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Research

Breeding status shapes territoriality and vocalization patterns in spotted owls

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Vocal territory defense can vary within a species due to many factors such as sex and breeding status, influencing territory size and thus population density across a landscape. Therefore, understanding what influences variation in territorial vocalizations can help to illuminate trade-offs between territoriality and other life history demands, which benefits our general understanding of animal ecology as well as helps to inform emerging passive acoustic monitoring approaches. Here, we investigated how sex and breeding status affected territoriality and vocal behavior in the California spotted owl *Strix occidentalis occidentalis* in the Sierra Nevada, California, USA, using high-resolution acoustic/GPS tags. We discovered that territorial vocal behavior was related to breeding status and to a lesser extent sex. Breeding owls with fledged young had a less diverse vocal repertoire, produced fewer and quieter territorial calls, and typically called only when close to their nest. Males were also more likely to engage in territorial calling than females. Breeding spotted owls also maintained significantly smaller territories – but utilized larger home ranges – than non-breeding individuals. Our results suggest that breeding spotted owls may reduce their investment in territorial behaviors to mitigate the demands and risks associated with rearing young. Further, our results have important implications for the passive acoustic monitoring of spotted owls and, more broadly, highlight the utility of using multiple call types to detect species of interest.

Keywords: acoustic tag, bioacoustics, ecoacoustics, passive acoustic monitoring, spotted owl

Introduction

Territory defense is an important ecological process shaped by many factors. Variation in territory defense within a species can be especially important to understand as this impacts resource partitioning and social hierarchies and, ultimately, influences

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population densities at landscape scales (Odum and Kuenzler 1955, Seyfarth and Cheney 2003). For vocally active species, a territory, defined as 'any defended area' (Noble 1939), is maintained through the production of specific vocalizations, yet these vocalizations are observed to be constrained in time and space, potentially in part due to direct energetic costs associated with vocally defending a large area (Schoener 1987, Ophir et al. 2010). Territorial vocalization can also entail indirect costs by reducing time for foraging and other activities (Gil and Gahr 2002), decreasing foraging success by alerting prey (Deecke et al. 2005) and attracting unwanted attention from predators or competitors (Haff and Magrath 2011). Consequently, for many vocally active animal species, territories are not infinitely large and the likelihood or intensity of territorial defense decreases with distance from an activity center (i.e. the location to which an individual returns after foraging bouts; Adams 2001), such that territories are often observed to be smaller than homes ranges (i.e. an individual's total area of use; Burt 1943, Grant et al. 1992, Anich et al. 2009).

Specific life history constraints such as those associated with sex and breeding status can also impact territorial vocal behavior. For many species, males are more likely to defend territories than females (Davies 1991, Fedy and Stutchbury 2005). Territory defense also typically fluctuates throughout the year, often peaking during courtship and decreasing after breeding (Odum and Kuenzler 1955, Finck 1990). Breeding is both risky and energetically costly, so reproductive individuals may exhibit weaker territorial behavior to increase the time and energy available for provisioning offspring and to reduce predation risks (Odum and Kuenzler 1955, Whitaker and Warkentin 2010). Many studies have examined how territoriality varies seasonally within a species (Odum and Kuenzler 1955, Finck 1990) but few examine how territory defense and vocal behavior might vary because of life history constraints such as breeding status within a season. Therefore, studying such variation in territory size and vocal behavior can illuminate trade-offs owing to competing life history demands and increase our knowledge of animal ecology.

Understanding how vocal behavior varies in space and time is also increasingly important for conservation, given the rapid emergence of bioacoustics as a population monitoring tool (Sugai et al. 2019). Passive acoustic monitoring can be especially effective for cryptic or rare species that are otherwise difficult to detect (Browning et al. 2017) but requires a detailed understanding of where and when different vocalization types are produced in order to best detect the species of interest and reduce false negatives (i.e. missing an individual when it is present). Further, when independent acoustic sampling units are not properly spaced in relation to the area over which an animal vocalizes, a single individual can be detected across multiple sampling locations, potentially interfering with the interpretation of acoustic data and subsequent population-level inferences (Reid et al. 2021). Thus, identifying and understanding spatiotemporal patterns in animal vocalizations can not only benefit our general understanding of animal ecology but also aids in monitoring and conservation efforts.

We investigated how life history constraints might affect territoriality and vocal behavior within a territorial species, the California spotted owl (*Strix occidentalis occidentalis*, hereafter 'spotted owl'), using acoustic/GPS tags that provided high-resolution, minute-by-minute location and audio data. Spotted owls are an ideal study species because their territorial vocalizations and various call types are well documented and easily identifiable, with novel acoustic/GPS tags developed and optimized for this species offering a unique opportunity to study their vocalizations at unprecedented levels of detail (Wood et al. 2021). Further, spotted owls are a focal species for the development of regional-scale, passive acoustic-based population monitoring programs (Wood et al. 2019a, Duchac et al. 2020) but their wide-ranging and cryptic nature has made it difficult to study their vocal behavior at an individual level until now (Wood et al. 2021). This is the first study to deploy acoustic/GPS tags on an owl species in the wild, and thus exemplifies the type of fine-scale information that can be gained when this technology is applied to novel taxa.

We investigated how spotted owl vocal behavior and territoriality were affected by sex and breeding status during the breeding season using fine-scale, spatiotemporal vocalization patterns obtained through acoustic/GPS tagging. Specifically, we assessed how the type, number and loudness of spotted owl vocalizations differed between males and females and breeders and non-breeders. We then examined how spatial vocalization patterns varied by sex and breeding status by examining the location of vocalizations relative to an individual owl's activity center (e.g. nest/roost). Finally, we examined how defended territory and home range size varied by sex and breeding status as well. Examining these patterns in territoriality and vocal behavior at a fine-scale, individual level with acoustic/GPS tagging technologies offers novel insights into spotted owl ecology and behavior, helping to elucidate some of the many trade-offs that shape territoriality and vocal behavior within a species.

Methods

Tagging

We conducted our study in the central and northern Sierra Nevada, California, USA (Fig. 1), where we deployed acoustic/GPS tags on adult spotted owls from May to July of 2019 and 2020. The primary vegetation type of our study area was Sierran mixed-conifer forest (Franklin et al. 2004, Tempel et al. 2014). Acoustic/GPS tags (Vesper 3.2 tag, manufactured by ASD, Haifa, Israel; encapsulated in epoxy by Lotek, Wareham, UK) contained a high sensitivity MEMS microphone to record audio continuously throughout the night at an 8 kHz sample rate, with data stored on-board in the Waveform audio file format; GPS locations were taken at one-minute intervals with a median error of 29 m based

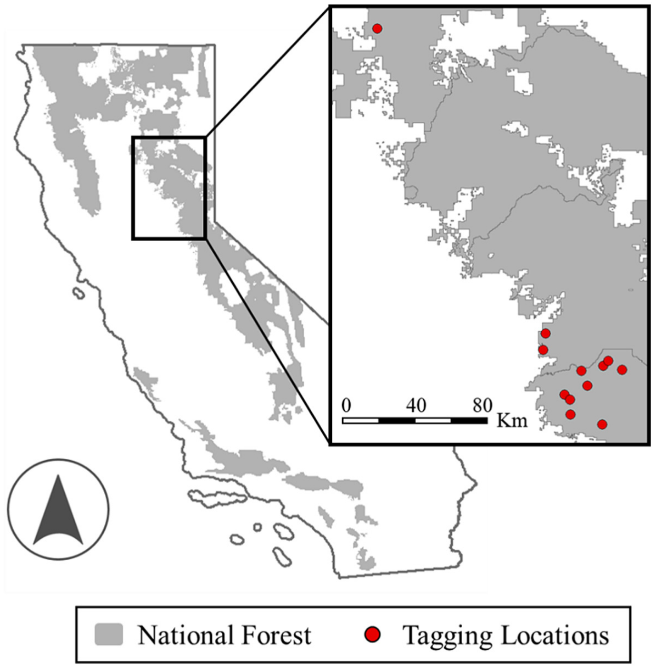


Figure 1. Study area in the Sierra Nevada, California, USA. Acoustic/GPS tagging locations are shown in red and were located primarily on the Eldorado National Forest, with additional locations on the Tahoe and Lassen National Forests.

on field tests. Tags weighed 11.6 g (approximately 2% of a spotted owl's body mass) and recorded from 1900 to 0500 PST each night, with a delayed start at 2100 PST on the first night to account for disturbance from capture. Tag battery life resulted in a tracking period of approximately 3–5 nights.

We captured 17 spotted owls and mounted the tags on their two central retrices so that individuals that were not recaptured would not be burdened with the devices beyond their next molt (all individuals in this study were recaptured, however). We tagged four breeding males, three breeding females, six non-breeding males and four non-breeding females during the breeding season (lasting from March to September in this species; Gutiérrez et al. 1995). All breeding owls were tagged during the fledgling period (the period after which young leave the nest but prior to juvenile dispersal, lasting from late May to September; Gutiérrez et al. 1995). Importantly, unlike many other avian species, spotted owls typically only attempt nesting once per season (Gutiérrez et al. 1995). Thus, if a nest fails or nesting was not attempted at all at the start of the breeding season, those owls remain non-breeding throughout the rest of the year. All tagged spotted owls resided within long-term, mark–recapture demographic study areas with their breeding status and activity center (e.g. nest/roost) locations ascertained as a routine part of demographic surveying following standard protocols (Franklin et al. 1996). For breeding birds, activity centers were considered the nest tree location or the first observed juvenile location if a nest tree was not found. For non-breeding birds, activity centers were considered the roost location or first daytime location at which the individual was observed if a roost was not found. While non-breeding roost locations can sometimes shift in space over the course of a season, spotted owl roost site fidelity is incredibly high and unlikely to shift over the shorter temporal scale studied here (Berigan et al. 2012).

Data analysis

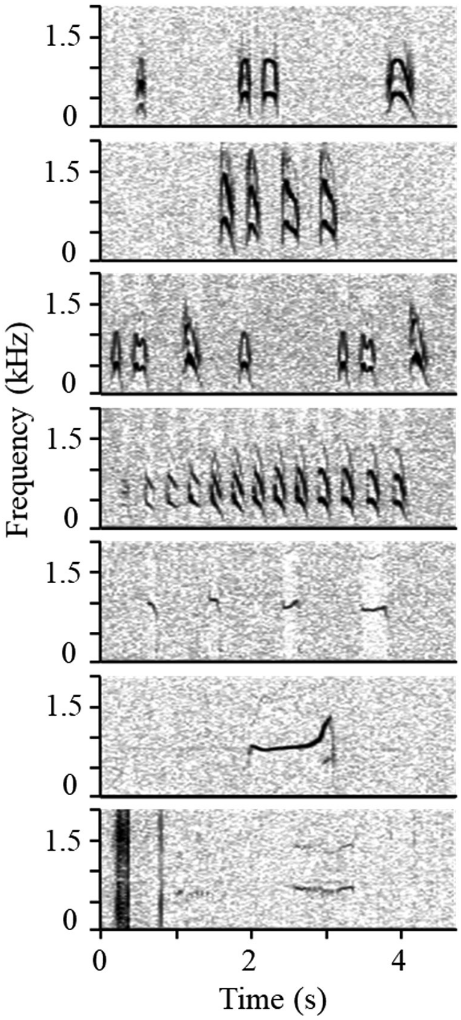
Acoustic data processing

We manually reviewed audio data using Raven Pro 2.0 (Cornell Lab of Ornithology, Ithaca, NY) to identify both the type of call (based on definitions by Forsman et al. 1984, Table 1), the average relative loudness of the call in decibels relative to full scale (dBFS, uncalibrated), and the exact time of vocalization. Average call loudness was calculated in Raven as the average value of the spectrogram's power spectral density per pixel of the call selection (Charif et al. 2010). We then classified calls as territorial if they a) were broadly recognized in the literature as a call given during territorial disputes (Table 1), and b) would indicate that the territory is occupied to any third-party observer – be that observer human, conspecific or other. Notably, many territorial spotted owl calls can also function as long-distance intrapair calls, but these are still considered 'territorial' as they are still indicative of territory occupancy to third-party observers. All calls were summarized by minute and linked to corresponding minute-by-minute GPS locations.

Territory and home range estimation

We estimated spotted owl territory and home range size using 95% fixed-kernel density estimators, considered an accurate and unbiased method of home range estimation (Seaman and Powell 1996). The 95% fixed-kernel density method generates a utilization distribution which estimates the relative amount of time an individual spends in a location and then creates a probability contour around the smallest area containing 95% of the distribution. The smoothing factor (h_{pi}) was calculated using the 'plug-in' method, considered an appropriate or even improved alternative to other smoothing factors (Gitzen et al. 2006, Walter et al. 2009). To estimate home range size, we utilized all GPS location points to generate 95% fixed-kernel density estimates using the *ks* package (Duong 2021) in Program R (ver. 4.0.3, <www.r-project.org>). To estimate territory size, we followed the same methodology but only used the locations at which a territorial vocalization was produced. We estimated home ranges for all 17 tagged spotted owls, and estimated territory sizes for 12 owls with $\geq$ 15 territorial vocalization locations – a threshold considered sufficient for reliable kernel estimation (Anich et al. 2009). The remaining five spotted owls – all breeding individuals – produced territorial vocalizations at eight or fewer locations over the tracking period, all within close proximity, resulting in a defended territory size that could not be properly estimated and was treated as effectively zero. Importantly, these estimates do not represent an individual's total territory or home range size because months of tracking are required to estimate the total area of use by

Table 1. Spectrogram and description for each of the seven spotted owl call types identified in the audio data. Definitions are adapted from Forsman et al. (1984).



Spectrogram	Call type	Definition	Primarily territorial?
	Four-note	This diagnostic call is commonly used to identify and locate spotted owls in the field. This call consists of three or four notes in a series; often the first note is dropped. It is produced by both sexes as a territorial challenge.	Yes
	Crowbark	This call consists of multiple loud, barking notes. It is given primarily by females during territorial disputes but is also produced by males.	Yes
	Agitated	This call is similar to the four-note call, but with the final note ending in a loud and higher-pitched 'ow!' Both sexes produce this call during territorial disputes, and it is also given during copulation.	Yes
	Series	This call consists of multiple hooting notes given in a rapid series which often crescendo in intensity. It is commonly given during territorial disputes.	Yes
	Coo	This call type includes soft whistles and cooing sounds. These calls are given by both sexes, commonly during copulation, roosting or allopreening.	No
	Contact	This call is a single, whistling 'cooo-weep' note ending in an upward inflection. It is primarily used to inform a mate or juvenile of an individual's location in order to coordinate prey deliveries and other activities.	No
	Chitter	This call consists of a rapid series of low chittering notes. It is produced by both sexes when allopreening or during copulation.	No

spotted owls (Forsman et al. 1984); rather, they provide a relative measure of home range and territory size during the 3–5-night tracking period.

Statistical analysis

We first examined general temporal patterns in spotted owl vocal behavior by exploring if call rate (calls/hour) varied by time of night, month or call type (territorial versus non-territorial). To do so, we constructed a linear mixed model in which hour, month and call type were fixed effects and owl and territory ID were nested random effects with the *lmerTest* package in R (Kuznetsova et al. 2017). We also examined the interaction of hour and call type in this model.

Next, we examined how the rate, type and loudness of spotted owl vocalizations varied by sex and breeding status. We first constructed a linear mixed model with the hourly rate of vocalizations as the dependent variable and breeding status, sex and call type (territorial versus non-territorial) as fixed effects and owl ID as a random effect. Only owl ID was included as a random effect in this model as the model did not converge when including both owl and territory ID as nested random effects. We also examined the interaction of call type and sex and call type and breeding status in this model. Then, we constructed a 2-way unbalanced ANOVA using the *car* package (Fox and Weisberg 2019) to examine if the proportion of territorial vocalizations owls produced varied by breeding status and sex. Finally, we also constructed a linear mixed model with the average relative loudness of territorial and non-territorial vocalizations (dBFS, uncalibrated) as the dependent variable and breeding status, sex and call type as fixed effects and owl and territory ID as nested random effects. We also examined the interaction of call type and sex and call type and breeding status in this model.

We then assessed spatial patterns in spotted owl vocal behavior by exploring how the spatial location of vocalizations relative to an owl's activity center varied by sex and breeding status. To do so, we first determined the distance between all vocalization locations and the owl's activity center. We then constructed a linear mixed model with the distance between vocalizations and the activity center as the dependent variable and breeding status, sex and call type as fixed effects and owl and territory ID as nested random effects. We also examined the interaction of call type and sex and call type and breeding status in this model.

Finally, we examined patterns in spotted owl territory and home range size by first performing a paired t-test in R to examine how mean territory size compared to mean home range size. We then performed two 2-way unbalanced ANOVAs to determine if territory and home range size varied by breeding status and sex. For all analyses, we assessed pairwise comparisons with Tukey's post hoc test as needed (Zar 2010) using the *emmeans* package (Lenth 2021). We assessed normality using Q–Q plots and the Shapiro–Wilk test (Shapiro and Wilk 1965) and found that most data were approximately normally distributed, with the exception of the calls per hour data which was somewhat normally distributed.

Results

Temporal vocal behavior patterns

Tags recorded acoustic data for an average of 40.6 h (range: 28.0–46.7, approximately 3–5 nights), and recorded an average of 1853 GPS locations (range: 1066–2394). Tagged owls produced an average of 521 vocalizations (range: 121–1101) over the tracking period at an average rate of 13 calls per hour (range: 4–26). Call rate did not vary by month ($F = 1.93$, $df = 2$ and 14.17, $p = 0.18$), however the interaction of time of night and call type was significant ($F = 5.73$, $df = 9$ and 1305.19, $p < 0.001$) with owls producing a higher rate of non-territorial vocalizations during the hours of 0300 (mean: 19 non-territorial calls/hour, 95% CI: 14–24; mean: 5 territorial calls/hour, 95% CI: 0–10) and 0400 (mean: 22 non-territorial calls/hour, 95% CI: 17–27; mean: 2 territorial calls/hour, 95% CI: 0–7). Overall, owls produced their highest rate of non-territorial vocalizations just before dawn, averaging a high of 22 non-territorial calls per hour at 0400 PST, while territorial vocalizations peaked at a high of 11 territorial calls per hour at 2000 PST (Fig. 2).

Rate, type and loudness of vocalizations

For call rate, the interaction between breeding status and type of call (territorial versus non-territorial) was significant ($F = 40.42$, $df = 1$ and 1322.16, $p < 0.001$). For non-territorial calls, breeders produced more calls per hour (mean: 13 calls/hour, 95% CI: 10–16) than non-breeders (mean: 6 calls/hour, 95% CI: 3–8), while for territorial calls, non-breeders produced more calls per hour (mean: 7 calls/hour, 95% CI: 4–9) than breeders (mean: 1 call/hour, 95% CI: 0–4). The interaction between sex and type of call was also significant ($F = 20.20$, $df = 1$ and 1322.16, $p < 0.001$). For non-territorial calls, females produced more calls per hour (mean: 12 calls/hour, 95% CI: 9–15) than males (mean: 7 calls/hour, 95% CI: 4–9), while territorial call rates were equivalent for both sexes (Fig. 3a).

The proportion of call types spotted owls produced was also affected by breeding status and sex. We found that a significantly higher proportion of the vocalizations of non-breeding owls consisted of territorial calls (mean: 0.51, 95% CI: 0.38–0.64) compared to breeding owls (mean: 0.13, 95% CI: 0.00–0.28) ($F = 17.24$, $df = 1$, $p = 0.001$). Male owls also produced a higher proportion of territorial calls (mean: 0.46, 95% CI: 0.33–0.59) than females (mean: 0.18, 95% CI: 0.02–0.33) ($F = 8.99$, $df = 1$, $p = 0.01$). In fact, we classified 70% of non-breeding male calls as territorial but classified practically no (< 0.01%) breeding female calls as territorial (Fig. 3). Overall, non-breeding birds displayed a more diverse

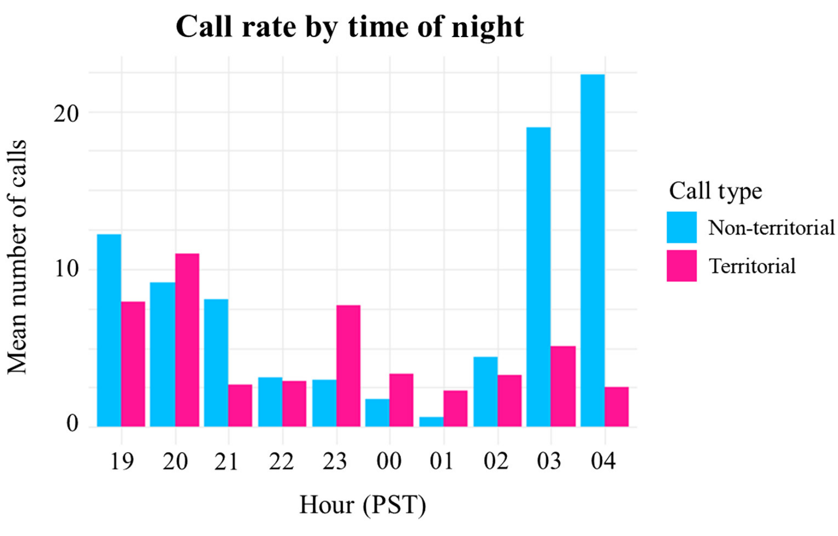


Figure 2. Average rate of territorial and non-territorial spotted owl vocalizations per hour by time of night. Territorial calls are shown in pink, with non-territorial calls shown in blue. Hour of the night is shown in military time, PST.

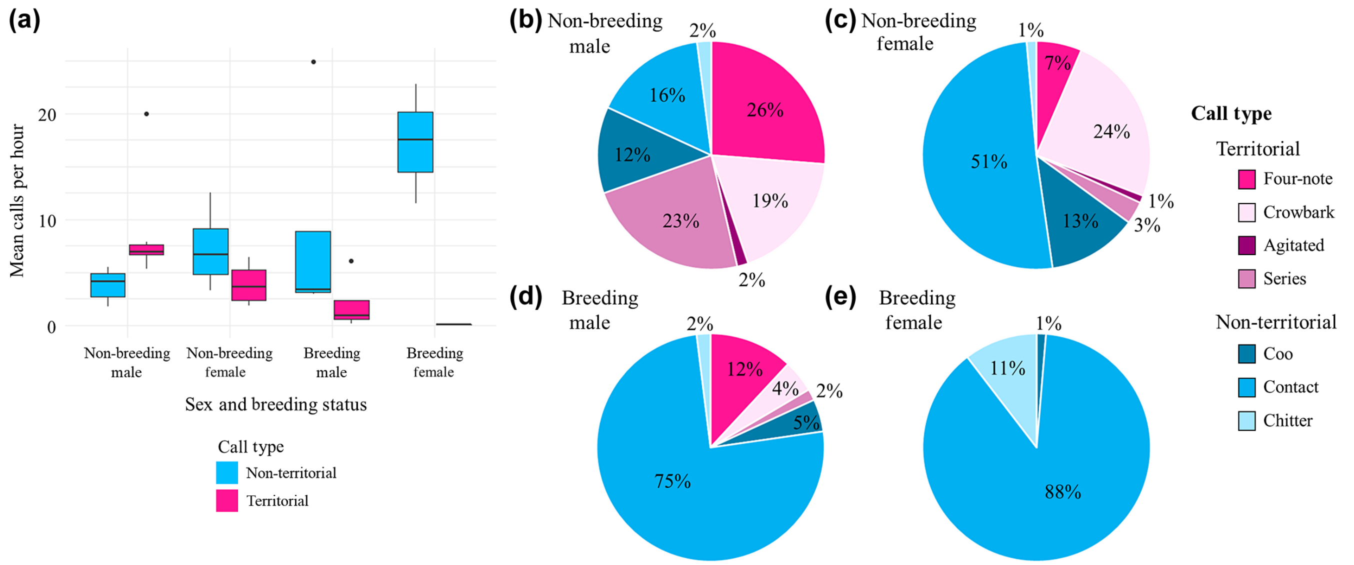


Figure 3. (a) Average number of territorial and non-territorial spotted owl vocalizations produced per individual per hour by sex and breeding status. Territorial calls are shown in pink, with non-territorial calls shown in blue. Pie charts show the proportion of each call type produced by (b) non-breeding males, (c) non-breeding females, (d) breeding males and (e) breeding females. Territorial calls are represented in pink shades, with non-territorial calls represented in blue shades.

vocal repertoire, with non-breeding males producing mainly territorial four-notes (26%) and series location calls (23%) while non-breeding females produced mainly non-territorial contact calls (a call type used for intrapair communication; 51%) and territorial crowbarks (24%) (Fig. 3b and c). In contrast, the majority of breeding male and female calls (75% and 88%, respectively) consisted of one call type: the contact call (Fig. 3d, e).

Call loudness was affected by the interaction between breeding status and call type (territorial versus non-territorial) ($F = 190.40$, $df = 1$ and 8811.8, $p < 0.001$). For territorial calls, non-breeders produced significantly louder calls (mean: −49.5 dBFS, 95% CI: −52.2 to −46.8) than breeders (mean: −58.2 dBFS, 95% CI: −61.3 to −55.0), while non-territorial calls were of similar volume for both breeders and non-breeders. Call loudness was also affected by the interaction between sex and call type ($F = 82.69$, $df = 1$ and 8821.3, $p < 0.001$). Males produced louder territorial calls (mean: −51.4 dBFS, 95% CI: −53.9 to −48.9) than females (mean: −56.3 dBFS, 95% CI: −59.2 to −53.3), while non-territorial calls were of similar volume for males and females (Fig. 4a). Overall, territorial calls were louder than non-territorial calls, with the loudest call type being the territorial four-note and the quietest the non-territorial chitter (Fig. 4b).

Spatial vocal behavior patterns

The spatial location of vocalizations was affected by the interaction between breeding status and call type (territorial versus non-territorial) ($F = 5.73$, $df = 1$ and 8772.7, $p = 0.02$). Breeding spotted owls produced non-territorial vocalizations closer to activity centers (mean: 184.0 m, 95% CI: 1.4–367.0)

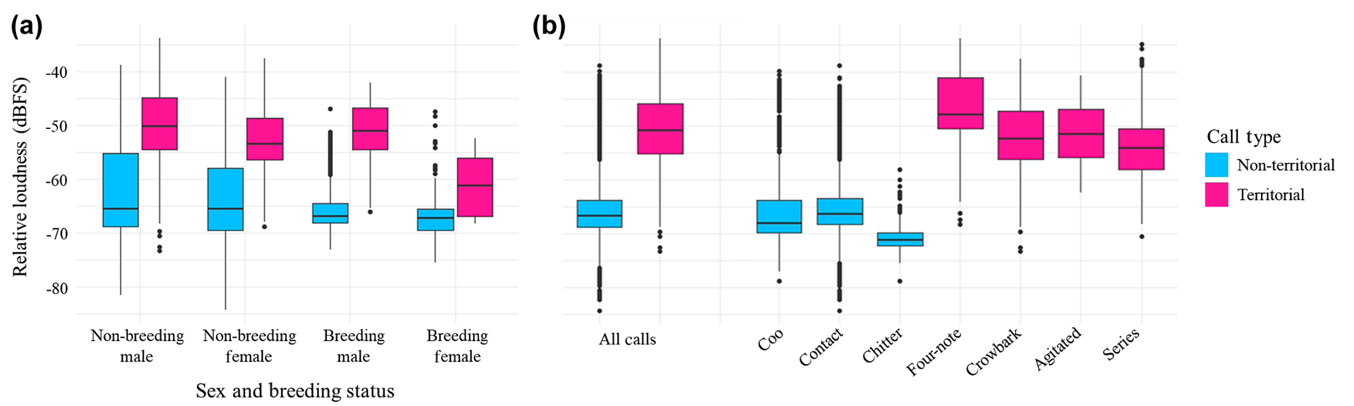


Figure 4. Average relative loudness of territorial and non-territorial spotted owl vocalizations in dBFS (uncalibrated). Boxplots show (a) the average loudness of vocalizations by sex and breeding status, and (b) the average loudness of all territorial and non-territorial calls as well as of specific call types. Territorial calls are shown in pink, with non-territorial calls shown in blue.

than non-breeders (mean: 508.0 m, 95% CI: 349.2–668.0), and also produced territorial vocalizations closer to activity centers (mean: 110.0 m, 95% CI: 0.0–300.0) than non-breeders (mean: 511.0 m, 95% CI: 352.1–671.0). The interaction between sex and call type was also significant ($F = 234.62$, df = 1 and 8822.9, $p < 0.001$). Males produced territorial calls at farther distances (mean: 387.0 m, 95% CI: 234.7–540.0) than non-territorial calls (mean: 247.0 m, 95% CI: 95.4–398.0), while females produced territorial calls at closer distances (mean: 234.0 m, 95% CI: 52.2–416.0) than non-territorial calls (mean: 446.0 m, 95% CI: 268.4–623.0). However, we found no significant difference in the spatial location of calls between males and females. Non-territorial call types tended to be produced closer to activity centers, with non-territorial chitters and contact calls produced the closest on average and territorial series and agitated calls produced the farthest (Fig. 5a). Overall, breeding spotted owls produced most of their vocalizations within close proximity to their activity center, with 95% of breeding owl vocalizations occurring within 300 m of an activity center (Fig. 5b). By comparison, non-breeding owl vocalizations occurred across a broader distribution of distances, with the majority (59%) produced > 300 m away (Fig. 5c).

Territory and home range size

Spotted owl territories (mean: 30.8 ha, range: 0.0–78.8) were significantly smaller than home ranges on average (mean: 112.2 ha, range: 34.0–296.5) ($t = -4.19$, df = 16, $p < 0.001$), with territories composing an average of 37% (range: 0–85%) of an individual's home range over the tracking period. Breeding owls maintained significantly smaller territories (mean: 0.8 ha, 95% CI: 0.0–16.6) than non-breeding owls (mean: 50.0 ha, 95% CI: 36.7–63.3) ($F = 26.44$, df = 1, $p < 0.001$). Breeders also maintained marginally non-significantly larger home ranges (mean: 147.5 ha, 95% CI: 97.8–197.0) than non-breeding owls (mean: 86.9 ha, 95% CI: 45.1–129.0) ($F = 4.06$, df = 1, $p = 0.06$), such that territories were very small relative to home ranges for breeding owls (Fig. 6). Males and females did not have significantly different territory ($F = 1.52$, df = 1, $p = 0.24$) or home range sizes ($F = 0.01$, df = 1, $p = 0.91$).

Discussion

Spotted owl territoriality and vocal behavior appeared to be strongly correlated to breeding status and, to a lesser extent, sex. Breeding individuals with fledged young exhibited weaker territorial behaviors: their territorial calls were quieter, produced at a lower rate and over a smaller area than those of non-breeding individuals. Breeding owls produced mainly non-territorial calls that were significantly more constrained in space, likely because of increased communication around the nest between mated pairs and their young to coordinate prey deliveries. Breeding females in particular almost never produced territorial vocalizations and mainly called to mates and juveniles. Non-breeding mated pairs could also be heard

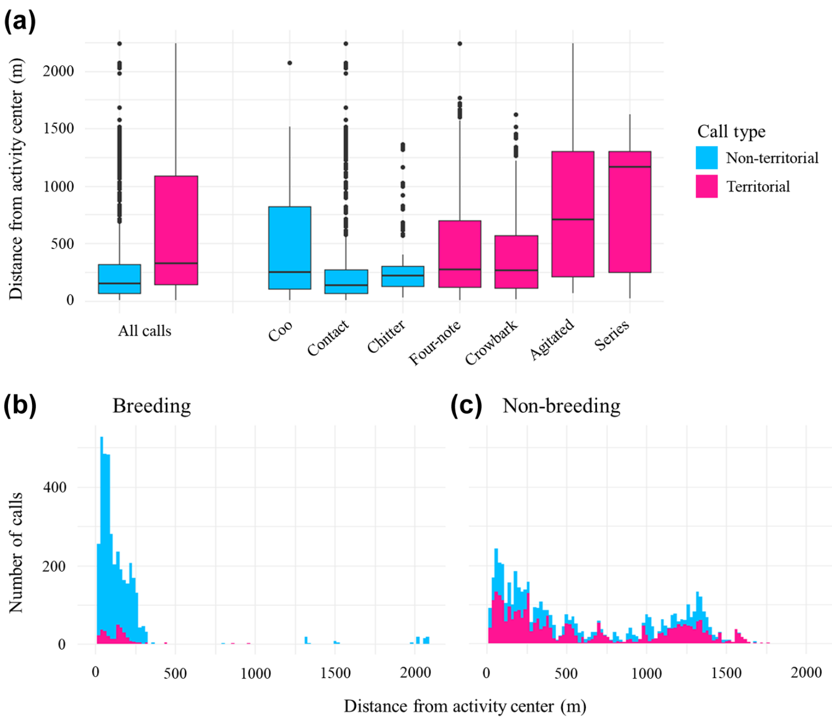


Figure 5. Distance between territorial and non-territorial spotted owl vocalization locations and the owl's activity center. (a) Boxplot shows distance from the call location to the activity center for all territorial and non-territorial calls as well as each specific call type. Histograms show the number of calls produced by distance from the activity center for (b) breeding owls, and (c) non-breeding owls. Territorial calls are shown in pink, with non-territorial calls shown in blue.

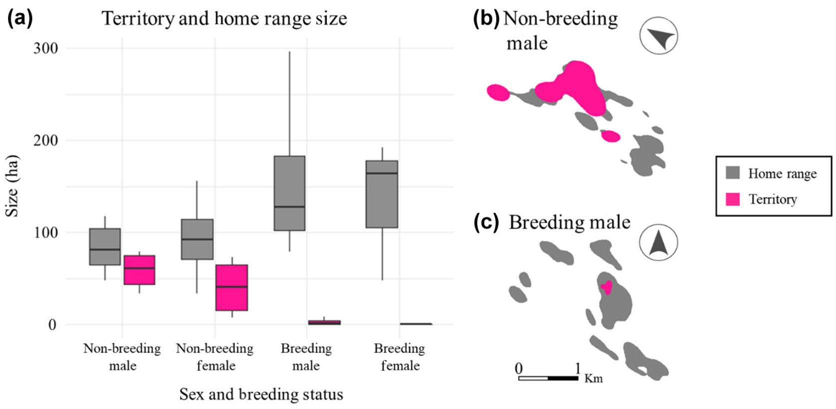


Figure 6. Spotted owl territory and home range size estimated using the 95% kernel density method. (a) Boxplot shows territory and home range size in hectares for breeding and non-breeding, male and female spotted owls. Maps represent the territory and home range estimates of (b) a non-breeding male owl (home range: 117.46 ha, territory: 78.78 ha), and (c) a breeding male owl (home range: 109.84 ha, territory: 2.97 ha). These two individuals represent the largest and smallest non-zero territory estimates, respectively. Territory size is indicated in pink, with home range size shown in gray.

communicating with each other throughout the audio, but these vocalizations consisted of a greater diversity of call types and were not constrained around an activity center. Male spotted owls – regardless of breeding status – were also more likely to engage in territorial calling than females, consistent with previous literature (Wood et al. 2019b). Overall, spotted owls tended to produce territorial vocalizations at farther distances from activity centers than non-territorial vocalizations, suggesting that these calls serve to maintain territory boundaries (Wood et al. 2019b).

Spotted owl territory and home range size over the tracking period was strongly correlated to breeding status but not sex. While defended territories were always smaller than home ranges, non-breeding owls maintained territories that were on average 25 times larger than the territories of their breeding counterparts over the tracking period. Home ranges, meanwhile, were two times larger on average for breeding owls than for non-breeding individuals. This was likely due to constraints associated with provisioning young where breeding owls spent more time foraging, resulting in a larger area of use and less time on territorial defense, resulting in smaller territories. Provisioning young spotted owls requires a significant time and energy investment, necessitating over 10 kg of prey to be delivered over the breeding season in order to produce a single offspring (Ward et al. 1998). Further, vocalizing while foraging can potentially alert prey to an individual's presence and decrease hunting success, with previous studies showing that spotted owls minimize territorial vocal activity in foraging habitat (Wood et al. 2019b). Thus, breeding spotted owls provisioning young have less time and energy available for territorial defense and are also not incentivized to produce loud, territorial calls while foraging. Breeding birds may also produce fewer and quieter territorial calls to decrease the likelihood of attracting potential predators or competitors such as northern goshawks *Accipiter gentilis* and great-horned owls *Bubo viginianus* that prey on juvenile spotted owls (Gutiérrez et al. 1995). Importantly, given the site-faithfulness and mate-faithfulness of spotted owls, it is generally assumed that the benefits of holding a territory are equivalent regardless of breeding status, thus we consider it unlikely that the variation in territory size we observed was due to other ecological factors (e.g. mate selection, etc.).

Our results indicate that breeding spotted owls likely reduce territoriality as a strategy to mitigate the demands and risks associated with provisioning and rearing young. While the acoustic/GPS tags used in this study provided a unique way to study the vocal behavior of spotted owls, previous studies of other owl species have observed similar trade-offs in territoriality such as with tawny owls *S. aluco* that showed decreased unprompted territorial vocal activity during the fledgling period (Zuberogoitia et al. 2019). In addition, other owl species have also shown decreased territorial vocal activity and defense in response to playback experiments following the hatching of offspring (Finck 1990, Flesch and Steidl 2007, Barnes and Belthoff 2008). Thus, our findings and previous literature suggest that owl species both decrease overall territorial maintenance (unprompted vocalizations) as well as show decreased territorial response to perceived intruders (playback experiments) during the fledgling period.

Territory size and vocal behavior commonly fluctuates throughout the breeding season in avian species and has been observed to be highly variable between individuals (Odum and Kuenzler 1955, Anich et al. 2009, Whitaker and Warkentin 2010), however few studies directly examine variation in territoriality and vocal behavior between breeding and non-breeding individuals during the breeding season (but see Barnes and Belthoff 2008). Even fewer have been able to examine territory size and vocal behavior in such a wide-ranging and cryptic species like the spotted owl with the high precision we achieved, highlighting the utility of acoustic/GPS tags for addressing such questions (Wood et al. 2021). The heterogeneity in territory size and vocal behavior that we observed between breeding and non-breeding spotted owls raises interesting questions regarding space use and population density for this species. Do breeding individuals experience more intrusions into their home range during the fledgling period because they only defend a small area? How does overlap in home ranges between adjacent owls change during this time depending on the breeding status of their neighbors? Our findings indicate a potential trade-off between territorial defense and parental care of offspring that resulted in significant spatiotemporal differences in vocal behavior owing to breeding status – differences with potential implications for the acoustic monitoring of spotted owl populations.

Implications for acoustic monitoring

Passive acoustic monitoring is increasingly used to monitor population trends of acoustically active species, with spotted owls at the forefront of this shift in approaches (Wood et al. 2019a, Duchac et al. 2020). Passive acoustic monitoring approaches for owls rely primarily on the detection of a single, diagnostic call – in this case, the territorial four-note – to identify the species. However, breeding spotted owls produce very few of these territorial four-notes and call over a limited area close to their activity center during the fledgling period. Previous studies have found that examining only the acoustic detections of female spotted owls, who produce fewer territorial vocalizations, reduces detection probability and decreases statistical power for monitoring programs (Wood et al. 2020); similar patterns are likely expected for breeding owls during the fledgling period as well. Importantly, breeding spotted owls may exhibit increased territorial calling earlier in the breeding season prior to fledging as has been found with other owl species (Finck 1990, Zuberogoitia et al. 2019). If passive acoustic surveys for spotted owls begin prior to fledging, decreased detectability of breeding owls may be less problematic. However, site accessibility as well as general resource constraints often limit survey effort early in the breeding season – an issue that is far from unique to our study species.

Another solution is to structure acoustic monitoring programs to identify species by both their territorial and non-territorial vocalizations, such as contact calls in our case, to help increase the detectability of breeding individuals. Fortunately, classifying multiple call types per species has become more feasible with the advent of machine learning algorithms trained on a wide range of calls (e.g. BirdNET; Kahl et al. 2021), which could present an effective way to detect species by both their territorial and non-territorial vocalizations. Classification of multiple call types also provides additional ecological information that can be used to strengthen inferences from passive acoustic surveys, potentially helping to locate nest stands, differentiate resident from transient individuals (Reid et al. 2021) and identify specific spotted owl behaviors.

Acoustic/GPS tagging and future research

The acoustic/GPS tags used in this study provided a wealth of information beyond vocal behavior and territoriality in our target species. Along with spotted owl vocalizations, tags recorded ambient noises such as running water, vocalizations from other species such as songbirds and frogs, and even the wing flaps of the tagged owl. Important events and behaviors such as prey kills, prey deliveries to begging juveniles, and allopreening by mated pairs could be identified in the audio as well. Acoustic/GPS tags have the potential to provide the spatial location not just of vocalizations but of specific behaviors (e.g. prey kills; Studd et al. 2021) that are otherwise difficult to observe in wide-ranging and cryptic species such as spotted owls. Further, this technology provides the ability to observe how mates or rivals interact when tagged simultaneously. While our tags resulted in a limited battery life, the highly detailed and fine-scale information they recorded could be used to pursue many further avenues of avian research.

Conclusions

Our study combined extensive background knowledge of spotted owl vocalization types and their meaning (Forsman et al. 1984) with cutting-edge tagging technologies (Wood et al. 2021), leading to new insights regarding spotted owl vocal behavior and life history trade-offs – along with the future potential to study many other aspects of owl behavior as well. We discovered that spotted owl vocal behavior and territoriality is strongly linked to breeding status, suggesting that population density and space-use are fluid across the landscape even for a site-faithful, highly territorial species. Further, our results are directly relevant to the passive acoustic monitoring of spotted owl populations, providing information on vocal behavior that could help improve detection probability and thus population estimates for this threatened species (Wood et al. 2019a, Reid et al. 2021). Thus, our findings provide insight into basic avian biology and offer potential benefits for the passive acoustic monitoring and conservation of a multitude of territorial species that likely face similar life history constraints in vocalization.

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Data availability statement

Data is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0cfxpnw51> (Reid et al. 2022).

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