



5-2023

Communication distance predicts territory size for an urban songbird

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Communication distance predicts territory size for an urban songbird

**A Thesis Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville**

**Ruth A. Simberloff
May 2023**

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ACKNOWLEDGEMENTS

Thank you to Jennifer Phillips, Graham Derryberry, Michael Mahoney, and, of course, Elizabeth Derryberry for all of your help with this work.

ABSTRACT

Many studies demonstrate that urban noise interferes with animal communication by masking acoustic signals such as birdsong, but the functional consequences of impaired communication are still not well understood. Although many bird species sing at higher amplitude in noise pollution, communication distance is still reduced in noisy urban soundscapes. Song is a long-distance signal that functions to attract a mate and defend a territory, so a reduction in communication distance could negatively influence a male's reproductive or competitive success. Reduced territorial success could manifest as more frequent territorial intrusions, reduced territory quality, or reduced territory size. We examined the relationship between communication distance and territory size in white-crowned sparrows (*Zonotrichia leucophrys*) across an urban-rural gradient in the San Francisco Bay Area in Spring 2021. We mapped the territories of male White-crowned sparrows and calculated territory size as the 75% utilization distribution using a kernel density estimator. We measured the amplitude of each male's songs as well as background and ambient noise levels on his territory, which we then used to calculate the communication distance of each song. We found the mean communication distance of each individual and assessed its relationship to territory size. the communication distance of a bird's songs significantly predict his territory size, such that birds with shorter communication distance tend to have smaller territories. This suggests that communication distance may influence the size of songbird territories. In keeping with this trend, urban birds had significantly smaller territories than rural birds. This finding strengthens our understanding of the link between communication and its fitness-related functions – an important frontier in the study of birdsong. It also underlines the potential complexity of the impacts of the anthropogenic soundscape upon animal behavior.

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PART ONE

INTRODUCTION

Literature review: birdsong and anthropogenic noise

Anthropogenic noise is a novel selective pressure facing animals in a world ever-more pervaded by manmade habitats and disturbances (Sih, 2013). Though noise affects many animal characteristics and behaviors (Kight & Swaddle, 2011; Swaddle et al., 2015), anthropogenic noise is especially disruptive to animals that rely on acoustic communication because it masks (i.e., limits detection of) acoustic signals (Brumm & Zollinger, 2013). A growing body of literature demonstrates that urban noise can interfere with animal communication (Cronin et al., 2022). However, the functional consequences of impaired communication are still not well understood (Slabbekoorn, 2013; Swaddle et al., 2015). Few studies do more than speculate about the functional implications of masked signals (Derryberry & Luther, 2021). Animal signals serve diverse and critical functions, from attracting a mate, to warning of nearby predators, to defending a breeding territory (Bradbury & Vehrencamp, 1998). These signal functions are critical to reproductive success and survival (Searcy & Nowicki, 2010). If noise reduces the distance at which a signal can be heard, it is reasonable to hypothesize that it also reduces the distance at which a signal can function (Naguib & Wiley, 2001). The bark of a dog, a cricket's chirp, a spoken word – all signals must be detected in order to elicit a behavioral response in a receiver. If the signal cannot be detected, then communication cannot occur. If noise reduces the communication distance of a signal, it may therefore also limit the range at which the signal can function.

Noise can reduce communication distance, the maximum distance from which a signal can be detected or discriminated by a conspecific receiver (Lohr et al., 2003). The ability of a receiver to detect or discriminate a signal depends, in part, on the signal-to-noise ratio (Brumm & Naguib, 2009). Background noise decreases the signal-to-noise ratio, and therefore reduces the communication distance of the signal (Brumm & Slabbekoorn, 2005). When animal signals must compete with high levels of anthropogenic noise pollution, the effect on communication distance can be substantial. For example, song communication distance nearly doubled when noise levels dropped during the 2020 COVID-19 lockdown for urban songbirds in heavily trafficked areas of San Francisco (Derryberry et al., 2020). This effect of noise on communication distance may be particularly relevant for long-distance signals, such as bird song.

Literature review: birdsong and territorial defense

Bird song has a growing number of recognized functions (Riebel et al., 2019), but one of the most evident and thoroughly documented functions of song is territorial defense (Catchpole & Slater, 2003). Males of most passerine species hold an individual territory during the breeding season, which they defend against conspecifics. Song is a critical component of passerine territory defense, and functions as a long-range “keep out” signal to neighbors and potential rivals. Evidence for this territorial function of song is plentiful. Observational studies note that birds start singing at the time of territory establishment (e.g., Catchpole, 1973), and sing most frequently when territory defense is most intense (e.g., Kramer & Lemon, 1983). Both natural and simulated territorial intrusions evoke changes in singing behavior, providing correlative evidence for the territorial function of song (e.g., Falls, 1981; Krebs et al., 1981).

Most convincing is evidence from experimental studies. Speaker occupation experiments remove the territorial male and replace him with a speaker broadcasting conspecific song. Territories occupied by a speaker broadcasting song experience fewer intrusions and remain vacant longer than control territories without a male or a speaker (Krebs, 1977; Falls, 1988; Nowicki et al., 1998). Similarly, in muting studies, when researchers surgically eliminate a territorial male's ability to produce song, muted males acquire territories later, experience more territorial intrusions, and are more likely to lose their territories than unmuted males (red-winged blackbird, Peek, 1972; Smith, 1976; Scott's seaside sparrow, McDonald, 1989). Muted males also experienced a reduction in territory area as neighbors encroached but recovered their original territory area when they regained their ability to sing (Smith, 1979). In short, ample evidence supports the importance of song for defense of a breeding territory.

Larger breeding territories may confer greater reproductive success. The most referenced explanation for territorial behavior is competition over limited space and resources (Kaufmann, 1983) – songbirds defend a territory in order to secure access to the food and/or nest sites required to breed successfully (Nice, 1941). Ample evidence supports a link between territory size and individual or reproductive fitness in birds, including findings that males on larger territories have higher survival (Both & Visser, 2000), higher rates of heterozygosity (Seddon et al., 2004), and fewer losses in paternity due to extra-pair fertilizations (Olsen et al., 2008). Offspring born on larger territories have been found to have higher survival, higher growth rates (Both & Visser, 2000), greater body mass, and higher long-term breeding success over the course of their lifetimes (Mumme et al., 2015). Therefore, any factor that might constrain territory size – such as reduced song communication distance – could impact reproductive success.

The factors influencing territory size have not been comprehensively described and are likely to be numerous and complex. Early considerations of territory size (e.g., Tinbergen, 1957) emphasized the primary role of individual territorial behavior in determining population density, and thus territory size. An alternate framework gained preeminence in the 1970s, based mainly on theoretical modeling, which centered resource density as the main determinant of territory size (e.g., Hixon, 1980). Abundant support exists for both viewpoints; some studies find that territories expand when resources are scarce, as predicted by the resource density framework (e.g., Stenger, 1958) while others find that territory size is insensitive to environmental variables and is likely governed by behavioral interactions (e.g. Krebs, 1971; reviewed in Adams, 2001). Individual characteristics that may influence an individual's ability to defend a territory (i.e., resource-holding potential) have also been found to correlate with territory size, providing further support for the importance of individual behavior. For example, older birds hold larger territories than younger birds across several species (Dhondt & Hublé, 1968; D. F. Mazerolle & Hobson, 2004; Ralph & Pearson, 1971). Similarly, individuals of larger size or better body condition tend to hold larger territories across several species (D. F. Mazerolle & Hobson, 2004; Pederson, 1984; Petrie, 1984). The anthropogenic landscape might influence territory size in either framework, either by altering resource availability or by altering behavioral interactions, for example through reduced signal range.

Aims and hypotheses

We investigated whether noise pollution impacts songbird territory size by reducing the effective range of birds' songs. We examined the relationship between communication distance and territory size in a common songbird, Nuttall's white-crowned sparrow (*Zonotricha leucophrys nuttalli*; NWCS), across a range of noise levels and habitat types in the San Francisco Bay Area, California, USA. We predicted that communication distance would decrease with increasing levels of background noise and that

territory size would vary with communication distance. Given this predicted relationship, we expected birds at urban sites with high noise levels to have smaller territories than birds at rural sites with low noise levels. We tested the effects of bird age and body condition, which may influence birds' ability to defend a territory irrespective of the role of song. We also investigated the relationship between background noise and territory size in case the urban acoustic environment impacts territory size independently from its effect on song. A relationship between communication distance and territory size would suggest that noise pollution can impact the behavioral ecology of animals reliant on acoustic territorial signals.

PART TWO

METHODS

Study system

This study was carried out in the spring of 2021 with territorial male Nuttall’s white-crowned sparrows (*Z. l. nuttali*; henceforth NWCS) in the San Francisco Bay Area. NWCS are a nonmigratory subspecies of white-crowned sparrow that occupies coastal scrub habitat in Central and Northern California. The white-crowned sparrow has long been used as a model organism in the study of animal communication – so much so that the bioacoustician Luis Baptista referred to it as the “white rat of ornithology” (Nelson 2004). NWCS are ideal for studying the impacts of urban noise upon bird communication because they are common year-round throughout both the city of San Francisco and the neighboring rural countryside of Point Reyes National Seashore.

We estimated territory size of 28 male NWCS across 4 locations: two urban areas in the city of San Francisco and two rural areas in Point Reyes National Seashore (Figure 1). Each site is home to a different cultural population of NWCS, characterized by discrete dialect differences in song traits (Derryberry et al., 2016). The two dialects recorded in San Francisco are known as San Francisco and Lake Merced (Luther & Baptista, 2010). The two dialects recorded in Point Reyes National Seashore are known as Clear and Drake (Baptista, 1975).

Study sites in Point Reyes National Seashore included both cattle rangeland and relatively intact coastal scrub habitat, whereas sites in San Francisco spanned developed urban parks, undeveloped or landscaped green spaces, and restored coastal scrub habitat. Each site spanned both locally high noise levels and locally low noise levels, with background noise stemming primarily from wind and surf at rural sites and from vehicular traffic at urban sites (Derryberry et al., 2016).

Individual identification

Individuals were sampled along preestablished transects designed to capture a representative range of local background noise levels (Berlow et al., 2021).

Territorial male NWCS were captured using mist nets and conspecific playback. Sex was confirmed by the presence of a cloacal protuberance or brood patch. We banded individuals with a numbered aluminum leg band and a unique combination of colored plastic leg bands to allow identification of individuals from a distance. Banding took place at least three days before the commencement of focal observations, to minimize the behavioral impacts of handling and band application.

Age

Previous studies of NWCS territories found age to predict territory size, with older males defending larger territories than second-year males (Ralph & Pearson, 1971). We therefore

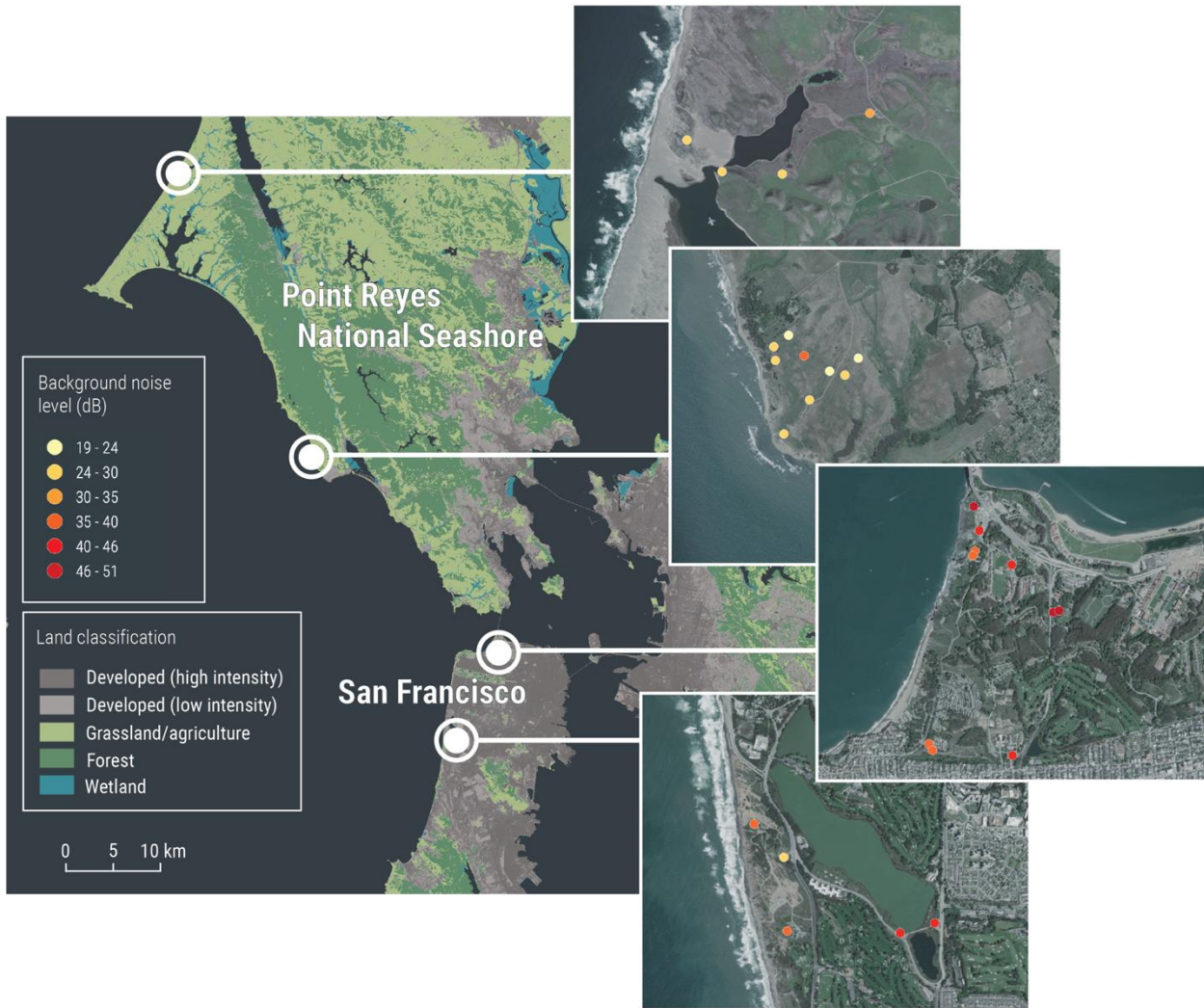


Figure 1. Map of study areas in the San Francisco Bay Area. Two rural sites were located in Point Reyes National Seashore, and two urban sites were located in the city of San Francisco. Inset maps show birds sampled at each site, colored by the average background noise level (LAF90) on each territory.

include bird age (second year or after second year) as a potential predictor variable in our analysis.

We estimated the age of each bird while it was in the hand using crown plumage. Second-year NWCS frequently retain some brown and tan feathers in their crown, while individuals after second year have fully black and white crowns (Pyle, 1997; Ralph & Pearson, 1971). We categorized males as “second year” (SY) if any brown at all was present in the crown, and “after second year” (ASY) if not.

Body condition

We measured the weight and wing length of each bird in order to estimate body condition. To calculate body condition, we used a scaled body mass index following Peig and Green (2009). This index is based on a regression of bird mass and bird wing length for all birds in the study.

Territory size

Territory size was measured between 15 March and 25 April in 2021. We selected this sampling period because it is after NWCS typically establish territories (Dewolfe et al., 1989) but before offspring are expected to fledge. Though Patterson and Petrinovich (1978) found that NWCS territories are very stable throughout the breeding season, we aimed to document territories of males at a similar reproductive stage to minimize potential differences in territorial behaviors during parental care.

We selected individuals for territory estimation based on responsiveness to playback during banding, which indicates territoriality, and on the individual’s continued presence at the same location at least 3 days after banding, which indicates site fidelity and provides further evidence of territory tenure. We selected territorial individuals at random locations along the banding transects at each site, and where possible we selected roughly equal numbers of SY and ASY territory holders.

Territories were estimated via observation of focal individuals. Observations were conducted according to a burst sampling protocol following Barg et al. (2005), in which we recorded the location of the focal male at short but regular time intervals (60 s) during 30-minute bursts to yield 30 observed locations per observation period. If observers lost sight of the focal individual (e.g., during an extra-territorial foray) they extended the focal observation period until either 30 locations were observed or a maximum of 40 minutes had elapsed since the beginning of the observation. Researchers conducted three “burst” observations of each bird, to yield a maximum of 90 observed locations per individual. Observations were separated by at least 40 hours and occurred at randomized times between 5:00 AM and 5:00 PM. Each bird underwent at least one focal observation before 10 AM (i.e. in the morning period of peak activity).

During focal observation periods, researchers identified the focal individual using his unique combination of colored leg bands. Two observers then followed the individual at a distance of at least 6 meters, which was sufficient to avoid disturbing the bird. One observer placed small flags at the bird’s location every 60 seconds while the other observer noted the bird’s position. If necessary, the observers waited for the bird to move a sufficient distance before placing the flag. The coordinates of each flag were collected with a handheld GPS unit (Garmin Rino 755t) to a precision of 4m.

Territory area was estimated using the kernel density utilization distribution – a probability distribution describing the likelihood that the bird is in any given location. In this analysis we considered territory

size to equal the area of the 75% utilization distribution (i.e., the area in which there is a 75% chance of recovering the individual; Figure 5). We thus defined the territory as the area in which the territorial male spends the bulk of his time, but this 75% threshold allows for fairly regular extraterritorial forays. Note that other kernel density thresholds were analyzed, and thresholds from 50-95% yield identical findings.

We calculated the smoothing parameter (kernel width; h) using the *ad hoc* method:

$$h = \sigma * n^{-1/6}$$

where

$$\sigma^2 = \frac{1}{2} * (var(x) + var(y))$$

We used the animal movement and home range analysis package *adehabitatHR* (Calenge & Fortmann-Roe, 2020) to calculate the kernel density utilization distributions.

To verify that we had collected sufficient location data to estimate territory area, we randomly resampled the set of recorded locations from each bird at different sample sizes and estimated territory area from each random sample. Most birds in this analysis had between 80 and 90 observed locations; from this data set, we sampled 100 random subsets of 10 locations, 20 locations, 30 locations, and so on until the full sample size was reached. If the number of sampled locations was insufficient, one would expect territory area to increase without bound as the number of sampled locations increased. However, we found that territory area reaches an asymptote before reaching the full sample size for all birds analyzed (Figure 4). For most individuals, roughly 50 observed locations sufficed to estimate territory area; this is consistent with the findings of Cooper et al. (2014) for American Redstart territories and indicates that we collected sufficient data to estimate NWCS territory areas accurately.

Territory noise level

We measured background noise at the approximate center of each territory following each focal observation, to yield three noise measurements from nonconsecutive days for each bird. We made noise measurements using a Model 831 Larson Davis sound level meter, omni-directional microphone and calibrated preamplifier with a windscreen to minimize wind noise. Following (Brumm, 2004), we recorded noise levels for one minute in each cardinal direction, with the sound level meter held vertically at chest height. The Larson Davis Model 831 sound level meter automatically calculates LAF90 (the maximum noise level experienced $\geq 90\%$ of the time; dB) for the length of the recording.

Background noise for each territory was calculated as the mean LAF90 of these three measurements.

Communication distance

We measured the amplitude of songs ($n = 260$ songs, median = 7 songs per bird) from each of the focal males between 28 April and 14 May 2021. Song amplitude was recorded from males actively singing spontaneous (i.e., unsolicited) song from an exposed perch. Measurements were made using the Model 831 Larson Davis sound level meter, which records sound pressure levels every 20ms. We included only

songs in which the bird was singing directly into the microphone and at the same height as the microphone and noted any changes in the bird’s position or head orientation that could affect the amplitude reading. We also identified segments of each amplitude recording that did not contain a song, which we used to measure background noise level as close in time as possible to the song. Recordists kept extensive notes on bird position during amplitude measurements, and only song segments in which the singer was oriented directly towards the microphone and was at the same height as the microphone were included in downstream analysis.

We calculated song amplitude and estimated communication distance following methods described in (Blickley & Patricelli, 2012; R. J. Dooling & Popper, 2007).

We measured the maximum energy level, Z-weighted with fast detection (LZF), per 1/3-octave frequency band for each song segment. From the “noise-only” segments we determined the average noise level per second for each frequency band that contained song. From each frequency band of the song segments, we then subtracted the amount of background noise calculated in that band. We extracted the largest LZF value per song (song peak LZF), noting the frequency band it occurred in and the LZ_{eq} for that band. Finally, we corrected for the distance between the recordist and the bird to determine the song peak LZF at 1 meter from the bird (Marten & Marler, 1977).

Our masking threshold was the greater of two values, either the absolute or the critical threshold. To determine the absolute threshold for each frequency band, we estimated an audibility curve (audiogram) for NWCS using previously published measurements of auditory brainstem responses of nine individual *Z. leucophrys* in response to a range of sound frequencies (500—7,000 Hz) in a quiet setting (Vélez et al., 2015). An audibility curve describes the minimum sound amplitude that an animal can perceive across its range of hearing. We modeled the audibility curve for NWCS with a nonlinear mixed-effects model fit by maximum likelihood using the function `nlme` in R, and we used this curve to model the ability of a receiver bird to perceive the song. To determine the critical threshold, we used the empirically determined masking function of the song sparrow (*Melospiza melodia*) (R. Dooling, 2002), a species closely related to white-crowned sparrows. The sum of the noise LZ_{eq} for a frequency band and the critical ratio (from the masking function) at that frequency is the critical threshold. We interpolated critical threshold values with a spline function. Finally, we used the masking threshold to calculate the detection distance:

$$Detection\ distance = 10^{\frac{song\ peak\ LZF - masking\ threshold - 3}{20}}$$

We calculated communication distance of each song as the distance from which at least 25% of the song could be detected (25% detection distance). We selected this measure because it is likely more biologically relevant than the maximum detection distance of a song, though we note that other detection distance thresholds were analyzed and yield identical findings.

We calculated the average communication distance for each bird by finding the mean communication distance across all recordings of his songs.

Statistical analysis

We calculated age ratios, median and range of territory noise levels (LAF90), mean communication distance, mean body condition, and median territory size for each of the four song populations examined.

We tested our expectation that communication distance will vary with background noise levels using a linear model.

We then employed model selection to investigate which of the four potential parameters (bird age, bird body condition, mean communication distance, and territory background noise level) are most likely to be informative predictor variables of territory area. We built 16 linear models of territory area as a function of the four parameters and selected the model that best fit the data using AICc (Akaike's Information Criterion corrected for small sample size) (Akaike, 1973). It is important to note that background noise level (LAF90) is not the same measure of noise level used in the calculation of communication distance, which relies on instantaneous noise measurements taken in the moment before the song production. Mean background noise level on territory and communication distance are not strongly colinear (Variance Inflation Factor < 2.5). Therefore, we included background noise level as a predictor independent of communication distance (citation for VIF/collinearity).

For each model, we inspected residual plots for non-normality and heteroscedasticity. We then conducted significance testing on the top-ranked model to evaluate the relationship between these predictor variables and territory area.

We then asked if urban populations had shorter communication distances and smaller territory sizes than rural populations using Welch's two sample t-tests. Data were square root transformed to meet model expectations.

We conducted all statistical analyses in R Studio (version 1.4.1717) using the packages AICcmodavg (M. J. Mazerolle, 2020) and nlme (Pinheiro & Bates, 2011).

Ethical note

This study complied with the with the standards of animal welfare established under United States law. All procedures were evaluated and approved by the University of Tennessee Institutional Animal Care and Use Committee (Protocol 2792). Researchers were permitted by the USGS (Federal Banding Permit 23900) and by the California Department of Fish and Wildlife (Scientific Collecting Permit S-202380004-20337-001). Local permissions were granted by the National Park Service (GOGA-2021-SCI-0025, PORE-2021-SCI-0013) and the San Francisco Recreation and Parks Department.

PART THREE

RESULTS

We collected data from 28 territorial NWCS across four song populations (Table 1). Territories in each population spanned a range of background noise levels depending on proximity to roads, shorelines, and windy cliffs. As expected, background noise levels were considerably higher in San Francisco than in Point Reyes National Seashore. We calculated communication distance from nearly 200 recorded songs (median = 7 songs/bird) and found, unsurprisingly, that urban birds had dramatically reduced communication distance compared to their rural counterparts.

Background noise reduces communication distance

As expected, average background noise level on a bird's territory significantly predicted the mean communication distance of his songs (linear model: communication distance ~ background noise level, $p < 0.0001$, adjusted $r^2 = 0.57$; Figure 6). Though birds experiencing higher background noise levels sing more loudly (Derryberry et al., 2017), this finding shows that increased amplitude does not compensate for the masking effect of background noise pollution. A NWCS song produced on a territory with an average background noise level of 40db (e.g., in an urban park near a busy road) is predicted to travel one third the distance of a song produced on a territory with an average background noise level of 20db (e.g., a remote inland valley of a national park).

Communication distance predicts territory area

We used AICc model selection to determine which of the four parameters to retain in the model of best fit. The highest ranked model included only bird age and communication distance as predictor variables. We report the top model, models within 2 Δ AICc, and the null model (Table 2; all models reported in Table 4).

In the top-ranked model, communication distance significantly predicts territory size ($p < 0.0003$, partial $r^2 = 0.40$, $\beta = 66.0$). Put simply, birds with greater communication distance have larger territories. In this study, a doubling of communication distance corresponded to a roughly 60% increase in territory area (Figure 2).

Bird age, though retained in the top-ranked model, does not significantly predict territory size ($p = 0.1$, partial $r^2 = 0.07$). There is a nonsignificant trend for older males (3+ years old) to hold larger territories than second-year males.

It bears noting that there is no meaningful difference between the top-ranked model and the next best model, which includes only communication distance as a predictor of territory area. The Δ AICc between these two models is only 0.38, and the difference in model probabilities (0.31 vs 0.26) is negligible. The inclusion of bird age as a predictor in the top ranked model lacks strong support (Burnham & Anderson 2002).

Table 1. Summary of data collected across four populations of NWCS

Song population	N	SY : ASY	Median territory noise level (LAF90)	Range of territory noise levels (max – min)	Median communication distance	Mean body condition	Median territory size
San Francisco	10	5:5	41.5	13.5	16.1	17.0	1595
Lake Merced	5	2:3	39.9	6.8	25.9	17.5	3038
Clear	9	3:6	26.0	10.6	77.3	18.0	5699
Drake	4	1:3	28.7	3.2	52.6	17.9	2379

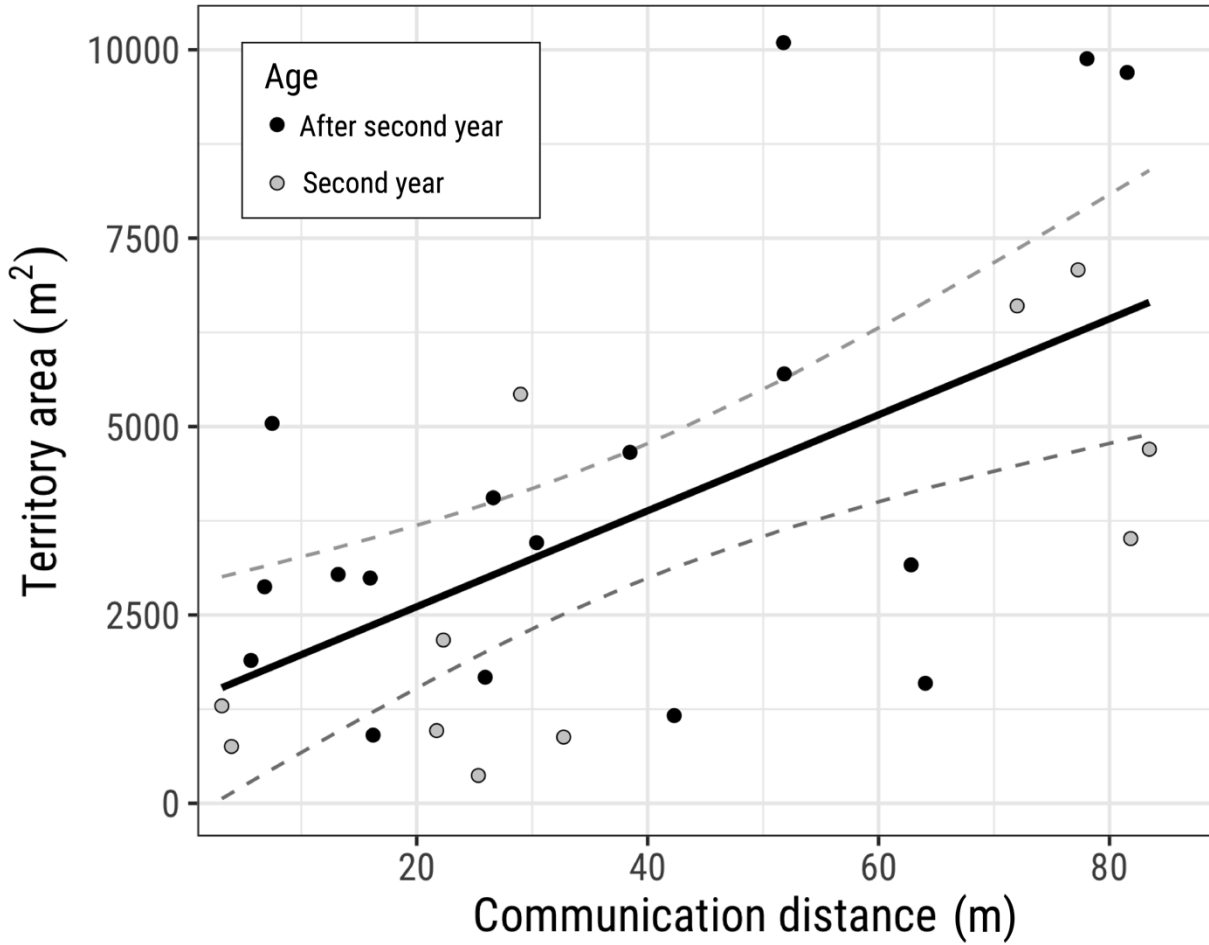


Figure 2. Plot of territory area as a function of mean communication distance for each bird. Dashed lines represent the 95% confidence interval. Second-year males (SY) are represented by gray circles, and after second year males (ASY) are represented by black circles. Males with greater communication distance have larger territories.

Because none of the candidate models emerged as a clear top choice (i.e., had model probability ≥ 0.90), we used multimodel inference to evaluate the relative importance of each parameter across the candidate model set. We calculated relative parameter importance by summing the model probabilities (Akaike weights) over the subset of candidate models that included each given parameter (Burnham & Anderson, 2002). This is a measure of the evidence in support of that parameter's inclusion in the top-ranked model. We report the relative importance of each parameter (Table 3). Though there are not standardized thresholds for evaluating relative parameter importance (Galipaud et al., 2014), 0.90 is considered a high value and strongly supports the inclusion of communication distance in the top-ranked model.

Urban birds have shorter communication distance and smaller territories than rural birds

“Urban” birds from the two study populations in San Francisco had significantly shorter communication distance than “rural” birds from the two study populations in Point Reyes National Seashore ($p < 0.0001$) (Figure 3). The mean communication distance of songs produced by urban birds was less than half the mean communication distance of songs produced by rural birds.

Moreover, in keeping with the linear model described above, urban birds had significantly smaller territories than rural birds (t-test; $p = 0.002$) (Figure 3). The mean territory size for a rural bird was 5440 m² (± 829 m²), while the mean urban territory size was less than half that, at 2328 m² (± 448 m²).

Table 2. Rank of models that describe territory area. The top model, models within 2 ΔAIC and the null are shown; K , number of parameters in the model; $AICc$, Akaike information criterion with a correction for finite sample sizes; $\Delta AICc$, difference between each model's $AICc$ and that of the top model.

Model	K	$AICc$	$\Delta AICc$	Model probability
Communication distance + age	4	517.24	0.00	0.31
Communication distance	3	517.62	0.38	0.26
Null (intercept only)	2	528.11	10.87	0.00

Table 3. Relative importance of each parameter based on sum of Akaike weights

Parameter	Relative importance
Communication distance	0.90
Bird age	0.49
Territory noise level	0.26
Bird body condition	0.23

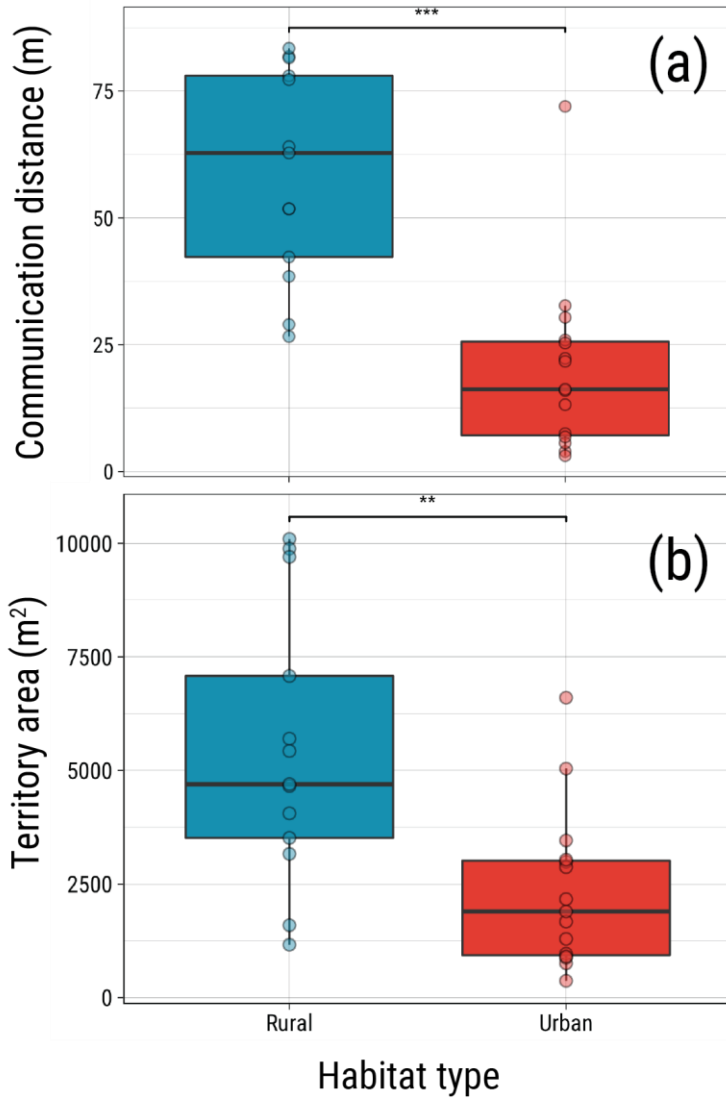


Figure 3 (a) Comparison of communication distances of rural and urban birds. Rural birds have significantly greater communication distance than urban birds. Mean rural communication distance was nearly 3 times greater than mean urban communication distance. (b) Comparison of territory area between rural and urban birds. Rural birds have significantly larger territories. The average rural territory is over twice as large as the average urban territory.

PART FOUR

DISCUSSION

White-crowned sparrows that produced songs with greater communication distance held significantly larger breeding territories. As a result of this trend, urban males held significantly smaller territories than rural males. Older males also tended to hold larger territories, although this trend was not significant. These findings suggest that the function of song as a territorial signal is reduced when the signal is masked by noise. Reduced functional range for this critical “keep-out” signal may limit territory size. It is, however, impossible to determine from these observational data whether reduced communication distance directly causes a reduction in territory size, or whether both variables are responding to some variation in the urban environment. The literature supports both the importance of environmental characteristics and the importance of territorial behaviors in determining territory size (Adams, 2001). Territory size has been shown to influence the reproductive success and demography of songbird populations, so this finding illuminates a complex and potentially important impact of the anthropogenic soundscape upon animal behavior.

Communication distance predicts territory size

We found that communication distance—the functional range of a bird’s song—predicts territory size. Communication distance was included as a parameter in the top-ranked model and had a high model-averaged parameter importance. In the top-ranked model, communication distance is the only parameter to predict territory area significantly.

One interpretation of our finding is that communication distance itself constrains territory size. The underlying mechanism of this relationship would be a loss of signal function when the signal is not detected. In other words, bird song functions as a territorial signal only when the song is heard by a receiver, and the area a territory holder is able to defend with this long-range signal is therefore determined by communication distance. This suggested mechanism is based on extensive research that establishes the importance of song for territory defense (e.g., McDonald, 1989; Nowicki et al., 1998). It also fits with work demonstrating that acoustic signals, in birds and beyond, lose their adaptive function when they cannot be detected and/or discriminated (Reed et al., 2021; Schmidt et al., 2014; Templeton et al., 2016). The suggestion that communication distance may constrain territory size emphasizes the importance of individual territorial behavior in determining the size of breeding territories. Though resource availability is often afforded primacy of place in regulating territory size, we are not the first to suggest that territory size may instead be governed by behavioral interactions between individuals. Several studies have found that bird breeding density, and thus territory size, is limited by territorial behavior and insensitive to changes in resource availability (Krebs, 1971; Newton, 1992; Stamps, 1990).

An alternative interpretation of this pattern is that communication distance is acting as a covariate for some feature of the urban environment that directly influences territory size. This interpretation would accord with the well-established theoretical approach to territory size as an optimality model, in which territory size is determined by the costs and benefits of territory defense (Hixon, 1980; Schoener, 1983; Stenger, 1958). Within this framework, territory size is primarily a function of resource availability. If resource availability determines territory size in this system, as suggested by the bulk of theoretical work

on this topic, then birds with lower communication distance in this study may defend territories in more resource-dense habitats.

One piece of evidence that undermines this interpretation is that communication distance outcompeted territory background noise as a predictor in our analysis. Background noise is a feature of the environment, and one might expect other habitat features to vary directly with background noise level. However, background noise level was not retained in the top-ranked model, and the candidate models including background noise level as a predictor had low model probabilities overall. It is less intuitively obvious why communication distance, which is not a feature of the environment but rather of bird behavior, would covary with habitat features such as resource density. Moreover, Phillips et al. (2018) found that urban NWCS in San Francisco have poorer body condition than rural NWCS in Point Reyes National Seashore. If urban NWCS have smaller territories because they reside in more resource-dense habitat, we might expect them to have comparable or better body condition than their rural counterparts. However, as the habitat characteristics affecting territory size may be complex and inconspicuous to a human observer, we cannot reject the possibility that communication distance in this study is a proxy for environmental variables.

We suggest that communication distance is one determinant of songbird territory size, but myriad other factors likely contribute. Habitat structure, including the types and density of vegetation as well as the presence of man-made paths and buildings, varied widely across the sites included in this study and may well influence territory size. Resource availability may also influence territory size, even if it is not the sole determinant. The observational data we present here do not contradict the potential importance of environmental factors in songbird territory size – rather, we offer communication distance as an additional explanatory variable that may influence territory size.

Age was also retained as a parameter in the top ranked model. Though its effect on territory size was not significant, its inclusion in the model indicates that the age of the territory holder may explain some variation in territory size. Across many bird species, older males have higher reproductive and territorial success than younger males. Older males have been shown to begin breeding earlier (Harvey et al., 1985; Nol & Smith, 1987), to fledge young at higher rates than second-year males, and to occupy disproportionately high-quality habitat compared to second-year males (Holmes et al., 1996). Of greatest relevance here, older males have been shown to defend larger territories than younger males in a number of bird species, including Nuttall's white-crowned sparrows (Cavé et al., 1989; Dhondt & Hublé, 1968; D. F. Mazerolle & Hobson, 2004; Ralph & Pearson, 1971). Though the mechanisms underlying this pattern remain unknown, many have speculated that older males may be more successful because of the benefits of experience in parenting, foraging, and territorial competition (Forslund & Pärt, 1995; Nol & Smith, 1987; Wunderle, 1991; Yakusawa, 1979). Age effects on breeding timing could also give rise to this pattern, as older males tend to arrive earlier at breeding sites in many bird species (Potts et al., 1980). This is likely to confer considerable competitive advantages, as established territorial residents almost always defeat challengers (Tobias, 1997), but may not be applicable to year-round resident species like NWCS. Age may also relate to other factors potentially important to territory size, including the strength of aggressive response to an intruder (Hyman et al., 2003) or the frequency of territorial intrusions (Arcese, 1987). The inclusion of age in the top model here accords with previous findings that age is important for territorial behavior in birds. However, we found that age does not explain a significant amount of variation in territory size. Age may therefore be informative but is likely less important than communication distance in explaining territory size, at least in this system.

Variation in territory size may be important for both individual fitness and the breeding density of the population for many bird species. Birds breeding on larger territories lay larger clutches and have higher survival rates (Valcu & Kempenaers, 2008), while chicks raised on larger territories have higher survival, growth rates, and higher breeding success over the course of their lives (Both & Visser, 2000; Mumme et al., 2015). On a population level, territory size is likely to be important to breeding density and the number of “floaters”, or non-breeding adults (López-Sepulcre & Kokko, 2005). If such trends exist in this system, then individuals with shorter communication distance may be likely to rear a smaller number of less successful offspring compared to individuals with longer communication distance. Populations with shorter communication distance, such as the white-crowned sparrows in noisy parts of San Francisco, may support higher breeding density with fewer floaters than populations with comparatively high average communication distance. While it remains unclear whether the relationship between communication distance and territory size is causal, communication distance may either indicate or influence a wide range of breeding characteristics for these songbirds.

Urban birds have shorter communication distance and smaller territories than rural birds

The urban NWCS in this study produced songs with significantly shorter communication distance than their rural counterparts (Figure 3a). Consistent with the relationship we found between communication distance and territory size, urban birds also held significantly smaller territories (Figure 3b). This finding contributes to a bustling frontier in urban ecology: understanding the effects of urban noise pollution upon animal behavior. Urban noise pollution is known to impact acoustic communication for a broad variety of taxa (Costello & Symes, 2014; Holt & Johnston, 2015; Parris et al., 2009; Slabbekoorn et al., 2003). Effects on communication can include changes in the characteristics of the acoustic signal, such as reduced trill frequency bandwidth in urban NWCS (Luther et al., 2016). Urban noise can alter the timing of signal production, with animals selectively signaling when noise levels are lowest (Fuller et al., 2007). Noise pollution can also impact the behavioral responses of signal receivers, for instance by preventing detection of the signal (Templeton et al., 2016), impairing the receiver’s ability to discriminate signal quality (Bent et al., 2021), or stimulating receiver aggression (Phillips & Derryberry, 2018). Despite agreement that acoustic signals serve important adaptive functions, and broad speculation about the possible ramifications of altered communication for urban animals, the second-order consequences of urban noise effects on animal communication have not yet been thoroughly charted (Derryberry & Luther, 2021; Gil & Brumm, 2014). In demonstrating that urban birds have smaller territories, and linking reduced territory size to reduced communication distance, we provide evidence that urban noise effects on communication matter more broadly: they are felt in other parts of the animals’ lives and ecosystems. NWCS songs are a functional part of their phenotype, influencing how birds interact with one another and their environment.

Here we have demonstrated one way in which the acoustic environment of urban spaces may alter the behavioral phenotype of one species in regard to one signal function, but the behavioral impacts of urban noise are likely to be as varied as animals’ reasons for signaling. Noise pollution may impact territorial signaling differently in different species, and other aspects of the urban environment, such as habitat quality, may impose different constraints on the behavior of urban animals. Other studies have recently found that some urban birds have larger territories than their rural counterparts, possibly as a response to lower resource density in urban areas (Juárez et al., 2020, 2021). Such contrasting patterns illustrate the complexity of urban effects upon animal behavior.

Conclusion

Speculation about the determinants of territory size is as old as the formal study of animal behavior (Hinde, 1956; Tinbergen, 1957). We found that the communication distance of songs may be one determinant of territory size for a model songbird. If territory size is reduced for birds in areas with higher noise levels, either as a function of reduced signal range or of some environmental variable not measured here, this could impact not only individual-level traits such as reproductive fitness (Both & Visser, 2000; Buchanan & Catchpole, 1997; Mumme et al., 2015), but also population-level traits such as breeding density (López-Sepulcre & Kokko, 2005). Anthropogenic habitats like downtown San Francisco present urban animals not only with novel physical environments, but with novel acoustic and social environments as well, which impact animal communication. Anthropogenic effects on communication may influence the extended phenotypes of our urban animal neighbors, as reflected in the reduced territory size of urban white-crowned sparrows in this study. Testing such relationships is key to understanding the myriad complex ways in which the human landscape interacts with the natural world. The world is growing noisier, and in order to manage and conserve wildlife effectively, we must understand not only the first-order impacts of this environmental change, such as impaired communication, but also the cascading second- and higher-order impacts such as constrained territorial defense and smaller territories.

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APPENDIX

Table 4

Model	K	AICc	ΔAICc	Model probability
Communication distance + age	4	517.24	0	0.31
Communication distance only	3	517.62	0.38	0.26
Communication distance + body condition	4	519.91	2.68	0.08
Communication distance + noise	4	519.92	2.68	0.08
Communication distance + age + body condition	5	520.13	2.90	0.07
Communication distance + age + noise	5	520.22	2.98	0.07
Noise only	3	521.34	4.11	0.04
Communication distance + body condition + noise	5	522.66	5.42	0.02
Body condition + noise	4	522.95	5.71	0.02
Communication distance + age + body condition + noise	6	523.41	6.17	0.01
Age + noise	4	523.46	6.22	0.01
Body condition only	3	523.77	6.53	0.01
Age + body condition + noise	5	525.34	8.10	0.01
Age + body condition	4	525.69	8.46	0.00
Null (intercept only)	2	528.11	10.87	0.00
Age only	3	529.44	12.20	0.00

All candidate models to describe territory area used in model selection in this analysis. Models are ranked by AICc. K, number of parameters in the model; AICc, Akaike information criterion with a correction for finite sample sizes; Δ AICc, difference between each model's AICc and that of the top model.

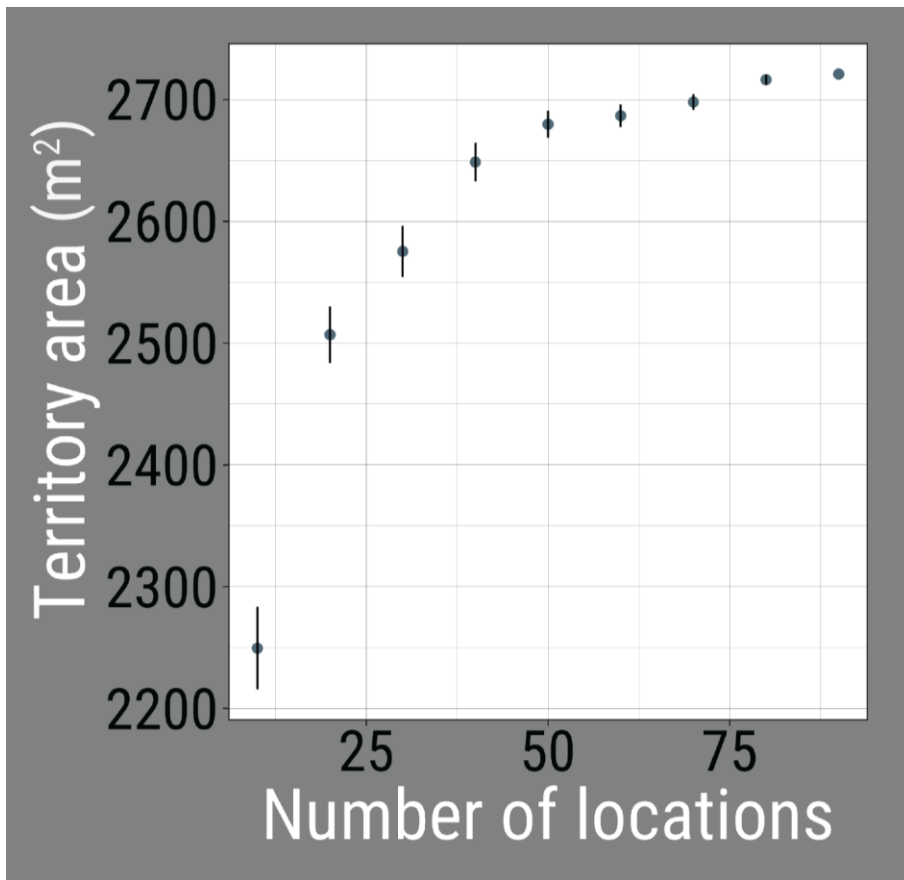


Figure 4

Validation of the territory estimation method. Shown is the territory area of one bird in this study as a function of the number of locations sampled. We subsampled the full dataset (90 locations) to attain various sample sizes, taking 100 random samples at each sample size. Territory area plateaus as more samples are added, indicating that the full set of sampled locations accurately captures the extent of the territory. All NWCS territories used in this study similarly plateau.

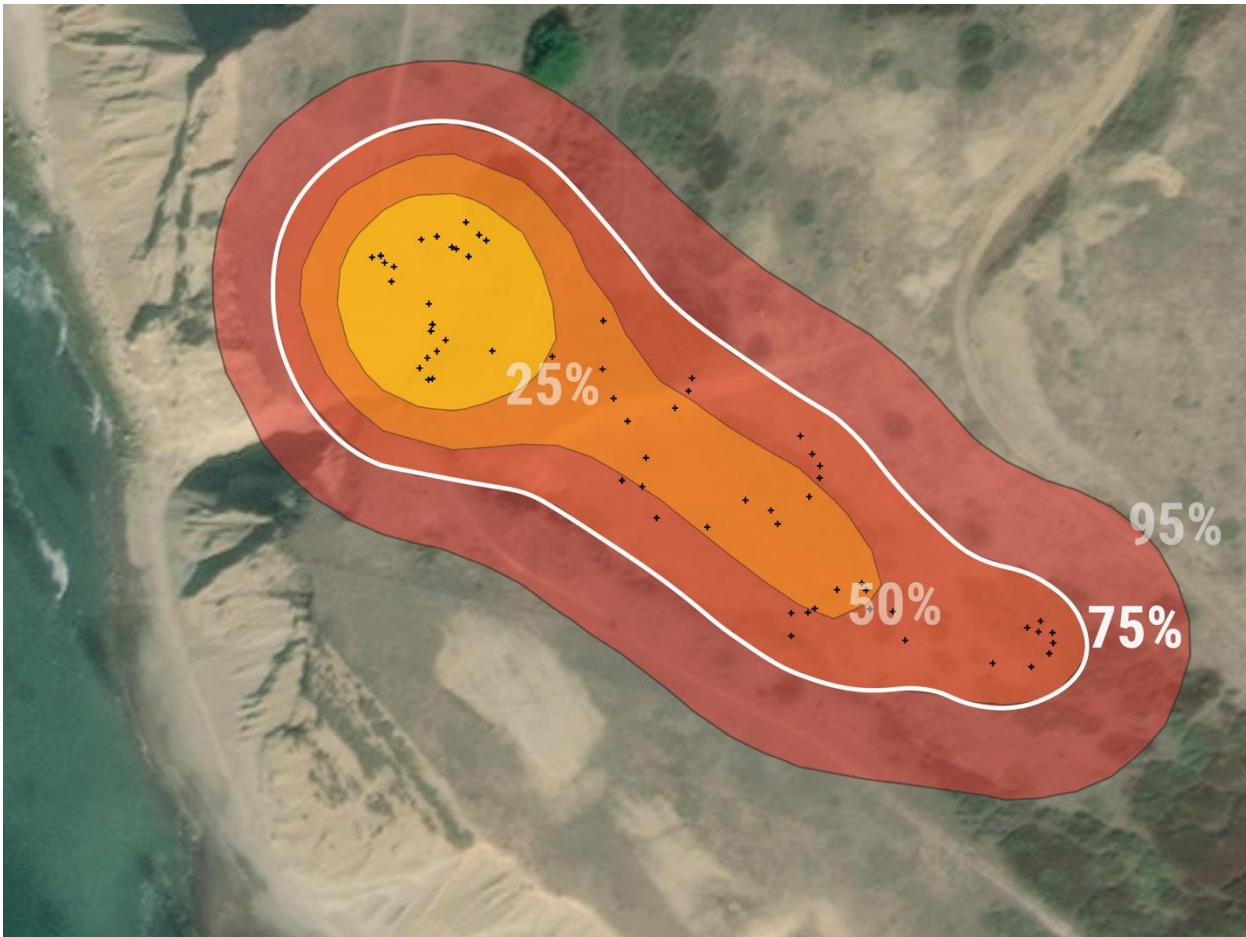


Figure 5

Map of one bird's breeding territory. Each black point represents a location observed during one of the three observation periods of this focal individual. The colored shape represents the territory area, calculated as a utilization distribution from these locations. The different colors and outlines indicate different kernel density thresholds. The 75% kernel density utilization distribution is highlighted in white, as this is the threshold used to estimate territory area in this study.

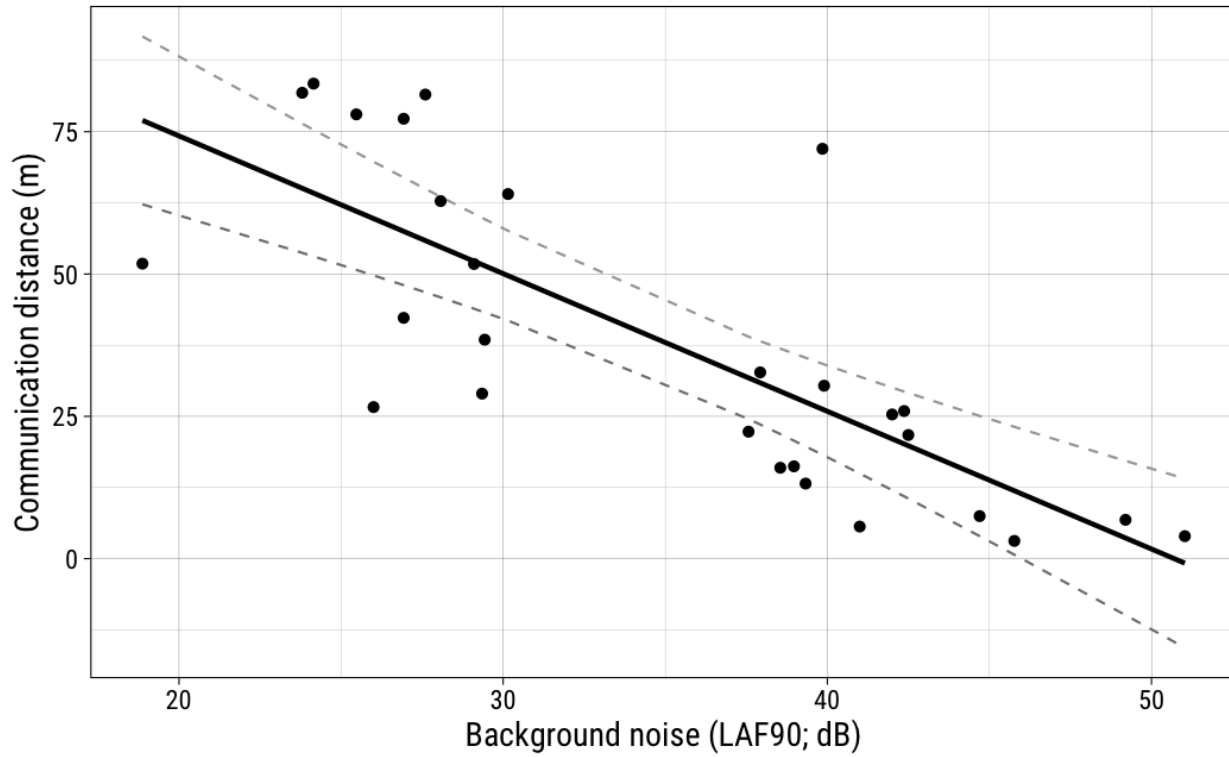


Figure 6

Plot of communication distance (averaged for each bird) as a function of background noise level. Dashed lines represent the 95% confidence interval.

VITA

Ruth Simberloff was born in 1995, and grew up in Knoxville, Tennessee. She began to develop her interest in animal communication and behavior as an undergraduate at McGill University, from which she graduated with honors in 2018. Simberloff entered The University of Tennessee, Knoxville, as a graduate student in the fall of 2020. She received her Master of Science degree in Spring 2023.