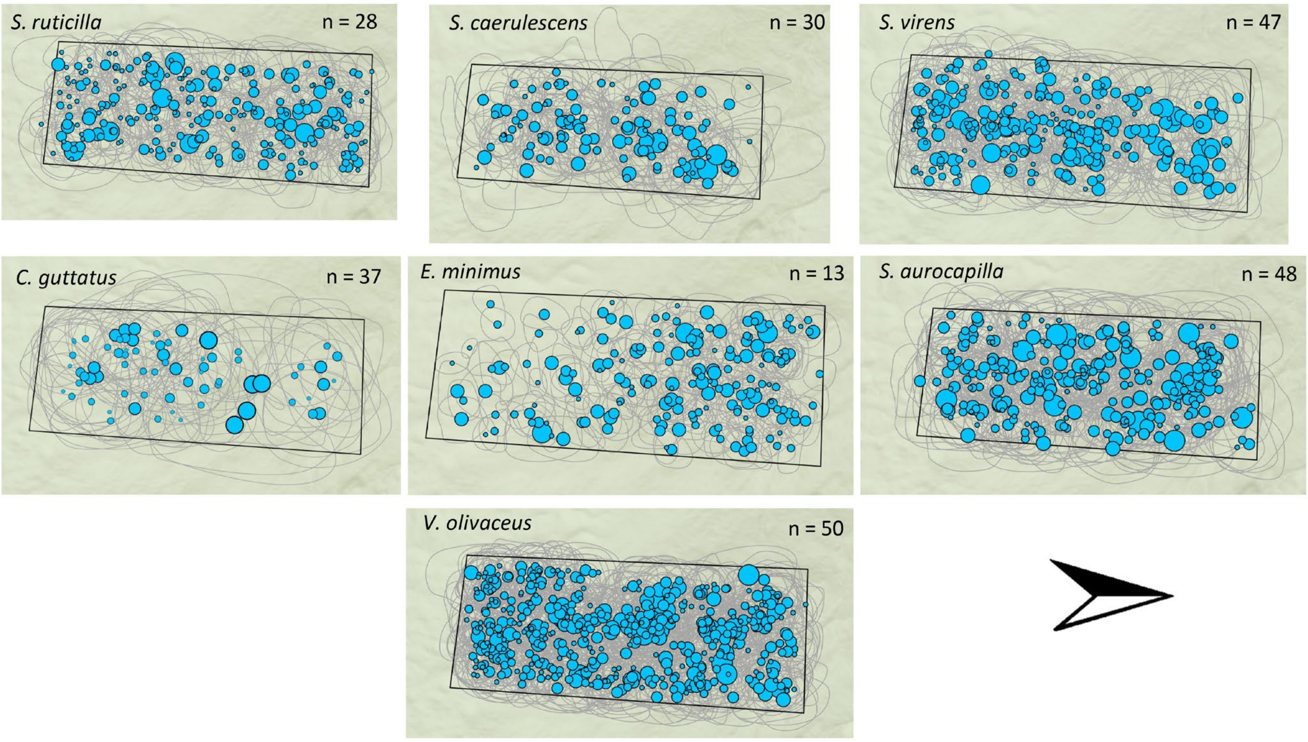

FIGURE 3 | Spatial patterns of territory size among all available years (n) for seven bird species at Hubbard Brook, 1969–2021. Five circle sizes represent different size classes of territories with larger circles representing larger territories. Individual territories are depicted as light grey outlines in the background. Rectangular frames show boundaries of the study plot.

region of larger territories near the centre of the plot). There was also some spatial structure to individual territory size for *S. virens* and *V. olivaceus*, both with a tendency for larger territories to occur towards the north end of the plot (Figure 3), but the spatial autocorrelations were minimal (Moran's I < 0.12; Figure S2).

3.2 | Habitat Preferences

All seven species showed clear patterns of habitat preference as measured by the annual probability of occupancy across the plot (Figure 4). Hot spot analyses supported the existence

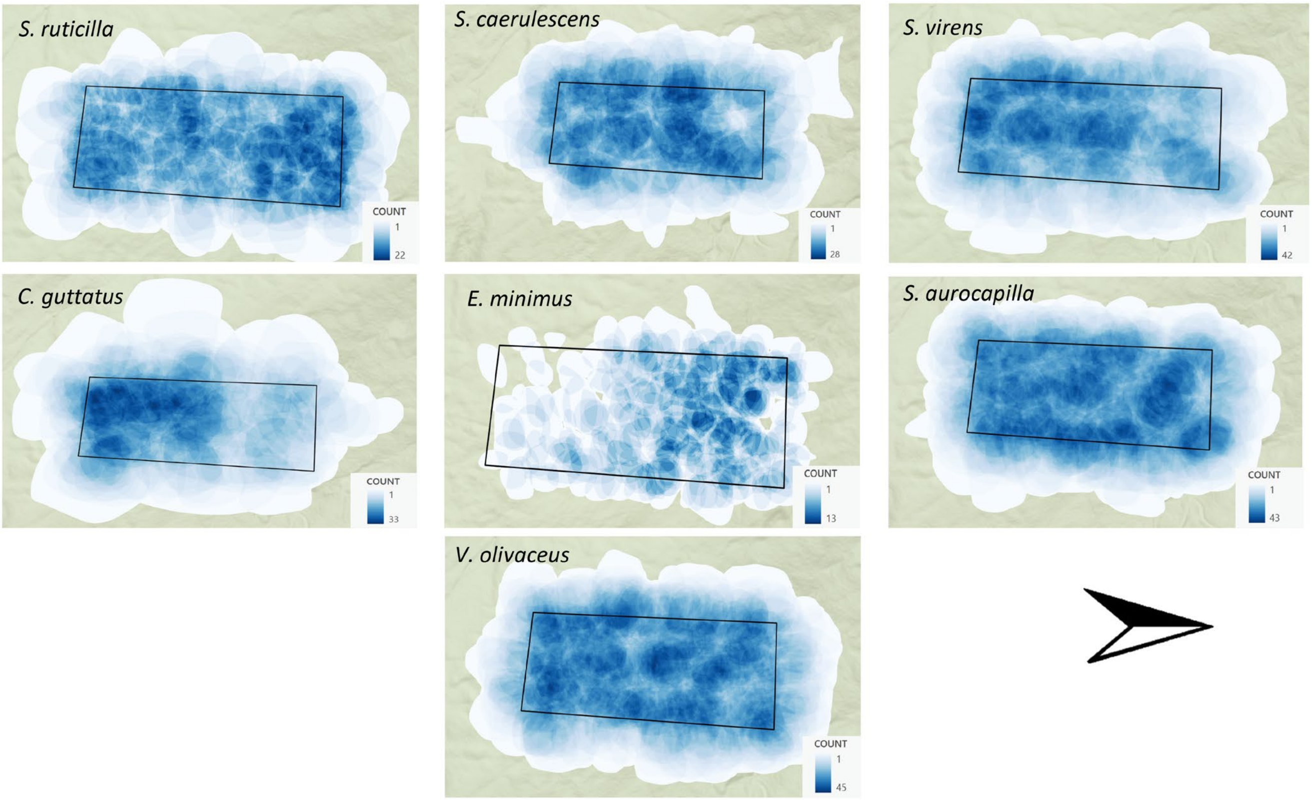

FIGURE 4 | Frequency of occupancy from overlapping territory maps across years for seven bird species at Hubbard Brook, 1969–2021. The intensity of blue shows annual probability of occupancy ranging from highest occupancy (dark blue) to unoccupied (white). Rectangular frames show boundaries of the study plot. See Figure S4 for the corresponding heat maps of occupancy.

of strong spatial patterning in preferences for all species (Figure S3). For each species, more than 50% of the 10-ha plot was significantly preferred or avoided ($|\text{Gi*-statistic}| > 1.96$; Figure S4). Patterns of spatial preference varied among species with some species showing broader spatial patterns and other species exhibiting finer scale patterns in their use of space. The statistical estimates of hot spots and cold spots varied slightly over decades (Figure S5), but there was no evidence for systematic changes for any species (no species displayed increasing dissimilarity with longer intervals of comparison; Figure S6).

3.3 | Abundances

The median number of breeding individuals on the 10-ha plot ranged from five for *C. guttatus* to 34 for *E. minimus* (Figure 1b). Variation in abundance ranged from twofold for *V. olivaceus* to 22-fold for the *S. ruticilla* across years. All species displayed variation among years in the number of individuals per plot (Figure S7). Two species that were initially very abundant disappeared from the study plot as the forest stand matured (*E. minimus* and *S. ruticilla*; Holmes and Sherry 2001). When we considered only the years when they were breeding on the plot, these two species still displayed the greatest interannual variation (5- to 13-fold range from 10th to 90th percentile; Table 2). The other five species ranged in abundance by a factor of 1.5–2.3 over the 52-year study period (Figure S7). The combination of interannual variation in abundance and spatial variation in habitat preferences presented the opportunity to test competing predictions of the ideal free and ideal despotic distributions.

3.4 | Ideal Free Distribution Versus Ideal Despotic Distribution

Overall, our results best matched the predictions of an ideal free distribution. All species showed a clear and significant decline in territory size when abundance increased (Figure 5). No species showed significant effects on territory size associated with variation in habitat preference or with the preference × abundance interaction (Table 3). The pattern of territory size (S) as a function of abundance (N), habitat preference (P) and the interaction between abundance and preference (NP), was qualitatively similar for all seven species (Figure 5; Table 3). The two species that came closest to displaying a significant interaction ($0.05 < p < 0.10$), *S. virens* and *V. olivaceus*, had parameter estimates for NP that went in opposite directions (Table 3). In *V. olivaceus*, effects of abundance were slightly greater in the least preferred habitats, in the direction predicted by the ideal despotic distribution, while in *S. virens*, the sensitivity of territory size to abundance was somewhat greater in the most preferred habitats (Figures 5 and 6). Visual comparisons of habitat preference maps (Figure 4) and territory size maps (Figure 3) suggested that *C. guttatus* had larger territories in less preferred habitats and that *S. virens* followed a similar pattern but with a weaker spatial structure. However, these relationships were not evident as statistically significant interactions between abundance and preference (Table 3).

TABLE 2 | Evaluation of changes in territory size as a result of increased abundance.

Species	Error degrees of freedom	β_0	β_1	SE(β_1)	Low abundance (10th percentile of individuals / 10-ha)	High abundance (90th percentile of individuals / 10-ha)	Expected territory size at low abundance (ha)	Expected territory size at 2× low abundance (ha)	Expected territory size at high abundance (ha)
S. ruticilla	237	0.389	−0.020	0.001	10.4	42.0	1.52	0.95	0.36
S. caerulescens	117	0.728	−0.046	0.006	8.5	15.0	2.18	0.89	1.10
S. virens	258	0.480	−0.027	0.003	8.5	18.5	1.76	1.03	0.94
C. guttatus	70	0.831	−0.072	0.013	3.0	7.5	4.11	2.49	1.96
E. minimus	187	0.196	−0.008	0.001	22.0	57.0	0.43	0.29	0.23
S. aurocapilla	252	0.576	−0.026	0.002	10.0	21.0	2.08	1.15	1.08
V. olivaceous	477	0.465	−0.021	0.001	18.5	30.0	1.12	0.43	0.64

Note: The model (log10(S) = $\beta_0 + \beta_1 \cdot N$) was fit to data for each species (Figure S6) and used to estimate average territory size at low abundance (defined as 10th percentile of historic values), at twice low abundance, and at high abundance (90th percentile of historic values). Territory size of all species decreased with abundance, but species differed in the relationship between territory size ($F_{12,1598} = 39.44$, $p < 0.0001$; Full vs. reduced model with full model allowing for difference in slope and intercepts among species). Error degrees of freedom for regression models = number of territories−2.

Bird species differed in the extent to which territory sizes varied with changes in abundance. Compressibility provides a measure of the amount that territory sizes decrease as a result of increasing abundance. We compared the compressibility of territory sizes in three different ways. From model fits of standardised data (Table 3), the slopes of territory size versus abundance differed significantly among species ($F_{6,1598} = 3.01$; $p = 0.0062$). Based on a comparison of these slopes, territory sizes of *S. ruticilla* and *S. aurocapilla* were most responsive to changes in abundance, and *E. minimus* was least responsive. By themselves, these slopes do not take into account the notable differences among species in how much abundance varied across years. For further comparisons, in nonstandardised units, we fit simple linear regressions for each species of S (log10-transformed) versus N and used these regressions to estimate the reduction in territory size (in original units of ha) with a doubling of abundance from low abundance (10th percentile) for that species (Table 2). From this perspective, *S. caerulescens* and *V. olivaceus* had the greatest compressibility in territory size (59% and 62% reduction with a doubling of N from low abundance respectively), and *E. minimus* had the least compressibility (33% reduction with a doubling of N), with *S. ruticilla* and *C. guttatus* also displaying relatively low compressibility (37% and 39% reduction with a doubling of N respectively). When we accounted for the full range of interannual variability in abundance expressed by each species (10th–90th percentile), *S. ruticilla* had the greatest range in expected territory size from low to high abundance: 1.52 to 0.36 ha as N ranged from 10 to 42 individuals per 10-ha (Table 2). The actual compressibility of territory size in *S. ruticilla* was even greater than indicated by these calculations because the log-transformation of S did not fully capture the strong nonlinear increases in territory size at low abundance for this species (note lack of fit at low abundance for *S. ruticilla* in Figure S8).

4 | Discussion

Our results indicated that territory size in all seven bird species decreased as local abundance increased, which was expected under the ideal free distribution. In general, when individuals establish territories that maximise their fitness relative to constraints of abundance in the area, it has the emergent effect of stabilising population growth rate leading to tighter population regulation and, therefore, reducing extinction risk in small populations (McPeek et al. 2001; Pulliam and Danielson 1991). Under Fretwell's model of despotic territoriality, socially dominant birds are predicted to occupy the most preferred habitats (and to hold the same territory size regardless of local abundance). If despots (sensu Fretwell) were present, this would have the effect of concentrating a larger fraction of expected annual reproduction in fewer individuals, which would increase extinction risks from stochastic events. That was, however, not the case in our study system (Figure 5).

Our results also support the early prediction by MacArthur (1958) that increased abundance leads to smaller territories with fewer resources and reduced per capita reproduction. This relationship

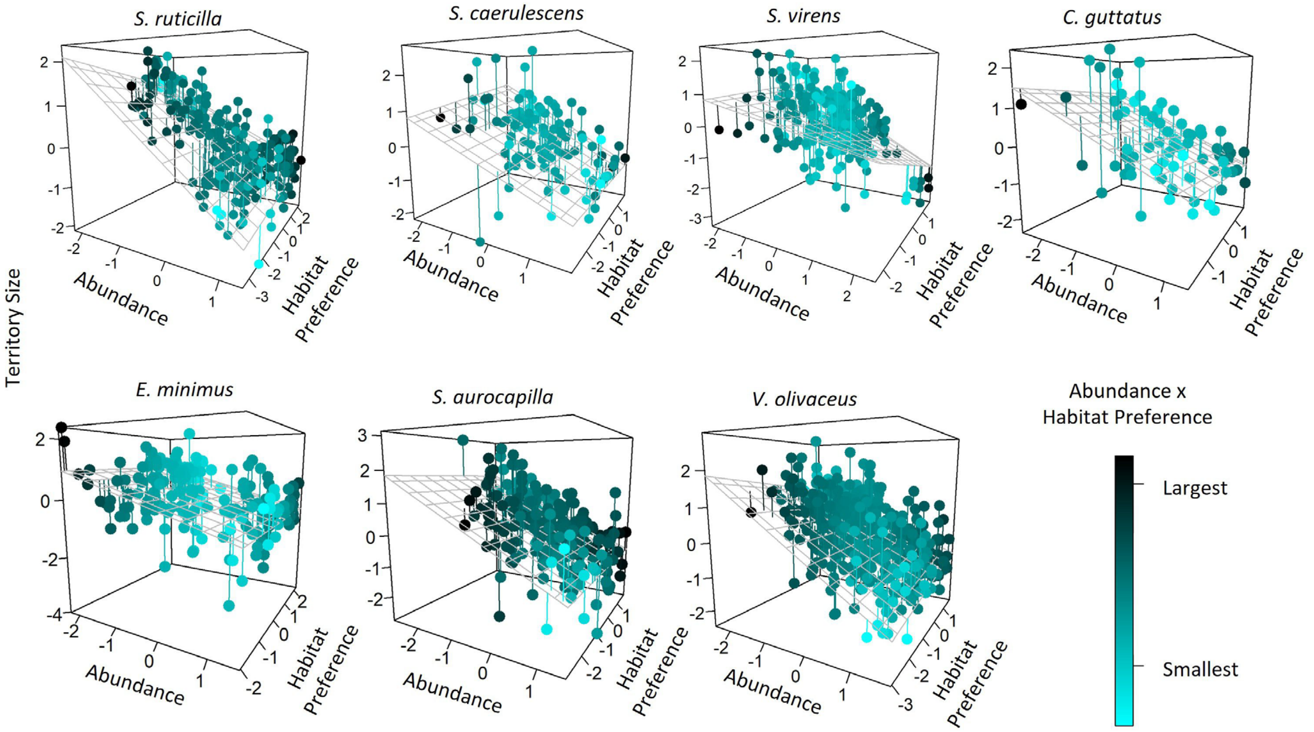

FIGURE 5 | Three-dimensional visualisation of the relationship between bird abundance, habitat preference and territory size for seven bird species at Hubbard Brook over 52 years. All variables were standardised prior to analysis (mean = 0, SD = 1), and territory size was first transformed as log10(S). Colours represent the interaction between abundance and the annual probability of occupancy from black (largest) to light blue (smallest). Further details are in Table 2. Alternative visualisation in Figure 6.

TABLE 3 | Summary of model estimates ± SE for effects of abundance, habitat preference and their interaction on territory size for seven bird species at Hubbard Brook.

Species	Abundance (N)	Habitat preference (P)	(NP)	df error	R^2 for full model
S. ruticilla	−0.74 ± 0.045***	0.01 ± 0.045	0.07 ± 0.046	235	0.54
S. caerulescens	−0.57 ± 0.077***	0.09 ± 0.077	−0.03 ± 0.087	115	0.32
S. virens	−0.50 ± 0.053***	−0.10 ± 0.053†	−0.10 ± 0.056†	256	0.28
C. guttatus	−0.53 ± 0.100***	−0.08 ± 0.100	−0.00 ± 0.097	68	0.30
E. minimus	−0.44 ± 0.079***	0.03 ± 0.080	0.01 ± 0.069	185	0.18
S. aurocapilla	−0.63 ± 0.049***	−0.01 ± 0.051	0.01 ± 0.051	250	0.40
V. olivaceus	−0.58 ± 0.037***	0.03 ± 0.037	0.07 ± 0.038†	475	0.34

Note: All coefficients for abundance were highly significant at $p < 0.001$.
$^{***}p < 0.001$.
$^{\dagger}0.05 < p < 0.10$.

was confirmed experimentally in one of our study species, *S. caerulescens*, by Sillett, Rodenhouse, and Holmes (2004). Furthermore, long-term studies of *S. caerulescens* at Hubbard Brook on a 64-ha plot indicate that local density is negatively related to average annual fledging success (Sillett, Holmes, and Sherry 2000; Sillett, Rodenhouse, and Holmes 2004). This results in an increase in the abundance of first-time breeders the next year, evidence that abundance (density) affects per capita reproduction (Sillett, Holmes, and Sherry 2000; Sillett, Rodenhouse, and Holmes 2004).

Contrary to Fretwell's (1972) model of an ideal despotic distribution, the birds in our study decreased their territory size with increasing abundance irrespective of spatial variation in habitat preference. We do not reject the possibility that some individuals in the species we studied exhibit social dominance. Larger territories may indicate despotic behaviour in the original sense of despotism, as these individuals are literally controlling a larger area, but the lack of relationships between habitat preference and territory size goes against Fretwell's definition of despotism.

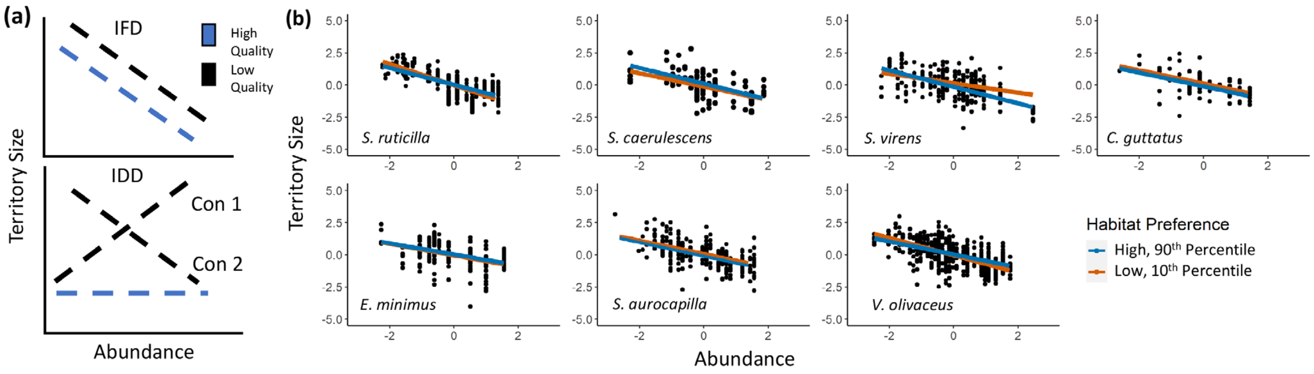

FIGURE 6 | (a) Theoretical relationships between territory size, abundance of conspecifics and habitat quality for the ideal free distribution (IFD) and ideal despotic distribution (IDD). Under IDD, territory size is predicted to be stable in high quality habitats and might go up (condition 1) or down (condition 2) in low-quality habitats. (b) Empirical results from analysis of data for the seven bird species at Hubbard Brook. Lines compare the expected territory size given abundance in low preference and high preference habitats, defined by the 10th and 90th percentile of the distribution of habitat preferences for the species (see text).

According to Fretwell (1972), there can be uncertainty about whether individuals can reach an 'ideal' state. This may not occur if individuals misread environmental cues when assessing habitat suitability or if the 'ideal' is simply never achieved. Sampling over several years is helpful to overcome uncertainties of individuals reaching an 'ideal' state and year-to-year variation (Fretwell 1972). Habitat preference is most likely linked to the life history of the species and fitness of individuals. Even if our measure of habitat preference is not the strongest indicator of habitat quality in that year, the preferences that we have observed may still be shaped by selection. Natural selection would favour individuals that choose habitats that increase their expected survival and reproduction (Krebs 2009). Our study species broadly conformed to the postulate of adaptive individual behaviour ('ideal') in the determination of territory size (Fretwell 1972; Fretwell and Lucas 1970).

In our study species (including *E. minimus* and *S. ruticilla* before their decline), the relative stability of abundances from year to year (Figure S7) is consistent with the stable population dynamics expected from a system that conforms, even approximately, to the ideal free distribution. Bird territory size, although it generally varied by at least twofold for each species across the 10-ha study plot, was not predicted by habitat preference (Figure 2; Figure 5; Table 3). All species showed clear patterns of preference for some areas of the study plot over others (Figure 4; Figure S3), but four of seven species showed no spatial structure at all in territory size (Figure S2), and the patterning of territory size for the three other species at best was only weakly related to habitat preference (Table 3). Generally, territories of similar sizes were not consistently located in preferred parts of the plot. Thus, our study provided little evidence of despotic territoriality as defined by Fretwell (1972). Only one species, *V. olivaceus*, showed the predicted signal of reduced compressibility of territory size in the most preferred habitats, and statistical support for the interaction term was marginal ($p = 0.08$). It may be relevant that *V. olivaceus* is a highly vocal species. Symes et al. (2022) analysed bioacoustic recordings from our study site at Hubbard Brook that included six of our study species (not *E. minimus*). *Vireo olivaceus* displayed an average of 181 songs per 10 min, which was more than sixfold greater than the second most vocal species in the community. Such high singing rates might make it easy for individual birds to assess occupancy patterns during territory establishment.

Our results and conclusions are contingent upon the spatial scale of our study (10-ha). It would be informative to have comparable data from more study plots that vary in habitat quality. For example, the model of site-dependent population regulation proposed by Rodenhouse, Sherry, and Holmes (1997); Rodenhouse et al. (2003) is based on the condition that birds settle first in the highest quality sites and then progressively in sites of decreasing suitability. We were unable to evaluate this model because it would most likely operate on a broader scale than that of our study plot. It is worth noting that inter-annual variation in the abundance of these species is well correlated across the White Mountains (Holmes and Sherry 1988, 2001; Jones, Doran, and Holmes 2003), so years of high abundance on our study plot tended to be years of high abundance throughout the broader region. Further studies with marked birds and greater variation in habitat quality would allow us to assess if floaters exist in our system and if so, whether they are more common in habitat of high or low quality (Brown and Long 2007).

Although territory size was generally unrelated to habitat preference, all of our study species showed notable variation in territory sizes each year within the 10-ha plot (Figure 2; Table S1). *Catharus guttatus* had the least variability in territory sizes associated with changes in abundance (factor of 1.36 from 10th to 90th percentile; Table 2). Lower variability in territory size may be related to body size, as *C. guttatus* is the largest of the species in our study and has the greatest energy requirement. However, territories varied in size among the parulid warblers which had similar body sizes and energy requirements (Table 1).

Though our analyses and the theoretical arguments of Fretwell (1972) focus on the role of intraspecific competition in habitat selection, interspecific competition may also affect territory size and location. Overlap among species in foraging zone and prey items could also influence territorial behaviour.

In our system, *E. minimus* and *S. ruticilla*, which forage in the same canopy zone, displayed about a threefold range of variation in territory size within years, the largest within-year range for our study species. It is possible that some of this within-year variation in territory size is related to spatial overlap with other species. *Empidonax minimus* clusters their territories together (Sherry and Holmes 1985; Tarof and Ratcliffe 2004) and regularly chase and attack other co-occurring species, including *S. ruticilla*, which is ecologically similar (Sherry 1979; Sherry and Holmes 1988). It could be expected that such clustering of territories would dampen the relationship between territory size and abundance, and indeed *E. minimus* had the lowest coefficient for territory size as a function of abundance (Equation (2); Table 3). Tarof and Ratcliffe (2004) hypothesized that the interspecific aggression displayed by *E. minimus* is an adaptation to limit interspecific competition for food resources. Other bird species in our community could also be responsive to heterospecifics in their territorial behaviour even if they do not display such overt interspecific aggression. Further studies of territory patterns in bird communities, such as those at Hubbard Brook, could test whether species with overlapping foraging habits adaptively adjust their territory sizes based partly on the occurrence of interspecific competitors.

For migratory birds, conditions on wintering grounds can have carryover effects influencing physiological condition, timing of migration and, subsequently, reproductive success on the breeding grounds (Marra, Hobson, and Holmes 1998; Norris et al. 2004; Woodworth et al. 2017). One mechanism by which some individuals may acquire bigger and better territories is to arrive at the breeding grounds earlier than their conspecifics (Marra, Hobson, and Holmes 1998; Kokko 1999; Rodenhouse et al. 2003). For example, *S. ruticilla* in higher quality wintering habitat, which tend to be older and more socially dominant males, arrive at their breeding grounds as much as a month earlier than individuals that spent the winter in lower quality habitat (Marra 2000; Marra, Hobson, and Holmes 1998; Norris et al. 2004). Heterogeneity in winter habitat quality may be among the reasons why *S. ruticilla* in our study displayed a particularly high range of territory sizes within years (Figure 2). On the other hand, Sung and Handford (2020) found territory size to be unrelated to arrival time in *Passerculus sandwichensis* (Savannah Sparrows). Our field protocol did not allow us to document arrival times as would be needed for testing this hypothesis.

It is also possible, albeit less parsimonious, that there is some heritable variation in traits that influence territorial behaviour. Heterozygosity is related to territory size and song structure in *Monias benschi* (Subdesert Mesite; Seddon et al. 2004). There is heritability to song characteristics in *Taeniopygia castanotis* (Zebra Finches; Forstmeier et al. 2009; Woodgate et al. 2014) and *Serinus canaria* (domesticated canaries; Trösch et al. 2017) but apparently not in *Ficedula hypoleuca* (Pied Flycatchers; Labra and Lampe 2018). In *Parus major* (Great Tits), exploratory behaviour is heritable and associated with dominance (Dingemanse et al. 2002; Dingemanse and de Goede 2004). Aggressive behaviour, including territoriality, is partly related to testosterone levels (Wingfield et al. 1997), which can vary among individuals and covary between siblings of *T. castanotis* (Kempenaers, Peters, and Foerster 2008). It is presently unknown if there are any heritable traits that might influence territory size in our study species.

Regardless of the proximate and ultimate causes of intraspecific variation in territory size, it seems likely that optimal territory size in our system varies over years. Optimisation of territory size can be considered in terms of a cost–benefit framework in which the benefit function is shaped by resource availability per area of habitat (Davies and Houston 1984; Hixon 1980; Schoener 1983). Presumably, the main benefit of increased territory size for insectivorous birds, like the ones we studied, is that larger territories hold more insect food resources. In our system at Hubbard Brook, the abundance of insects fluctuates greatly from year to year (e.g., > 20-fold interannual variation in caterpillar biomass per 2000 leaves over 25 years) and is spatially synchronous to a scale at least several hundred kilometres, while varying little among replicate transects within years (Jones, Doran, and Holmes 2003; Lany et al. 2016; Reynolds et al. 2007; Zammarelli et al. 2022). Thus, given the same cost function, optimal territory size would be expected to vary over years (Avgar, Betini, and Fryxell 2020).

Nest predation is another process that may influence territory size. Our study system also displays high interannual variation in the abundance of nest predators (Holmes 2011; Nagy and Holmes 2004), which could affect annual differences in territory size. Some studies (e.g., Dunn 1977; Schmidt and Whelan 1999; Zimmerman 1984), but not others (Reitsma 1992), have reported density-dependent nest predation in birds. Where present, density-dependent nest predation may tend to favour larger territories when nest predators are abundant and smaller territories when nest predators are rare.

Consistent with cost–benefit optimisation models, the clades in which territoriality is common tend to be those in which territories are established via signalling rather than physical aggression, which presumably lowers the cost function and makes it more likely that there will be an evolutionarily stable strategy that includes territoriality. Conformity to the ideal free distribution in our study system is apparently facilitated by the use of singing to establish and maintain territory boundaries. Singing offers some advantages over other modalities in that it travels farther and is more omnidirectional than visual signals and is more immediate and adjustable than olfactory signals (Podos and Webster 2022). While singing may expose birds to predators, birds can rapidly adjust the signal to reduce their detectability or switch to an alarm call (Podos and Webster 2022; Symes et al. 2022). Singing is not free but the energetic costs for songbirds are not very great (estimated increase of 2%–36% in oxygen consumption; Oberweger and Goller 2001). In our study system, it appears to be singing that allows male birds to assess the number of individuals contending for territories and adapt their territory sizes in a manner that approximates the 'ideal' postulated by Fretwell (1972).

One of the most consequential predictions of the ideal free distribution is that fitness is equalised across habitats of intrinsically different quality. We were unable to evaluate this prediction because we lacked complete fitness measurements for our study species. However, because average territory size was not generally smaller in the most preferred habitats and not generally larger in less preferred habitats, it seems unlikely that fitness is equal across habitats. Furthermore, in the simplest version of the ideal free distribution, territory sizes would be similar among individuals occupying habitats of similar quality, which was not the case in our study species. The traditional dichotomy of ideal free distribution vs. ideal despotic distribution, therefore, may not be sufficient for understanding the patterns of habitat selection and territory size. Other mechanisms, besides variation in territory quality, should be considered when assessing how individuals within a species select and space themselves across habitats.

Where territoriality exists, it elevates the evolutionary importance of agonistic behaviour (Maynard Smith 1982). It also may frequently influence mate choice and sexual selection (Stamps 1983) with fundamental consequences for population regulation (Brown 1969; Hoover et al. 2020; Howard 1920; Rodenhouse, Sherry, and Holmes 1997; Treinys, Bergmanis, and Väli 2017; Wolff 1997). The ideal free distribution is derived under the assumption that individuals behave to maximise their own fitness but has the emergent consequence of stabilising population dynamics and promoting the persistence of local populations (McPeek et al. 2001). The strong general, multidecadal pattern of decreasing territory size with increasing abundance in multiple species that we have shown here may thus contribute to the maintenance of diversity in forest bird communities.

Author Contributions

Richard T. Holmes led the field data collection, made all bird abundance estimates and drew bird territorial boundaries in collaboration with his census team. Miranda B. Zammarelli digitised the maps. Spatial analyses were conducted by Miranda B. Zammarelli and David A. Lutz. Other data analyses were completed by Miranda B. Zammarelli and Matthew P. Ayres. Miranda B. Zammarelli led the writing of the manuscript. All authors contributed to conceptual design and writing, and all authors approved of the final version of the manuscript.

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Data Availability Statement

Original images of maps are available in the Environmental Data Initiative (EDI) at https://doi.org/10.6073/pasta/df93595ba8df60570d472f6e6f58839e. Data and code supporting the manuscript are available on the Environmental Data Initiative (EDI) at https://doi.org/10.6073/pasta/a2ff072d5d2d8fc4034d2bc9e199b4a5.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.