


# Effects of age, breeding strategy, population density, and number of neighbors on territory size and shape in *Passerculus sandwichensis* (Savannah Sparrow)

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## ABSTRACT

The size and shape of an animal's breeding territory are dynamic features influenced by multiple intrinsic and extrinsic factors and can have important implications for survival and reproduction. Quantitative studies of variation in these territory features can generate deeper insights into animal ecology and behavior. We explored the effect of age, breeding strategy, population density, and number of neighbors on the size and shape of breeding territories in an island population of *Passerculus sandwichensis* (Savannah Sparrow). Our dataset consisted of 407 breeding territories belonging to 225 males sampled over 11 years. We compared territory sizes to the age of the male territorial holder, the male's reproductive strategy (monogamy vs. polygyny), the number of birds in the study population (population density), and the number of immediate territorial neighbors (local density). We found substantial variation in territory size, with territories ranging over two orders of magnitude from 57 to 5,727 m<sup>2</sup> (0.0057–0.57 ha). Older males had larger territories, polygynous males had larger territories, territories were smaller in years with higher population density, and larger territories were associated with more immediate territorial neighbors. We also found substantial variation in territory shape, from near-circular to irregularly shaped territories. Males with more neighbors had irregularly shaped territories, but shape did not vary with male age, breeding strategy, or population density. For males that lived 2 years or longer, we found strong consistent individual differences in territory size across years, but weaker individual differences in territory shape, suggesting that size has high repeatability whereas shape has low repeatability. Our work provides evidence that songbird territories are highly dynamic, and that their size and shape reflect both intrinsic factors (age and number of breeding partners) and extrinsic factors (population density and number of territorial neighbors).

**Keywords:** geographic information system, GIS, neighborhood size, *Passerculus sandwichensis*, population size, resource defense, Savannah Sparrow, territoriality, territory shape

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## LAY SUMMARY

- The size and shape of birds' territories can affect survival and reproduction.
- Over an 11-year period, we measured the territory size and shape for 225 male *Passerculus sandwichensis* (Savannah Sparrow).
- We explored relationships between territory size and shape versus male features (male age, breeding strategy, and number of neighbors), and population features (population density).
- Territory sizes were highly variable, ranging from 57 to 5,727 m<sup>2</sup> (0.0057–0.57 ha).
- Larger territories were held by males who were older, males with multiple mates, and males with more neighbors.
- Territories were larger during low-density years.
- Territory shapes were also variable, and males with more neighbors had more oddly shaped territories.
- We conclude that territory size and shape are dynamic features influenced by diverse factors.

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## Efectos de la edad, la estrategia reproductiva, la densidad poblacional y el número de vecinos en el tamaño y la forma del territorio en *Passerculus sandwichensis*

### RESUMEN

El tamaño y la forma del territorio de reproducción de un animal son características dinámicas influenciadas por múltiples factores intrínsecos y extrínsecos y pueden tener importantes implicaciones para la supervivencia y la reproducción. Los estudios cuantitativos de la variación en estas características territoriales pueden generar conocimientos más profundos sobre la ecología y el comportamiento animal. Exploramos el efecto de la edad, la estrategia reproductiva, la densidad poblacional y el número de vecinos en el tamaño y la forma de los territorios de reproducción en una población isleña de *Passerculus sandwichensis*. Nuestro set de datos consistió en 407 territorios de reproducción pertenecientes a 225 machos muestreados durante 11 años. Comparamos los tamaños de los territorios con la edad del macho poseedor del territorio, con la estrategia reproductiva del macho (monogamia vs. poliginia), con el número de aves en la población de estudio (densidad poblacional) y con el número de vecinos territoriales inmediatos (densidad local). Encontramos una variación sustancial en el tamaño del territorio, con territorios que varían en dos órdenes de magnitud de 57 a 5727 m<sup>2</sup> (0.0057–0.57 ha). Los machos mayores tenían territorios más grandes, los machos polígamos tenían territorios más grandes, los territorios eran más pequeños en años con mayor densidad poblacional y los territorios más grandes estaban asociados con más vecinos territoriales inmediatos. También encontramos una variación sustancial en la forma del territorio, desde territorios casi circulares hasta territorios de forma irregular. Los machos con más vecinos tenían territorios de forma irregular, pero la forma no variaba con la edad del macho, la estrategia reproductiva o la densidad poblacional. Para los machos que vivieron dos años o más, encontramos fuertes diferencias individuales en el tamaño del territorio a lo largo de los años, pero diferencias individuales más débiles en la forma del territorio, lo que sugiere que el tamaño tiene una alta repetibilidad mientras que la forma tiene una baja repetibilidad. Nuestro trabajo proporciona evidencia de que los territorios de las aves canoras son altamente dinámicos y que su tamaño y forma reflejan tanto factores intrínsecos (edad y número de parejas reproductivas) como factores extrínsecos (densidad poblacional y número de vecinos territoriales).

**Palabras clave:** defensa de recursos, forma del territorio, *Passerculus sandwichensis*, SIG, sistema de información geográfica, tamaño del vecindario, tamaño poblacional, territorialidad

### INTRODUCTION

Given that territories allow for the acquisition of resources (Nice 1941), mating, and rearing of young (Brown 1964), and concealment from predators (Tinbergen 1957), the size and shape of an animal's territory can have important implications for animal survival and reproduction. Many migratory songbirds establish territories upon arrival to the breeding grounds and may invest significant time and energy in defending them from conspecific neighbors. In most of these species, males arrive first on the breeding grounds and typically establish territories prior to female arrival (Brown 1964). Males that successfully defend larger territories are more attractive to females (Potter 1972, Reid and Weatherhead 1990) and have greater reproductive success (Krebs 1971, Best 1977, Peterson and Best 1987, Evans 1996, Both and Visser 2008, Flockhart et al. 2016). By documenting the factors that influence territory size and shape, we can develop a better understanding of animal fitness.

Territory size may vary with a variety of features related to the individual defending the territory. In birds, for example, larger territories are associated with males that are heavier (Petrie 1984, Adams 2001), larger (Price 1984, Duca et al. 2006), and more aggressive (Watson and Miller 1971). Older males generally defend larger territories, possibly due to the experience they gain over successive breeding seasons (Reid 1988, Ralph et al. 1971, Smith and Moore 2005) or because of age-related differences in body size or hormones (Reid 1988, Cavé et al. 1989). Variation in territory size may also reflect relative differences between males and their neighbors. In *Fulica americana* (American Coot), for example, males occupy larger territories if they are older and larger bodied than their neighbors (Cavé et al. 1989). The territorial animal's breeding strategy may also influence territory size (McLaren 1972). Under the resource defense polygyny model, polygyny is understood to be associated with larger territories and territories with more resources (Emlen and Oring 1977). Empirical studies support this idea: in *Lagopus*

(Willow Ptarmigan) and *Vanellus vanellus* (Northern Lapwings), for example, males that breed polygynously defend larger territories than males that breed monogamously (Hannon and Dobush 1997, Parish and Coulson 1998).

In addition to intrinsic factors, territory size may also be influenced by extrinsic factors, such as conspecific density (Nice 1941). At higher population densities, competition increases between individuals, resulting in decreased resources available per capita (Brown 1964). In response to increased population densities, several species of bird defend smaller territories, including, for example, *Cardellina canadensis* (Canada Warbler, Flockhart et al. 2016), *Parus major* (Great Tit; Krebs 1971); and three antbirds—*Thamnophilus caerulescens*, *Dysithamnus mentalis*, and *Pyriglena leucoptera* (Duca et al. 2006). A similar phenomenon exists at a neighborhood scale: territory size is smaller when an animal's territory is surrounded by more neighbors, including, for example, among *Passerculus sandwichensis princeps* (Ipswich Sparrows; Reid and Weatherhead 1990) and *Formicivora serrana* (Serra Antwren; Chaves et al. 2019). Removal experiments further confirm that the number of neighbors influences territory size at a local scale (Adams 2001); in several species, territories expand when neighbors are removed, including in *P. major* (Krebs 1971) and *L. lagopus* (Hannon 1983). Investigating the effects of population and local density, as well as intrinsic male features such as male age and breeding strategy, will deepen our knowledge of the factors influencing territory size.

Breeding territories vary not only in size but also shape. Territory shape may reflect the influence of habitat features (Adams 2001). *Todiramphus gambieri* (Tuamotu Kingfisher), for example, defend fewer circular territories within slender habitat patches (Kesler 2012). In the case of *Paroaria gularis* (Red-capped Cardinals), birds defend small sections of shoreline of the opposite sides of a narrow waterbody rather than one long section on a single shoreline (Eason 1992). Territory shape may also be influenced by population density. At high-population densities in homogenous environments, territories

tend to converge on circular or hexagonal shapes, although with variation in shape which is thought to reflect variation in nest placement, movement costs, and fighting abilities (Adams 2001, Maynard Smith, 1974). In *Sylvia undata* (Dartford Warblers), for example, territory roundness varies positively with the size of the territory and the density of the population (Pons et al. 2008). Variation in territory shape is poorly studied relative to territory size, making it an important area for further exploration.

In this study, we quantify the territory size and shape of *Passerculus sandwichensis* (Savannah Sparrow) on Kent Island, New Brunswick, Canada and examine how both size and shape vary with male age, breeding strategy, population density, and number of neighbors (local density). Given prior mechanisms and evidence outlined above, we predicted that territory size would show a positive association with age, that territories would be larger when males bred polygynously versus monogamously, and that territory size would show a negative relationship with population density and local density. Given that territory shape is poorly studied compared to territory size (Adams 2001), rather than testing specific predictions, we examined variation in territory shape from an exploratory perspective, investigating relationships between territory shape and male age, breeding strategy, population density, and local density. Our goal was to better understand variation in the size and shape of breeding territories in a migratory temperate songbird using a multi-year dataset of individually marked birds that were closely observed over the entire breeding period.

## METHODS

### Study Species and Re-sighting Locations

*Passerculus sandwichensis* are migratory songbirds that inhabit grasslands throughout North America (Wheelwright and Rising 2020). Our study population breeds on a 10-ha plot located on Kent Island, in the Bay of Fundy, New Brunswick, Canada (44.58254°N, 66.75604°W), where birds have been individually marked and studied since 1987 (Woodworth et al. 2017, Burant et al. 2021). Our study area was subdivided into 50 × 50 m squares via mowed paths, with grid markers denoting each square. The mowed paths were established in 1987 to facilitate researchers' movements through the grassland habitat without disturbing birds' nests. These paths have been maintained annually in the same positions and our observations suggest that the gridlines do not impact the sparrows' territorial behavior. The meadows of Kent Island provide *P. sandwichensis* with suitable nesting sites (Mitchell et al. 2012) and males defend abutting and contiguous breeding territories from conspecific rivals by engaging in singing bouts, fights, and chases (Potter 1972, Thomas et al. 2021). The breeding population occupies a homogenous habitat made up of *Vaccinium angustifolium* (blueberry), *Chamaenerion angustifolium* (fireweed), *Solidago rusa* (goldenrod), *Rubus idaeus* (raspberry), and several species of grasses (Dobney et al. 2023). Our analyses focus on variation in territory size and shape, rather than variation in territory quality.

Male *P. sandwichensis* arrive first from migration and establish breeding territories in late April and early May; females arrive from migration several weeks later in mid-May and nesting begins soon thereafter (Woodworth et al.

2016). *Passerculus sandwichensis* spend the majority of the breeding period on their territory, although they often fly off territory to the inter-tidal zone or the forest tree line to forage, and males will intrude onto other birds' territories to seek extra-pair copulations (Wheelwright and Rising 2020). In these circumstances when males are off their territory, they do not sing or display other territorial behavior (D.R.N., D.J.M. personal observation). Most male *P. sandwichensis* form socially monogamous pair bonds, but between 15% and 43% of males are polygynous (multiple females nesting on the same territory) in any given year (Wheelwright et al. 1992) and rates of extrapair paternity are relatively high (70% of adults in our study population produce extrapair offspring and more than half the eggs in a socially monogamous male's nest may be the genetic offspring of another male; Freeman-Gallant 1997, Freeman-Gallant et al. 2006).

Each year, we captured all previously unmarked adults (birds who were typically second-year birds) using mist nets and attached a unique combination of 4 leg bands (2 on each leg): 1 USGS aluminum leg band and 3 colored leg bands. We found the nest of every female within the study area and, on day 7, we banded the nestlings using a single aluminum band on one leg and a single, colored band on the opposite leg. If a formerly banded nestling returned to breed the following year, it was re-captured and given two additional colored leg bands, forming a unique combination. Individuals in the study population show a high degree of site philopatry, where nestlings typically return to establish territories within 200 m of their natal site and adults disperse an average of 40 m between successive breeding seasons (Wheelwright and Mauck 1998, Hensel et al. 2022). Among birds that return to breed in their second year, longevity ranges from 1.5 to 8 years (Wheelwright and Rising 2020).

To estimate territory size, we compiled a sample of locations over the breeding season from each uniquely marked breeding male. Each May and June, our team of field researchers documented the space use of males within the study area on a daily basis by re-sighting leg bands. Daily field observations of territory boundaries were recorded on paper maps, guided primarily by observations of male behavior, including frequented areas, singing perches, and nest locations (Woodworth et al. 2017). Positions of birds and their territory boundaries were made with reference to grid points (spacing: 50 × 50 m), trees, bushes, and positions of numbered nest boxes for *Tachycineta bicolor* (Tree Swallow). Singing perches were of special interest because males sing solely within the bounds of their territory.

Over the period of 2011–2022, field mapping techniques were taught to each year's team of 2–4 field researchers by the same principal investigator (D.R.N.) and the same uniform-scale base maps were used throughout this period, ensuring consistency in the field mapping protocols. Each member of the field team used a new blank map to record territorial positions each day, documenting the position of banded animals relative to key landmarks on the study site. We estimate that re-sighting locations were accurate to within 5 m. Over the course of the breeding season, each male was re-sighted at least 20 times on different days, providing a robust dataset for estimating territory boundaries. Once every 2–3 weeks, the mapping locations were used to develop “summary maps” of territory boundaries based on the positions shown in the

daily territory maps. These summary maps were regularly updated throughout the field season, refining and incorporating any small changes in territory boundaries. We used the “final” summary map to calculate territory size and shape in the current investigation. Importantly, we have no reason to expect any systematic bias in territory mapping in relation to any of the independent variables that we tested: male age, breeding strategy, population density, or local density. Indeed, we mapped territories before we had the idea to conduct the current investigation and our goal at the time that we created the maps was simply to describe the space occupied by each territorial male so that they could be found by our field team.

### Territory Quantification and Calculations

We used ArcGIS Pro (ver. 3.0) to georeference and digitize summary maps of male Savannah Sparrow territories from 2011 to 2022. No data were collected in 2020 due to the Covid-19 pandemic. We created 11 feature layers reflecting the 11 years of field data. We projected each layer of digitized territories into the NAD83 New Brunswick Stereographic projection, the standard current survey projection of New Brunswick (Surveys Act, RSNB 2011, c 226, <https://canlii.ca/t/52j8h>). We saved all territory layers to a single geodatabase, identified by the year and the color-band combination of the territorial male. Many males were present in multiple years, and we accounted for this repeated sampling in our analyses (see Statistical Analyses below).

To quantify the size and shape of each territory, we performed geometric calculations to obtain the following territory response variables: area, perimeter, and shape. We calculated territory area (m<sup>2</sup>) using the *Calculate Geometry (Area)* function in ArcGIS Pro. We calculated territory perimeter (m) using the *Calculate Geometry (Perimeter Length)* function in ArcGIS Pro. We computed territory shape using the *Compactness* equation in ArcGIS Pro, which describes territory shape relative to a circle ( $\frac{4\pi \times \text{area}}{(\text{perimeter})^2}$ ) with values ranging from 0 to 1. Territories with higher values of compactness are more circular (i.e., the highest possible compactness score is 1.0 for a perfectly circular territory), whereas territories with smaller values of compactness indicate more irregularly-shaped territories.

### Male Age

For males that were born in the study population and returned to breed as adults, we recorded their birth year as the year they were banded as nestlings. Birds that were not banded as nestlings were identified, in the hand, as either “second-year” or “after-second-year” based on their plumage characteristics (Pyle 1997). Most unbanded birds that we captured as adults in spring were second-year birds ( $n = 214$  birds including males and females), and we estimated their birth year as the year before they were first banded. Unbanded adults captured in spring were rarely determined to be after-second year birds, except in 2021, given that pandemic restrictions prevented us from conducting field work in 2020. For these birds, we used the plumage features to differentiate second-year and after-second-year birds. In our dataset, we categorized male age into 4 bins (1 year, 2 years, 3 years, or 4 years, and older) and treated age as an ordinal variable.

### Monogamy versus Polygyny

To determine whether males were socially monogamous (one social partner) or polygynous (multiple social partners), we

noted how many uniquely banded females nested within each male’s territory. We also noted whether each male was observed to associate regularly with more than one female, regularly copulate with more than one female, and exhibit mate-guarding behavior with more than one female. We also noted the number of females’ nests at which he was observed feeding nestlings. Generally, all of these criteria resulted in the same assignment of monogamous or polygynous for a male, but in cases where there was disagreement, which occurred rarely, we relied on observations of a male repeatedly feeding nestlings at two females’ nests. We recorded a male as polygynous if he paired with two females with overlapping nesting periods (i.e., simultaneous polygyny, not sequential polygyny). If a male associated with only one female at a time, he was recorded as monogamous. In any cases where the presence of a second female was uncertain, we excluded that territory from our comparison of monogamous versus polygynous territories. This gave rise to a dataset comprising 419 territories associated with 230 different males over the 11-year study where we were confident in our assignment of a monogamous versus polygynous breeding strategy.

### Population Density

For each year, we estimated population density as the total number of males that defended territories within the 10-ha study area (Woodworth et al. 2017). Given that the spatial extent of the study area remained consistent across this period, the total number of males served as a measure of density. We note that an individual territory is typically occupied by two birds (the breeding male and female), and that some territories are occupied by polygynous groups (one breeding male and two breeding females). Consequently, the number of territories was not an exact measurement of population density but it was a compelling proxy of population density.

### Local Density

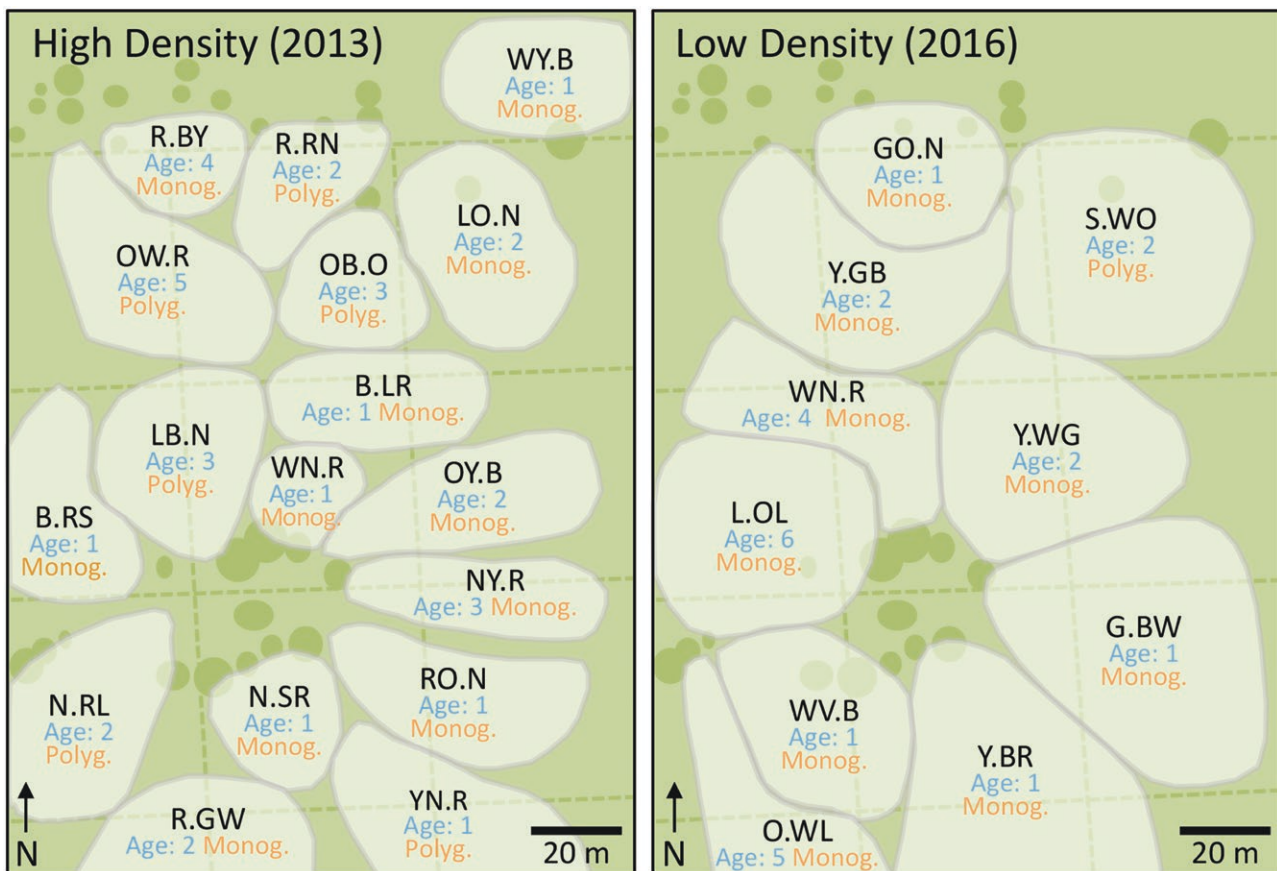
We calculated local density as the number of male territorial neighbors for each focal territory, using the spatial join tool in ArcGIS Pro. We defined a “neighbor” as any territory found within 10 m of the edge of any given focal territory. We chose a 10-m distance to include adjacent territories with which the resident male of the focal territory would have regular interactions during territory establishment. When we experimented with radii > 10 m, we found that this included territories that were not immediate neighbors. We applied this criterion through the *minimum distance* parameter in ArcGIS Pro, returning the number of territories found within 10 m of each territory. The tool appended these counts to the territory attribute table in ArcGIS Pro. We verified the accuracy of the number of neighbor calculations by manually counting all territories within a 10 m radius of each focal territory and confirmed that the GIS approach yielded reasonable values.

The first author (S.P.S.S.) calculated all territory size and shape measurements prior to accessing male age data, breeding strategy data, or density data. Therefore, our assessment of territory size and shape was not influenced by any preconceived ideas about male age, breeding strategy, or density.

### Statistical Analyses

We calculated territory size for 407 territories, representing 225 unique Savannah Sparrow males, sampled over 11





**FIGURE 1.** Maps of breeding territories of *Passerculus sandwichensis* on Kent Island, New Brunswick, Canada during the highest (left) and lowest (right) population density years of the study. Only a portion of the 10-ha study site is shown with dashed lines outlining each 50 × 50 m grid. Each territory is identified by the letters corresponding to each male's colored leg bands, followed by the age of the male and his breeding strategy (monogamous or polygynous).

breeding seasons, where we were confident in our assignment of male age and breeding strategy. We used principal components analysis (PCA) to summarize our 3 measurements of the territories (area, perimeter, and compactness). Principal components analysis yielded one principal component with an eigenvalue greater than 1 (PC1; eigenvalue: 2.0) which had strong positive loading from both territory area (eigenvector: 0.65) and territory perimeter (eigenvector: 0.70). Hereafter, we refer to this principal component as “territory size,” where large PC1 values reflect territories with larger areas and bigger perimeters. The second principal component (PC2) had an eigenvalue of 0.97 with strong loading only from compactness (eigenvector: 0.92); instead of reporting this principal component we chose to use the original variable, compactness, in our analyses. We refer to this variable as “territory shape,” noting that the primary source of variation in shape was territories that varied from circular to an irregular amoeboid shape (Figure 1).

We ran 2 mixed-effects models, one for territory size (PC1) as the dependent variable and one for compactness as the dependent variable; both models included male age, breeding strategy, population density, and number of neighbors as independent variables with male identity and year as random effects. All analyses were conducted using the R statistical environment (v. 4.2.3; R Core Team 2023).

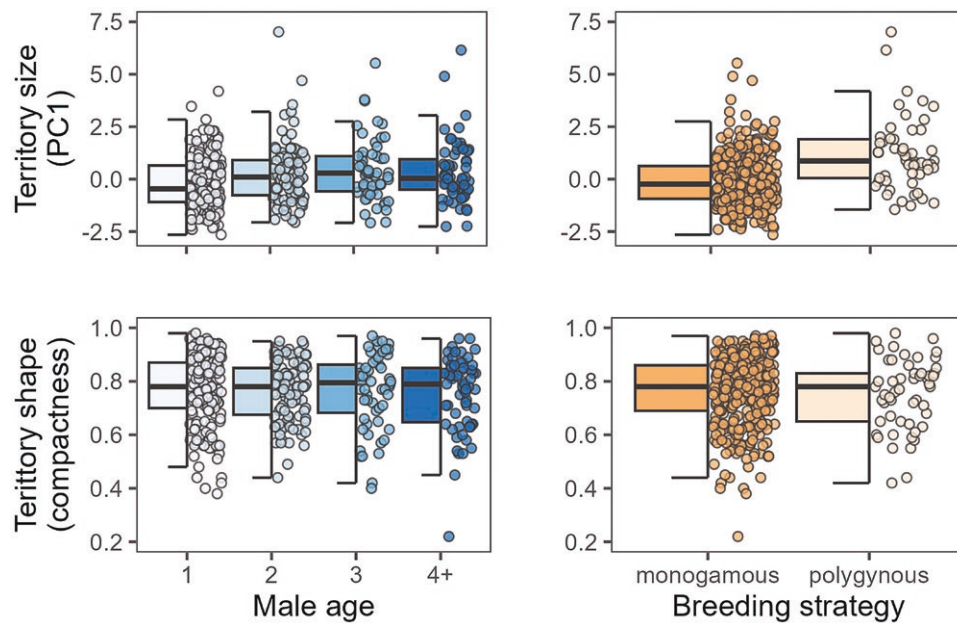
## RESULTS

Over the 11-year study period, *P. sandwichensis* breeding territories showed substantial variation in size, both within and across years. Across all years, territory area ranged from 57 to 5727 m<sup>2</sup> (0.006 to 0.57 ha) with a mean of 1,563 m<sup>2</sup> (0.16 ha). Territory perimeter ranged from 27 to 342 m with a mean of 157 m. Within a year, the largest difference in territory area was 1,429 m<sup>2</sup> (in 2011 the largest territory was 2,522 m<sup>2</sup> and the smallest was 1,093 m<sup>2</sup>), and the largest difference in territory perimeter was 203 m (in 2022 the largest territory was 342 m and the smallest was 139 m). There was also substantial variation in territory shape: compactness (bounded by 0 and 1) varied from 0.98 (i.e., a nearly circular territory) to 0.22 (i.e., a territory with an irregular, amoeboid shape; Figure 1). Across 407 nests where we could confidently determine breeding strategy, 87% of males were socially monogamous and 13% of males were polygynous.

*Passerculus sandwichensis* territory size varied with male age, breeding strategy, population density, and number of neighbors (Table 1). Territories were smallest for males in their first breeding season (average area: 1,443 m<sup>2</sup>; average perimeter: 150 m) and largest for males in their third breeding season (average area: 1,722 m<sup>2</sup>; average perimeter 168 m; Figure 2), with males in their second and fourth breeding

**TABLE 1.** Details of 2 linear mixed-effect models explaining variation in the size and shape of territories of *Passerculus sandwichensis*. Fixed effects include male age (1, 2, 3, or 4+ years), breeding strategy (monogamy versus polygyny), population density, and local density ( $n = 407$  measured territories from 225 color-banded males over 11 years); random effects include year and male identity (some males were sampled repeatedly across years).

	Territory size (PC1)					Territory shape (compactness)				
	Estimate	SE	df	<i>t</i>	<i>P</i>	Estimate	SE	df	<i>t</i>	<i>P</i>
<b>Fixed effects</b>										
(intercept)	2.63	0.74	399	3.57	<0.001	0.84	0.07	399	11.36	<0.001
Male age	0.16	0.05	399	3.16	0.002	0	0.01	399	-0.76	0.45
Breeding strategy	1.13	0.16	399	6.86	<0.001	-0.02	0.02	399	-1	0.318
Population density	-0.07	0.02	399	-4.6	<0.001	0	0	399	0.25	0.802
Number of neighbors	0.08	0.04	399	2.05	0.041	-0.02	0	399	-4.63	<0.001
<b>Random effects/<math>R^2</math></b>										
Residual	1.008					0.012				
Variance	0.133 male, 0.203 year					0.002 male, 0.002 year				
Marginal $R^2$ /conditional $R^2$	0.33/0.50					0.05/0.27				



**FIGURE 2.** Male age (left) and male breeding strategy (right) versus territory size (top) and shape (bottom) in *Passerculus sandwichensis*. Territory size is a principal component score, with strong loading from both territory area and territory perimeter, where high scores indicate a large territory. Territory shape is measured as compactness, where higher scores indicate more circular territories and lower scores indicate more irregular territories. Older males had larger territories than younger males (top left). Polygynous birds had larger territories (top right). There was no evidence of a relationship between male age and territory shape (bottom left) or male breeding strategy and territory shape (bottom right).

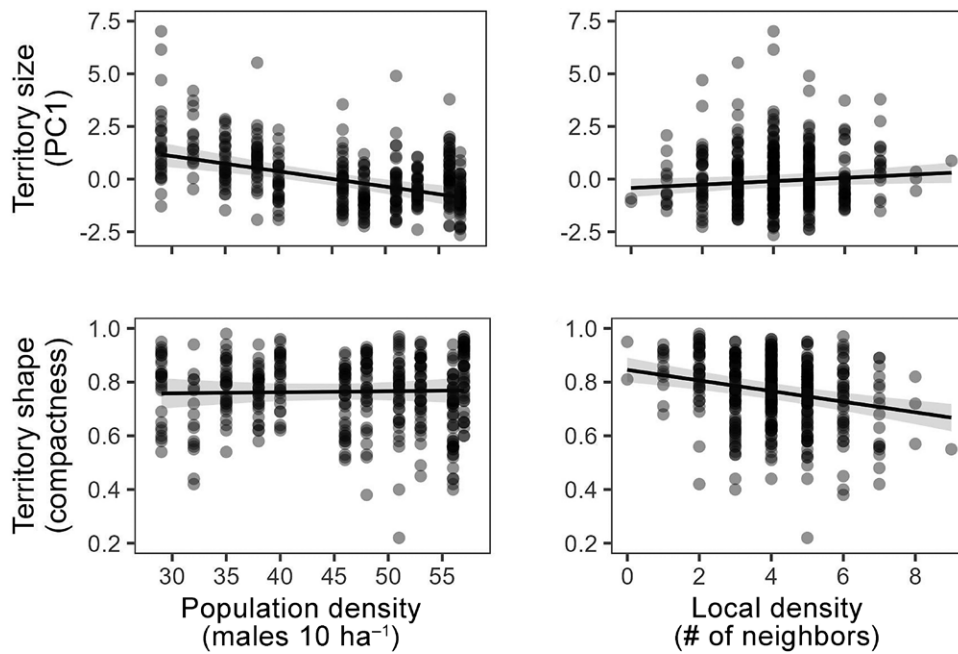
seasons defending territories of intermediate size, on average. Territories of polygynous males were ~50% larger by area and 26% larger by perimeter (average area: 2,264 m<sup>2</sup>; average perimeter: 191 m) compared to monogamous males (average area: 1,499 m<sup>2</sup>; average perimeter: 155 m). In the year with the lowest population density, territories were more than twice as large by area, and more than 50% larger by perimeter (2016: average area: 2,613 m<sup>2</sup>; average perimeter: 202 m; density: 29 males per 10 ha) compared to the highest density year (2013: average area: 1,174 m<sup>2</sup>; average perimeter: 132 m; density: 57 males per 10 ha). Finally, territory size varied with local density in the opposite direction to our prediction: males with more immediate territorial neighbors had larger territories (Figure 3). For example, the territories of males with 7 territorial neighbors were larger (average area: 1,655

m<sup>2</sup>; average perimeter: 153 m) than the territories of males with only one territorial neighbor (average area: 1,408 m<sup>2</sup>; average perimeter: 142 m).

Territory shape, in contrast, showed no relationship with male age (Table 1; Figure 2), breeding strategy (Table 1; Figure 2), or population density (Table 1; Figure 3). Territory shape, however, varied with local density (Table 1): males with more neighbors had territories that were more irregular in shape (Figure 3).

## DISCUSSION

We examined how variation in both territory size and territory shape are related to male age, breeding strategy, population density, and local density in *P. sandwichensis* over a span



**FIGURE 3.** Population density (left) and local density (right) versus territory size (top) and shape (bottom) of male *Passerculus sandwichensis*. Territory size is a principal component score, with strong loading from both territory area and territory perimeter, where high scores indicate a large territory. Territory shape is measured as compactness, where higher scores indicate more circular territories, and lower scores indicate more irregular territories. Territories were smaller in years with high population density (top left). No relationship was found between population density and territory shape (bottom left). Territory showed a positive relationship with local density (top right). Territories were more circular when there was low local density (i.e., fewer territorial neighbors; bottom right). Raw data are shown as well as the line of fit from the general linear model with a 95% confidence band shown in grey.

of 11 breeding seasons. Our results suggest that males held larger territories if they were older, polygynous, and bred in years of low population density. Contrary to our prediction, we also found that males with larger territories had more immediate neighbors (higher local density). We did not find any relationship between the shape of territories and male age, breeding strategy, or population density. Interestingly, we found that territory shape was positively related to local density: males with fewer neighbors had more circular territories whereas males with more neighbors had irregularly shaped territories.

While our finding of a positive relationship between male age and territory size is similar to studies on a number of other species, including *Fulica atra* (Eurasian Coot; Cavé et al. 1989), *Larus glaucescens* (Glaucous-winged Gull; Reid 1988), *P. major* (Duca et al. 2006, Both and Visser 2008), and *C. canadensis* (Flockhart et al. 2016), the specific mechanism by which older birds obtain and defend larger territories than younger birds remains unclear. Given their experience arising from previous reproductive seasons, one possibility is that older males may be better skilled at defending and maintaining territories (Ralph and Pearson 1971). Unfortunately, we have no data to support or refute this hypothesis, although future investigations could feasibly explore territorial behavior of males of different age, possibly by following the approach used by Thomas et al. (2021) involving acoustic analysis of aggressive interactions. Another possibility is that older males returning to a previously defended area place a higher value on that area, and, therefore, exhibit stronger territory defense behaviors (i.e., the value asymmetry hypothesis; Beletsky and Orians 1987). Given that adults in our study site typically occupy the same area from year to year (mean breeding

dispersal distance is 40 m; Wheelwright and Mauck 1998, Hensel et al. 2022), it seems likely that strong site fidelity could contribute to differences in territory size between age classes. Interestingly, in migratory birds, overwintering latitude and timing of spring migration could be a logical mechanism by which older males can establish higher quality and larger territories because they tend to arrive earlier than younger males (Lozano et al. 1995, Potti 1998, Cadahía et al. 2017; but see Petrie 1984). However, there is no evidence for a difference in arrival time between age classes in Kent Island *P. sandwichensis* (Woodworth et al. 2016). This suggests that the mechanisms driving age-related differences in territory size play out once birds have begun to interact on the breeding grounds.

In addition to the effects of male age, we also found that when males bred polygynously, which occurred in 13% of the birds in this study, territories were almost 1.5 times larger than when males bred monogamously. However, rather than breeding strategy influencing territory size, it seems more likely that, following the polygyny threshold model (Orians 1969), territory size influences whether or not males are able to acquire a second mate. Several studies have shown that females prefer males with larger territories, including *Geospiza fortis* (Darwin's Finch; Price 1984) and closely-related *P. sandwichensis princeps* (Reid and Weatherhead 1990). In Kent Island *P. sandwichensis*, males tend to pair with secondary females well into the breeding season, after territorial boundaries have largely been established and primary females have started nesting. Males with larger territories may be more attractive to secondary females, either because the territory is of higher quality or because there is more space for secondary females to establish nests, as well as feed young after



they have left the nest. When there are two nesting females on a single territory, the secondary female typically builds a nest on the other side of the territory (D.R.N. personal observation), suggesting that she may be aware of the primary female and is attempting to maximize the distance between them. The relationship between polygyny and territory size does not hold true in all species such as *Protonotaria citrea* (Prothonotary Warbler; Petit 1991), suggesting that this is a worthwhile area for further research.

In addition to age and breeding strategy, we also found a strong, negative relationship between population density and territory size, similar to other species such as *Spizella breweri* (Brewer's Sparrow; Wiens 1985); *C. canadensis* (Flockhart et al. 2016); *Parus major* (Krebs 1971); and *T. caerulescens*, *D. mentalis*, and *P. leucoptera* (Duca et al. 2006). Territories are traditionally thought of as fixed areas that play an important role in limiting and regulating population size through despotic processes (Fretwell and Lucas 1969, Rodenhouse et al. 1997). While territories may play an important role in these processes, it is also likely that many species, such as *P. sandwichensis*, constrict territory size at high-population densities (Huxley 1934, as cited in Fretwell and Lucas 1969), which may act to buffer negative effects of density. Given that territory size is a balance between the benefits of resource acquisition and the costs of defense, there is presumably a species-dependent threshold at which maintaining a certain territory size is no longer beneficial (Hixon et al. 1983). We do not know the lower threshold for *P. sandwichensis*, but our measurements reveal that territories can reach several orders of magnitude less than their average size. Understanding variation in territory size within a population, as well as the fitness effects of occupying different sized territories, will be an important component of understanding population regulation over the long-term. It is possible that models that fail to account for effects of elasticity in territory size could overestimate the role of negative density-dependence in regulating populations.

Interestingly, in contrast to population density, we found the opposite effect for local density: males with larger territories had more neighbors. This result makes logical sense; as the size of a territory increases it is more likely that it will come into contact with the territories of more neighbors. This relationship appears to be driven by larger territories in years with high population density. In these years, males with larger territories have up to 8 adjacent neighbors. This is perhaps a cautionary result, suggesting that scale is important when examining the effects of density on territory size, given that different patterns may be evident for local density versus population density.

In terms of territory shape, we found that males with many immediate territorial neighbors had more irregularly shaped territories, whereas males with fewer immediate territorial neighbors had more circular territories. This pattern may reflect the idiosyncratic nature of territory defense in a migratory songbird, where males arrive at different times from migration. Upon arrival males begin to carve out territories through interactions with neighboring males who have already arrived, and parts of their territories may be contested as new males arrive. A circular territory may be the most optimal shape for animals with continuously distributed resources, with the greatest ratio of territory area to territory perimeter, but this shape may be manifested only in situations with low local density. At higher local density,

deviation from circular territories is expected, possibly toward a hexagonal shape when density becomes very high (Adams 2001). A study of *S. undata* (Dartford Warbler) showed that territory roundness increased with territory size, reflecting the energetic constraints of defending a larger area, and also at higher densities of conspecifics, reflecting the influence of territorial neighbors (Pons et al. 2008). Our study shows deviation from compact territories not with population density, but with the number of local neighbors. Male age, breeding strategy, and population density showed no relationship with territory shape in any of our analyses, suggesting that it is interactions between local neighbors, not broader population level features or features of individual territorial males, that affect territory shape in *P. sandwichensis*.

Many males were sampled repeatedly across years and a comparison of the random effects in our statistical models yields an interesting insight into territory size and territory shape. The variance estimate for the random effect of male identity in the model of territory size was several orders of magnitude higher than the same estimate in the model of territory shape (Table 1). This suggests that there were stronger consistent individual differences in territory size across years for a given male, whereas there were much weaker individual differences in territory shape for males across years (Table 1). Territory size is likely associated with male quality and, therefore, should be more predictable across individuals and through an individual's lifetime; territory shape, by contrast, is likely more idiosyncratic, associated with the particular territorial interactions and boundary compromises that occur while a male establishes his territory through his interactions with neighbors. Our model results further support this idea: male age, which is associated with male quality in *P. sandwichensis*, predicts territory size but does not predict territory shape (Table 1).

In conclusion, our study reveals that territory size and shape are highly variable traits influenced by both individual-level and population-level parameters. Territory size is influenced by male age, breeding strategy, population density, and local density, and there are consistent individual differences in size across years. In contrast, territory shape is only influenced by local density, and there are weak individual differences in shape across breeding seasons. Although both territory size and shape appear to be influenced by density-dependent factors, they occur at different spatial scales (population vs. local) and, therefore, are likely driven by different mechanisms. While this study explicitly informs our understanding of *P. sandwichensis* breeding territories, it can arguably relate to a broader array of avian species that maintain territory boundaries. Our results highlight the importance of considering both intrinsic individual-level features and extrinsic neighbor-level and population-level features in studying territory size and shape.

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## Ethics statement

This research was approved by the University of Windsor Animal Care Committee. All bird banding was conducted by experienced bird banders with required permits from the Canadian Wildlife Service. We attempted to minimize stress during capture and handling by checking mist nets frequently (typically, nets were observed by the banders and birds were extracted as soon as they hit the net). We held the birds for the minimum amount of time possible (typically, less than 15 min) keeping them in a cloth bag until they were measured, banded, and released.

## Conflict of interest statement

The authors report and confirm that they have no conflict of interest in this work.

## Author contributions

S.P.S.S., D.R.N., and D.J.M. conceived the idea, design, and experiment. S.P.S.S., S.L.D., D.R.N., S.M.D., A.E.M.N., J.B.B., I.G.M., S.D.M., H.A.S., and D.J.M. collected data and conducted the research. S.P.S.S., S.L.D., D.R.N., S.M.D., J.B.B., I.G.M., S.D.M., H.A.S., and D.J.M. wrote the paper (or substantially edited the paper). S.P.S.S., D.R.N., and D.J.M. developed or designed methods. S.P.S.S., D.R.N., J.B.B., S.D.M., S.D.M., and D.J.M. analyzed the data. S.P.S.S., D.R.N., S.M.D., A.E.M.N., and D.J.M. contributed substantial materials, resources, or funding.

## Data availability

Analyses reported in this article can be reproduced using the data provided by [Suarez Sharma et al. \(2024\)](#).

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