

## DISTINGUISHING SEX OF NORTHERN SPOTTED OWLS WITH PASSIVE ACOUSTIC MONITORING

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**ABSTRACT.**—Northern Spotted Owls (*Strix occidentalis caurina*) are of management and conservation concern in the US Pacific Northwest where populations have been monitored since the 1990s using mark-resight methods. Passive acoustic monitoring has the potential to support monitoring efforts; however, its use is currently primarily restricted to determining species presence rather than breeding status. Distinguishing female from male Northern Spotted Owl vocalizations could facilitate determination of pair status using passive acoustic methods, greatly enhancing inference derived from noninvasive monitoring data. In 2017, we deployed 150 autonomous recording units (ARUs) within 30 5-km<sup>2</sup> hexagons overlapping recently occupied owl territories in Oregon and Washington, USA, where mark-resight methods were simultaneously occurring. We collected approximately 150,000 hours of recordings and detected 22,458 Northern Spotted Owl vocalizations at 76 ARUs. We summarized vocalizations by call type and found differences in the proportion of call types made by single, paired, and nesting owls. We used expert opinion to classify 2812 four-note location calls as female or male. We summarized inter-sex variation within 19 acoustic attributes of the four-note location call and its subcomponents, and developed a mixed logistic regression model to classify sex based on call-segment acoustic attributes. Males generally called at lower frequencies than females, with mean fundamental frequencies of 556 Hz and 666 Hz, respectively. Male four-note location calls were also longer than female calls, with signal median times of 1.99 s and 1.71 s, respectively. The middle-two-note and the full-call segment of the four-note location call were both useful for classifying sex of the calling owl. Our top-ranked models were able to predict 82–83% of our testing data consistent with expert classification as either male or female with 98–99% accuracy (17–18% of test set was classified as unknown). Our results suggest that acoustic characteristics of Northern Spotted Owl calls captured with ARUs can be used to identify whether sites have males and/or females present, and we suggest that further investigation into the full repertoire of Northern Spotted Owl call types is warranted.

**KEY WORDS:** *Northern Spotted Owl*; *Strix occidentalis caurina*; *bioacoustics*; *passive acoustic monitoring*; *vocal distinction*.

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## DISTINGUIENDO EL SEXO DE *STRIX OCCIDENTALIS CAURINA* MEDIANTE MONITOREO ACÚSTICO PASIVO

**RESUMEN.**—*Strix occidentalis caurina* es una especie de interés para la gestión y conservación en la región noroeste del Pacífico de los EEUU donde sus poblaciones han sido seguidas desde la década de 1990 mediante métodos de marcado y reavistamiento. El monitoreo acústico pasivo tiene el potencial de apoyar los esfuerzos de seguimiento; sin embargo, su uso está principalmente restringido a determinar la presencia de especies en lugar del estatus reproductivo. Distinguir las vocalizaciones entre hembras y machos de *S. o. caurina* utilizando métodos acústicos pasivos podría facilitar la determinación del estatus de las parejas reproductoras, mejorando ampliamente la inferencia derivada de los datos de seguimiento mediante métodos no invasivos. En 2017, colocamos 150 unidades de grabación autónomas (UGA) dentro de 30 hexágonos de 5 km<sup>2</sup> cubriendo los territorios recientemente ocupados por estos búhos en Oregon y Washington, EEUU, donde simultáneamente se utilizaban métodos de marcado y reavistamiento. Colectamos aproximadamente 150,000 horas de grabaciones y detectamos 22,458 vocalizaciones de *S. o. caurina* en 76 UGAs. Resumimos las vocalizaciones por tipo de llamada y encontramos diferencias en la proporción de tipos de llamadas realizadas por búhos solteros, en parejas y anidando. Utilizamos la opinión de expertos para clasificar 2812 llamadas de ubicación emitidas por machos o por hembras. Resumimos la variación entre sexos considerando 19 atributos acústicos de la llamada de ubicación de cuatro notas y sus subcomponentes, y desarrollamos un modelo de regresión logística mixto para clasificar el sexo en función de los atributos acústicos de segmentos de la llamada. Los machos generalmente cantan a frecuencias más bajas que las hembras, con frecuencias fundamentales medias de 556 Hz y 666 Hz, respectivamente. Las llamadas de ubicación de cuatro notas emitidas por los machos también fueron más largas que las llamadas emitidas por las hembras, con tiempos medios de señal de 1.99 s y 1.71 s, respectivamente. La nota dos del medio y el segmento de llamada completo de la llamada de ubicación de cuatro notas fueron útiles para clasificar el sexo del búho que emite la llamada. Nuestros modelos mejor clasificados fueron capaces de predecir el 82–83% de nuestros datos de testeo de acuerdo con la clasificación de expertos como macho o hembra, con una precisión del 98–99% (17–18% del set de testeo se clasificó como desconocido). Nuestros resultados sugieren que las características acústicas de las llamadas de *S. o. caurina* registradas con UGAs pueden utilizarse para identificar la presencia de machos y/o hembras en estos sitios. Finalmente, sugerimos que es necesario continuar investigando el repertorio completo de los tipos de llamadas emitidas por *S. o. caurina*.

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## INTRODUCTION

Northern Spotted Owls (*Strix occidentalis caurina*) are a species of management and conservation concern in the US Pacific Northwest and adjacent southwestern Canada (US Fish and Wildlife Service [USFWS] 1990, Lamberson et al. 1992, Lesmeister et al. 2018). Northern Spotted Owls are an obligate dweller of old-growth forest and populations have continued to decline with loss of these forests in the 21st century (USFWS 2020). However, more recent population declines have been exacerbated by the invasion of Barred Owls (*Strix varia*) in the Pacific Northwest (Peterson and Robins 2003, Dugger et al. 2011, Yackulic et al. 2019, Franklin et al. 2021, Wiens et al. 2021). Northern Spotted Owl population trends have been closely monitored with mark-resight and call-broadcast surveys for the past three decades (Franklin et al. 2021). Passive acoustic monitoring via autonomous acoustic recording units

(ARUs) offers an effective passive alternative to survey and monitor diminishing populations of Northern Spotted Owls (Duchac et al. 2020; Ruff et al. 2020; Lesmeister et al. 2021, 2021).

Passive acoustic monitoring produces recordings of behaviors and interactions within and between species unsolicited by surveyors, creating a permanent record of natural behavior (Laiolo 2010). Northern Spotted Owl vocalizations occur primarily at night and are an important aspect of social behavior and pair communication. The Northern Spotted Owl vocal repertoire contains 13 distinct call types, including some often associated with mated-pair communication and others mostly used by just one sex (Forsman et al. 1984). The full repertoire of Northern Spotted Owl vocalizations is an underutilized and potentially valuable monitoring tool if call types can be linked to a site's occupancy and breeding status (Wood et al. 2019, 2020).

Variation in acoustic properties within call types may provide valuable population information. The structural characteristics of calls, whether measured acoustically or examined visually using spectrograms, are useful indicators for distinguishing among different species (Duchac et al. 2020, Ruff et al. 2020), among call types within species (Ruff et al. 2021), and potentially among individuals (Odom and Mennill 2010, Zhou et al. 2020). The four-note location call is considered the primary call type of Spotted Owls and comprises four distinct hoots (or notes) that vary in pitch between females and males with females typically calling at a higher pitch (Ligon 1926, Forsman et al. 1984, Ganey 1990). This location call has also been used as a target of automated Northern Spotted Owl vocalization detection programs (e.g., Ruff et al. 2020). A preliminary spectrogram investigation of the Mexican Spotted Owl (*S. o. lucida*) four-note location call suggested that quantitative analysis of acoustic metrics could distinguish between calls made by individual owls (Kuntz and Stacey 1997). However, the difference between male and female Spotted Owl calls has not been systematically confirmed nor has call component variation within and between sexes been thoroughly described for any of the three Spotted Owl subspecies. Rather, thresholds of call frequency bounds from manually identified pair duets have been used to identify sex. For example, Wood et al. (2020) reported a threshold of 631 Hz to distinguish between the four-note location calls of male and female California Spotted Owls (*S. o. occidentalis*). The difference in pitch between sexes has also been documented in other raptors. Quantitative vocal analysis using acoustic metrics from recordings of Eurasian Eagle-Owls (*Bubo bubo*) and Barred Owls suggest the females of those species tend also to call at a higher pitch than males (Grava et al. 2008, Odom and Mennill 2010).

Our goals for the present study were to: (1) use ARU data to quantify inter-sex variation within acoustic metrics derived from the Northern Spotted Owl four-note location call and its sub-components, and (2) develop and test a predictive model to classify Northern Spotted Owl four-note location calls as male, female, or unknown with associated confidence levels to reduce the necessity of manual human review. We also summarized patterns of call types from sites associated with nesting pairs, non-nesting pairs, and unpaired Northern Spotted Owls.

## METHODS

**Passive Acoustic Monitoring.** We conducted passive acoustic monitoring targeting territorial pairs of Northern Spotted Owls concurrent with demography surveys that provided supporting information regarding social status and productivity (Duchac et al. 2020) from March–July 2017. We conducted surveys on three established Northern Spotted Owl demographic study areas on US Government lands in western Oregon and Washington, USA: the Klamath Mountains (KLA), the Oregon Coast Range (COA), and the Olympic Peninsula (OLY, see Duchac et al. 2020 and Franklin et al. 2021 for site descriptions). Demography surveys determined site occupancy status of historical territories as unoccupied or as occupied by an unpaired Northern Spotted Owl, a nesting pair, or a non-nesting pair (defined as a territorial pair with no evidence of breeding behavior; Franklin et al. 2021). The sampling design for passive acoustic surveys is described in detail in Duchac et al. (2020). We overlaid a grid of 5-km<sup>2</sup> hexagons across study areas and nonrandomly selected 10 nonadjacent hexagons in each study area that overlapped spatially with Northern Spotted Owl territories that were occupied in 2016 (D. Lesmeister unpubl. data). Within each of our 30 hexagons, we deployed five ARUs (Wildlife Acoustics Song Meter SM4s, Wildlife Acoustics, Maynard, MA, USA;  $n = 150$ ) in random locations with the following stipulations: US Government lands,  $\geq 250$  m apart,  $\geq 200$  m from the edge of a hexagon, and on mid-to-upper slopes (Duchac et al. 2020). We set ARUs to record from 1 hr before sunset to 2 hr after sunrise each night, 11–14 hr per night. We deployed ARUs for 3–4 mo (average 94 d, range 26–130 d). Hexagons were slightly larger than a Northern Spotted Owl territory core area (Glenn et al. 2004) and therefore recordings from within a single hexagon could represent a single territory or two nonoverlapping adjacent territories.

**Acoustic Data Processing.** We identified Northern Spotted Owl vocalizations within the acoustic recordings using the *simple clustering* feature of Kaleidoscope Pro (version 4.5; Wildlife Acoustics, Inc.), which detects sounds meeting user-defined criteria and sorts them into clusters by similarity, allowing efficient user review and application of identification tags corresponding to species and/or vocalization type (Duchac et al. 2020). We used this method to search for sounds between 0.5 and 7.5 s in duration with a maximum inter-syllable gap of 2 s, and between 0 and 1200 Hz in frequency, which was

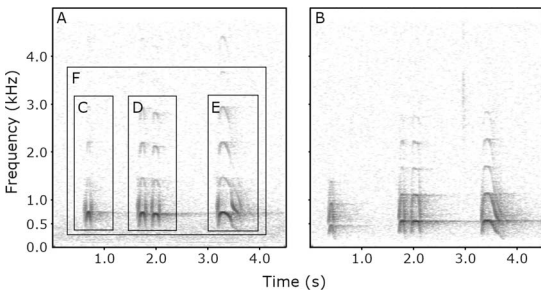


Figure 1. Spectrogram representing components of the four-note location call for (A) female, and (B) male Northern Spotted Owls where each component is represented as the (C) first note, (D) middle-two notes, (E) fourth note, and (F) full call.

effective in detecting a variety of vocalizations commonly produced by adult Northern Spotted Owls (Forsman et al. 1984, Duchac et al. 2020).

We isolated Northern Spotted Owl calls as short (8–12 s) clips and annotated by call type following characteristics described by Forsman et al. (1984) including: four-note location call, series location call, agitated location call, contact call, agitated contact call, bark series call, nest call, juvenile begging call, *wraack* call, and duets. Duets consisted of vocal exchanges between females and males. Some audio clips had multiple call types present. We summarized the proportion of call types observed within each hexagon and compared these with the Northern Spotted Owl pair status of each hexagon based on overlapping 2017 demography survey data.

We focused our sex classification analysis on the four-note location call (Fig. 1) because it is frequently produced by both sexes and has been observed to differ in pitch between females (Fig. 1A) and males (Fig. 1B; Ligon 1926, Forsman et al. 1984, Ganey 1990, Wood et al. 2020). We categorized recordings of four-note location calls by quality (high, moderate, and poor). High-quality calls contained little-to-no interfering background noise with a distinct, visible call signal on the spectrogram (high signal-to-noise ratio). Moderate-quality calls either had some background noise with a clearly visible signal or minimal background noise with a faint visible signal. Poor-quality calls had a weak signal barely distinguishable from background noise; we included these calls in the demographic analyses but excluded them from acoustic analyses.

We used an expert-opinion-based approach to classify the sex of all high- and moderate-quality

Northern Spotted Owl four-note location calls (2812 calls from 19 hexagons). Five experts with extensive Northern Spotted Owl field experience (5–30 yr each) performed individual blind classifications (audio and spectrogram were available for review) on a subset of 400 randomly selected high- and moderate-quality calls taken from hexagons known to contain pairs of owls where both members of each pair vocalized. The remainder of calls were classified by a single reviewer (S. Dale). We acknowledge that these classifications made by manually reviewing calls may not always result in correct classification of owl sex and that the sex of owls making calls in our sample was unknown; however, there was 96.5% agreement among the five experts' classifications for female and male four-note location calls, which we considered strong support for the accuracy of the remaining call classifications and correct classification of sex.

Some notes or segments of a call may be more variable than others (e.g., Rognan et al. 2009). We assessed call components to determine whether a portion of the four-note location call was more consistent for classifying female and male Northern Spotted Owl calls. We initially tested four segment options: the first note (Fig. 1C), the middle-two notes (Fig. 1D), the fourth note (Fig. 1E), and the full call (Fig. 1F). We edited recordings manually in Kaleidoscope Pro by drawing a bounding box around the call segment in the spectrogram viewer and applied a high-pass filter to remove any unrelated signals that overlapped the call at higher frequencies. We quantified 19 acoustic attributes from call segments relating to pitch, duration, and shape of the distribution of energy using the function *specan* in R package *warbleR* (Supplemental Material Table S1; Araya-Salas and Smith-Vidaurre 2017, R Core Team 2019). Metrics relating to call duration, maximum and minimum frequencies, and time have previously been used to differentiate calls of individual owls (Freeman 2000, Appleby and Redpath 2008) and to differentiate calls of female and male Barred Owls (Odom and Mennill 2010) and Great Spotted Kiwis (*Apteryx haastii*; Dent 2013). Initial tests of acoustic metrics generated from a random sample of each of the four call segments indicated that testing only the middle-two-note and full-call segments rather than the first-note and fourth-note segments was most useful (Supplemental Material Table S2, S3). Thus, we report complete results for only the full-call and middle-two-note segments.

**Female and Male Classification Analysis.** We compared male and female four-note location call segment metrics using mixed linear regression models with a fixed effect of sex. We generated 95% bootstrapped confidence intervals for modeled acoustic metric mean values using 100 simulations. We developed mixed logistic regression models to predict sex of calling owls (male = 1, female = 0) using an information-theoretic approach, with models ranked using Akaike's Information Criterion adjusted for sample size ( $AIC_c$ ). All models included a random effect of hexagon on the intercept to account for both repeated measures and uneven samples of calls within hexagons. Because our hexagons approximated the size of a Northern Spotted Owl territory core, calls originating from a hexagon likely came from the same individual(s) but may have come from adjacent territories overlapping a hexagon or non-territorial individuals. All analyses were run in program R (R Core Team 2019) using package *lme4* (Bates et al. 2015).

Prior to constructing models, we randomly split samples into training (80%) and testing (20%) subsets. We generated and ranked logistic regression models using the training subset and generated model performance metrics using the testing subset. We set our logistic regression classification threshold to 0.5. Because we wanted to be conservative in our classification of sex based on model predictions, we used prediction intervals (PI) to classify test samples as male, female, or unknown. Prediction intervals are more conservative than confidence intervals and incorporate variation due to random effects. We classified a test-set call segment as male if the entire 95% PI was  $> 0.5$ , classified a sample as female if the entire 95% PI was  $< 0.5$ , and classified any sample for which the 95% PI included 0.5 as unknown. We generated prediction intervals for our test data set using 1000 simulations with the *predictInterval* function from R package *merTools* (Knowles and Frederick 2020). We calculated five measures of model prediction accuracy. First, we calculated the proportion of the test set classified as unknown for each model (PU). Next, using confusion matrix terminology, we calculated the accuracy of male predictions ( $A_M$ ), accuracy of female predictions ( $A_F$ ), and accuracy of both female and male predictions ( $A_{All}$ ) as  $[True\ Positives]/[True\ Positives + False\ Positives]$ , omitting samples labeled "unknown." Finally, we estimated an overall model performance score (PS) as the ratio of  $A_{All}$  to PU,

where a higher PS indicates higher predictive performance.

We used a multi-stage model development strategy (Morin et al. 2020) to develop our model sets. We started by fitting and ranking single-variable models, considering models with single variables as useful in classifying calls as female and male if they ranked above the intercept-only model. After ranking the single-variable models, one single-variable model represented 100% of the model weight for both the full-call segment and middle-two-note segment training data sets. To evaluate if more complex models had higher support (i.e., lower  $AIC_c$  values) and/or improved model performance (higher PS score), we used a build-up strategy by adding additional supported and uncorrelated (Spearman's rank correlation  $< |0.70|$ ) variables to the top-ranked single-variable models and subsequent top-ranked multi-variable models (Supplemental Material Table S4, S5).

We performed k-means clustering using fixed variables from the top-ranked logistic regression models as a blind test of classification accuracy (Maechler et al. 2021). K-means clustering is a blind clustering method where each observation is sorted into one of k clusters, in this case  $k = 2$  for females and males. We reported the percent of females and males (assigned by experts) from our entire sample that were sorted into each blind cluster. Assuming that our experts' classifications were correct, a useful set of variables should produce a cluster with more of one sex than the other. We also classified ten confirmed female and 50 confirmed male call recordings collected in northern California, USA (M. Higley, A. Pole, H. Hooran, pers. comm.), using top models with 95% prediction intervals.

## RESULTS

We manually classified 19,953 recordings of vocalizations of Northern Spotted Owls to call type from 76 ARUs in 25 hexagons overlapping historical territories monitored by demographic crews in 2017 (Table 1). We detected the highest number of calls from hexagons overlapping territories with pairs of Northern Spotted Owls. One ARU was placed at random within 20 m of a nest and recorded  $> 7000$  Northern Spotted Owl vocalizations, which accounted for approximately 36% of all calls identified from all ARUs in the study. We detected the four-note location call in all 25 hexagons and did not detect any other call types in the two hexagons occupied by single owls or in the two hexagons that demography

Table 1. The proportions of call types of Northern Spotted Owl vocalizations detected in recordings from autonomous recording units (ARUs) in 5-km<sup>2</sup> hexagons overlapping Northern Spotted Owl historical territories surveyed in Washington (OLY) and Oregon (COA and KLA), USA, in 2017. Hexagons are grouped by occupancy status as determined by field crews performing concurrent demographic surveys.

| HEXAGON | STATUS            | ARUS <sup>b</sup> | PROPORTIONS OF CALL TYPES <sup>a</sup> |      |        |        |        |        |      |        |        |        |        |
|---------|-------------------|-------------------|----------------------------------------|------|--------|--------|--------|--------|------|--------|--------|--------|--------|
|         |                   |                   | CALLS                                  | FNLC | SLC    | ALC    | CC     | ACC    | NC   | JBC    | WC     | BS     | DUET   |
| COA 9   | Unoccupied        | 1                 | 1                                      | 1.00 | 0.00   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| KLA 6   | Unoccupied        | 3                 | 18                                     | 1.00 | 0.00   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| COA 4   | Single (unpaired) | 1                 | 13                                     | 1.00 | 0.00   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| OLY 4   | Single (unpaired) | 2                 | 71                                     | 1.00 | 0.00   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| COA 1   | Paired            | 5                 | 226                                    | 1.00 | < 0.01 | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| COA 2   | Paired            | 2                 | 28                                     | 0.96 | 0.04   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| COA 7   | Paired            | 5                 | 52                                     | 0.56 | 0.02   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.42   | 0.00   |
| COA 8   | Paired            | 4                 | 1469                                   | 0.34 | 0.62   | 0.02   | 0.05   | < 0.01 | 0.00 | 0.01   | < 0.01 | 0.06   | 0.01   |
| KLA 1   | Paired            | 5                 | 2973                                   | 0.91 | 0.20   | 0.00   | < 0.01 | 0.00   | 0.00 | 0.00   | 0.00   | 0.02   | < 0.01 |
| KLA 2   | Paired            | 5                 | 495                                    | 0.58 | 0.09   | 0.00   | 0.02   | 0.00   | 0.00 | 0.00   | 0.00   | 0.34   | 0.01   |
| KLA 4   | Paired            | 4                 | 181                                    | 0.81 | 0.18   | 0.03   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.01   | 0.04   |
| KLA 5   | Paired            | 4                 | 1040                                   | 0.40 | 0.18   | 0.01   | 0.12   | 0.01   | 0.05 | < 0.01 | < 0.01 | 0.35   | 0.02   |
| KLA 7   | Paired            | 5                 | 1670                                   | 0.49 | 0.21   | 0.01   | 0.15   | 0.00   | 0.08 | 0.00   | 0.00   | 0.19   | 0.04   |
| OLY 2   | Paired            | 2                 | 201                                    | 0.92 | 0.04   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.07   | 0.00   |
| COA 3   | Nesting           | 4                 | 112                                    | 0.99 | 0.03   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| COA 5   | Nesting           | 4                 | 1517                                   | 0.46 | 0.62   | < 0.01 | 0.04   | 0.00   | 0.00 | 0.00   | < 0.01 | 0.03   | 0.01   |
| COA 6   | Nesting           | 1                 | 1                                      | 1.00 | 0.00   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| KLA 3   | Nesting           | 3                 | 652                                    | 0.48 | 0.45   | 0.00   | 0.15   | 0.00   | 0.01 | 0.00   | < 0.01 | 0.09   | 0.01   |
| KLA 8   | Nesting           | 3                 | 7141                                   | 0.17 | 0.19   | 0.01   | 0.65   | < 0.01 | 0.05 | 0.02   | 0.00   | 0.03   | 0.08   |
| KLA 9   | Nesting           | 3                 | 758                                    | 0.92 | 0.03   | < 0.01 | 0.07   | 0.00   | 0.00 | 0.00   | 0.00   | 0.01   | 0.04   |
| KLA 10  | Nesting           | 5                 | 1030                                   | 0.92 | 0.25   | 0.00   | < 0.01 | 0.00   | 0.00 | 0.00   | 0.00   | < 0.01 | 0.00   |
| OLY 1   | Nesting           | 1                 | 140                                    | 0.16 | 0.02   | 0.00   | 0.77   | 0.03   | 0.00 | 0.00   | 0.00   | 0.07   | 0.01   |
| OLY 3   | Nesting           | 1                 | 13                                     | 1.00 | 0.00   | 0.00   | 0.00   | 0.00   | 0.00 | 0.00   | 0.00   | 0.00   | 0.00   |
| OLY 5   | Nesting           | 2                 | 81                                     | 0.82 | 0.05   | 0.03   | 0.24   | 0.00   | 0.00 | 0.11   | 0.00   | 0.03   | 0.10   |
| OLY 6   | Nesting           | 1                 | 70                                     | 0.11 | 0.14   | 0.01   | 0.70   | 0.06   | 0.00 | 0.00   | 0.00   | 0.10   | 0.04   |

<sup>a</sup> Proportion of call types within our sample of isolated Northern Spotted Owl calls. We considered each 8–12 s audio clip as a call which could contain more than one call type; thus proportions do not always sum to 1. Abbreviations: FNLC is four-note location call, SLC is series location call, ALC is agitated location call, CC is contact call, ACC is agitated contact call, NC is nest call, JBC is juvenile begging call, WC is wrack call, BS is bark series call, and DUET comprises vocal exchanges between females and males including any of these call types other than WC.

<sup>b</sup> The number of ARUs within a hexagon that recorded a Northern Spotted Owl call that we were able to identify.

surveys considered unoccupied by Northern Spotted Owls (Table 1). We found between one and nine call types in hexagons with confirmed nesting pairs (11 hexagons), and one to eight call types in hexagons overlapping territories occupied by non-nesting pairs (10 hexagons). The four-note location call was the most abundant call type for all but five occupied hexagons. At one hexagon with a non-nesting pair and one hexagon with a nesting pair, the series location call was the most common (62% of calls) and at three hexagons with confirmed nesting pairs, the contact call was most frequently recorded (64–77% of calls; Table 1).

We classified 2812 four-note location calls from 19 hexagons as high- or moderate-quality. The middle-

two-note segment data set included 1015 calls classified as females and 1797 calls classified as males (training subset, F = 809, M = 1414; testing subset, F = 206, M = 383). Our full-call segment data sample included 1017 calls classified as females and 1744 calls classified as males (training subset, F = 811, M = 1371; testing subset, F = 206, M = 373). The difference in sample sizes among call segment groups was due to the inability of the function *specan* to summarize metrics for some of the calls.

Nine full-call segment metrics had bootstrapped 95% confidence intervals for male and female calls that did not overlap (Table 2). Time metrics (see Supplemental Material Table S1 for description of metrics and associated abbreviations) for the full-call

Table 2. Acoustic metrics of female and male full-call segments of the Northern Spotted Owl four-note location call and bootstrapped 95% confidence intervals (CI). Metric means and bootstrapped 95% CI lower (lcl) and upper limits (ucl) from linear mixed-effect models of a fixed effect of sex and random effect of hexagon. Northern Spotted Owl calls were collected in 2017 with autonomous acoustic recorder units in western Oregon and Washington, USA.

| METRIC <sup>a</sup>   | FEMALE  |         |         | MALE    |         |         |
|-----------------------|---------|---------|---------|---------|---------|---------|
|                       | MEAN    | LCL     | UCL     | MEAN    | LCL     | UCL     |
| DUR <sup>b</sup>      | 3.45    | 3.34    | 3.60    | 3.96    | 3.85    | 4.09    |
| TIME.IQR <sup>b</sup> | 1.75    | 1.64    | 1.81    | 1.94    | 1.84    | 2.01    |
| TIME.MDN <sup>b</sup> | 1.71    | 1.63    | 1.78    | 1.99    | 1.91    | 2.05    |
| TIME.Q25 <sup>b</sup> | 0.91    | 0.88    | 0.96    | 1.14    | 1.11    | 1.20    |
| TIME.Q75 <sup>b</sup> | 2.66    | 2.56    | 2.75    | 3.08    | 2.97    | 3.17    |
| FUN.MIN <sup>b</sup>  | 0.56    | 0.55    | 0.57    | 0.48    | 0.47    | 0.50    |
| FUN.MAX <sup>b</sup>  | 0.74    | 0.73    | 0.76    | 0.61    | 0.60    | 0.63    |
| FUN.MN <sup>b</sup>   | 0.67    | 0.65    | 0.68    | 0.56    | 0.54    | 0.57    |
| FREQ.IQR              | 0.52    | 0.46    | 0.57    | 0.54    | 0.48    | 0.60    |
| FREQ.MDN              | 0.51    | 0.46    | 0.58    | 0.49    | 0.44    | 0.55    |
| FREQ.Q25              | 0.28    | 0.20    | 0.38    | 0.25    | 0.18    | 0.35    |
| FREQ.Q75              | 0.28    | 0.20    | 0.37    | 0.25    | 0.18    | 0.35    |
| PEAKF <sup>b</sup>    | 0.65    | 0.63    | 0.67    | 0.53    | 0.52    | 0.54    |
| FREQ.MN               | 0.58    | 0.52    | 0.63    | 0.56    | 0.50    | 0.61    |
| PEAKF.MN              | 0.35    | 0.31    | 0.41    | 0.29    | 0.24    | 0.34    |
| SD                    | 0.41    | 0.39    | 0.44    | 0.40    | 0.38    | 0.44    |
| HARM                  | -2.80   | -3.53   | -2.02   | -2.17   | -3.01   | -1.50   |
| KURTOSIS              | 3260.00 | 2568.06 | 3980.24 | 3824.00 | 3146.09 | 4499.80 |
| SKEW                  | 50.47   | 43.15   | 59.27   | 55.28   | 48.03   | 63.32   |

<sup>a</sup> Abbreviations: DUR is duration, FREQ.MN is mean frequency, SD is standard deviation of frequency, FREQ.MDN is median frequency, FREQ.Q25 is first quartile frequency, FREQ.Q75 is third quartile frequency, FREQ.IQR is interquartile frequency range, TIME.MDN is signal median time, TIME.Q25 is first quartile time, Time.Q75 is third quartile time, TIME.IQR is interquartile time range, SKEW is asymmetry of the spectrum, KURTOSIS is peakedness of spectrum, PEAKF.MN is mean peak frequency, PEAKF is peak frequency, HARM is harmonics, FUN.MN is mean fundamental frequency, FUN.MAX is maximum fundamental frequency, and FUN.MIN is minimum fundamental frequency. See Supplemental Material Table S1 for further descriptions of these metrics.

<sup>b</sup> These metrics have 95% CIs that do not overlap.

segments were greater for male calls than female calls including duration (DUR), interquartile time range (TIME.IQR), median time (TIME.MDN), first quartile time (TIME.Q25), and third quartile time (TIME.Q75; Table 2). Metrics describing fundamental frequency measured across the acoustic signal (FUN.MIN, FUN.MAX, and FUN.MN) and the frequency with the highest energy (PEAKF) were greater for female calls than male calls (Table 2). The top-ranked full-call segment mixed logistic regression model, with 65% of the model set weight, included mean fundamental frequency, median time, interquartile frequency range, and harmonics (HARM; Table 3, Supplemental Material Table S6). Male calls had a lower mean fundamental frequency ( $\beta = -4.19$ , 95% CI = -4.80, -3.60), a longer median time ( $\beta = 1.35$ , 95% CI = 1.13, 1.67), a higher interquartile frequency range ( $\beta = 0.41$ , 95% CI = 0.17, 0.74), and lower harmonics ( $\beta = -0.32$ , 95% CI = -0.55, -0.06) than females (Table 4). All top-ranked full-call

models performed similarly based on testing subset performance metrics (Table 3). The top-ranked model classified 83% of the test data set as either male or female and 17% as unknown based on our 95% prediction interval (Table 3; Fig. 2). Ninety-nine percent of all predicted male and female calls were correctly classified. The top-ranked single-variable model (FUN.MN,  $\beta = -0.32$ , 95% CI = -0.58, -0.09) had an overall accuracy score of 0.98, 1% lower than the accuracy of our top-ranked multivariate model and classified a similar proportion of male and female calls. K-means blind clustering using the four variables in the top-ranked model performed well, with one cluster including 84% of total females and the second cluster containing 96% of total males. Our full-call model classified 98% of control calls (i.e., known-sex vocalizations) accurately (8 female, 45 male). One female call was misclassified as a male call and six control calls (1 female, 5 male) were classified as unknown.

Table 3. Model selection and classification accuracy scores for the top-ranked mixed logistic regression models for distinguishing male and female full-call segments and middle-two-note segments of the Northern Spotted Owl four-note location call. Calls were collected in 2017 with autonomous acoustic recorder units in western Oregon and Washington, USA. The intercept-only model is also included for reference. K is the number of parameters, LL is the log-likelihood,  $\Delta AIC_c$  is the difference in Akaike’s Information Criterion adjusted for sample size from the top model, w is the Akaike’s weight,  $A_{All}$  is overall prediction accuracy score,  $A_M$  is the prediction accuracy score for males,  $A_F$  is the prediction accuracy score for females, PU is the proportion of the test dataset classified as “unknown” based on 95% prediction intervals, and PR is the overall model performance score.

| CALL<br>SEGMENT | RANK | MODEL <sup>a</sup>                      | K | LL       | $\Delta AIC_c^b$ | w    | $A_M$ | $A_F$ | $A_{ALL}$ | PU   | PR   |
|-----------------|------|-----------------------------------------|---|----------|------------------|------|-------|-------|-----------|------|------|
| Full-call       | 1    | FUN.MN + TIME.MDN+ FREQ.IQR + HARM      | 6 | -272.63  | 0.00             | 0.65 | 0.99  | 0.99  | 0.99      | 0.17 | 5.97 |
|                 | 2    | FUN.MN + TIME.MDN + FREQ.IQR            | 5 | -275.76  | 4.23             | 0.08 | 0.99  | 1.00  | 0.99      | 0.17 | 5.86 |
|                 | 3    | FUN.MN + TIME.MDN + PEAKF.MN + HARM     | 6 | -274.94  | 4.61             | 0.06 | 0.99  | 1.00  | 0.99      | 0.16 | 6.17 |
|                 | 4    | FUN.MN + TIME.MDN + FREQ.IQR + PEAKF.MN | 6 | -275.09  | 4.92             | 0.06 | 0.99  | 0.99  | 0.99      | 0.17 | 5.91 |
|                 | 5    | FUN.MN + TIME.MDN + PEAKF.MN            | 5 | -276.58  | 5.88             | 0.03 | 0.99  | 1.00  | 0.99      | 0.16 | 6.04 |
|                 | 6    | FUN.MN + TIME.MDN + HARM                | 5 | -276.69  | 6.10             | 0.03 | 0.99  | 1.00  | 0.99      | 0.16 | 6.04 |
|                 | 7    | FUN.MN + TIME.MDN                       | 4 | -278.13  | 6.96             | 0.02 | 0.99  | 1.00  | 0.99      | 0.16 | 6.04 |
|                 | 44   | NULL (intercept only)                   | 2 | -1118.76 | 1684.23          | 0.00 | 0.98  | 0.00  | 0.98      | 0.91 | 1.08 |
| Middle-two-note | 1    | FUN.MAX + FUN.MIN + TIME.IQR + PEAKF.MN | 6 | -325.57  | 0.00             | 1.00 | 0.99  | 0.96  | 0.98      | 0.18 | 5.52 |
|                 | 35   | NULL (intercept only)                   | 2 | -1164.40 | 1669.63          | 0.00 | 0.98  | 0.00  | 0.98      | 0.91 | 1.08 |

<sup>a</sup> All models included a random effect of hexagon to account for repeated samples coming from within individual 5-km<sup>2</sup> hexagons that approximated Northern Spotted Owl territory core areas. Covariate abbreviations are defined in the footnote of Table 2 and in Table S1 of the Supplemental Material.

<sup>b</sup> The  $AIC_c$  value for the top-ranked full-call segment model set was 557.307 and the  $AIC_c$  value for the top-ranked middle-two note segment model set was 663.174.

Table 4. Parameter estimates and 95% bootstrapped confidence intervals for fixed effects from the two top-ranked mixed logistic regression models for distinguishing male and female full-call segments and middle-two-note segments of the Northern Spotted Owl four-note location call. Calls were collected in 2017 with autonomous acoustic recorder units in western Oregon and Washington, USA.

| SEGMENT         | PARAMETER <sup>b</sup> | MODEL 1 <sup>a</sup> |              | MODEL 2  |              |
|-----------------|------------------------|----------------------|--------------|----------|--------------|
|                 |                        | ESTIMATE             | 95% CI       | ESTIMATE | 95% CI       |
| Full-call       | Intercept              | 3.05                 | 1.81, 4.31   | 3.02     | 1.80, 4.90   |
|                 | FUN.MN                 | -4.19                | -4.80, -3.60 | -4.10    | -4.59, -3.61 |
|                 | TIME.MDN               | 1.35                 | 1.13, 1.67   | 1.37     | 1.10, 1.66   |
|                 | FREQ.IQR               | 0.41                 | 0.17, 0.74   | 0.30     | 0.08, 0.56   |
|                 | HARM                   | -0.32                | -0.55, -0.06 | -        | -            |
| Middle-two-note | Intercept              | 2.93                 | 1.58, 4.13   | 2.86     | 1.81, 3.79   |
|                 | FUN.MAX                | -3.80                | -4.41, -3.41 | -3.83    | -4.30, -3.39 |
|                 | FUN.MIN                | -0.87                | -1.10, -0.66 | -1.03    | -1.22, -0.85 |
|                 | TIME.IQR               | -0.50                | -0.84, -0.29 | -0.37    | -0.65, -0.14 |
|                 | PEAKF.MN               | -0.52                | -0.77, -0.24 | -        | -            |

<sup>a</sup> Model 1 full-call segment = FUN.MN + TIME.MDN+ FREQ.IQR + HARM, Model 2 full call segment = FUN.MN + TIME.MDN + FREQ.IQR, Model 1 middle-two-note segment = FUN.MAX + FUN.MIN + TIME.IQR + PEAKF.MN, Model 2 middle-two=note segment = FUN.MAX + FUN.MIN + TIME.IQR.

<sup>b</sup> Covariate abbreviations are defined in the footnote of Table 2 and in Table S1 of the Supplemental Material.

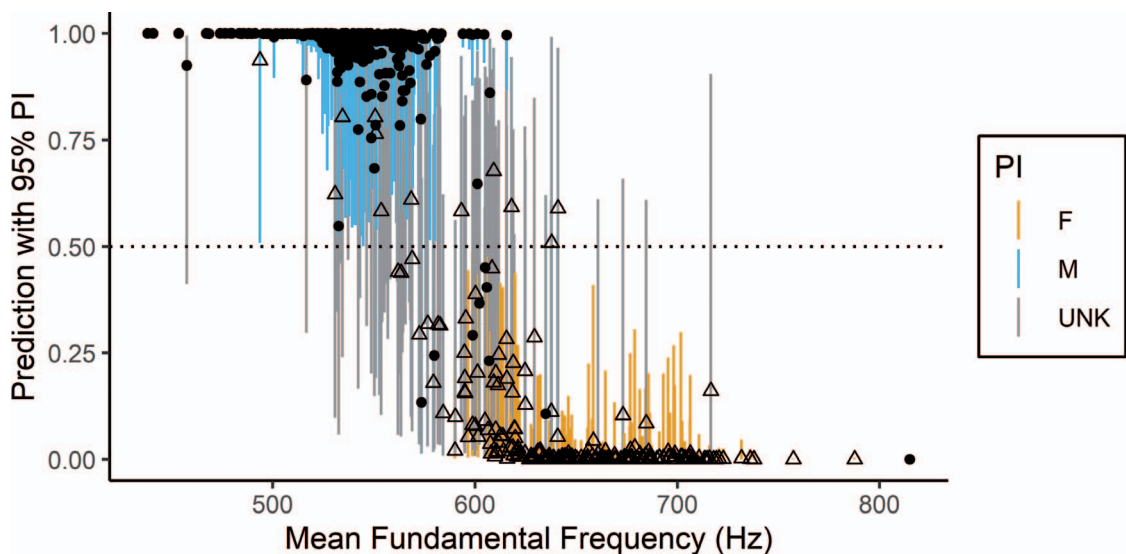


Figure 2. Training-set mean and 95% prediction intervals (PI) generated using the top-ranked logistic regression model from the full-call segment of the Northern Spotted Owl four-note location call plotted with mean fundamental frequency. Samples that were classified as male or female by our manual reviewers are shown as black dots and triangles, respectively with model 95% PI colored according to classification as male (M), female (F) or unknown (UNK). Calls were collected in 2017 with autonomous acoustic recorder units in western Oregon and Washington, USA.

The bootstrapped 95% confidence intervals did not overlap between male and female middle-two-note segments for four metrics that described fundamental frequency measured across the acoustic signal (FUN.MIN, FUN.MAX, and FUN.MN) and the frequency with the highest energy (PEAKF), which were greater for female calls than male calls (Supplemental Material Table S7). The top-ranked middle-two-note segment mixed logistic regression model, with 100% of the model-set weight, included: maximum fundamental frequency, minimum fundamental frequency, interquartile time range, and mean peak frequency (PEAKF.MN; Table 3, Supplemental Material Table S8). Compared to females, males had a lower FUN.MAX ( $\beta = -3.80$ , 95% CI: -4.41, -3.41), lower FUN.MIN ( $\beta = -0.87$ , 95% CI: -1.10, -0.66), shorter TIME.IQR ( $\beta = -0.50$ , 95% CI: -0.84, -0.29), and shorter PEAKF.MN ( $\beta = -0.52$ , 95% CI: -0.77, -0.24; Table 4). The top-ranked model classified 82% of the test data set as either male or female and 18% as unknown based on our 95% prediction interval (Table 3; Fig. 3). Ninety-eight percent of all predicted male and female classifications matched our manual classification. The top-ranked single-variable model (FUN.MAX,  $\beta = -4.03$ , 95% CI = -4.67, -3.58) also had an overall accuracy score of 0.98 with a slightly

higher number of unknowns (PU = 0.20). K-means clustering using variables from the top-ranked logistic regression model of the middle-two-note segment clustered 85.4% of male calls together and 81.4% of female calls together. Our middle-two-note call model classified 100% of control vocalizations accurately (8 female, 49 male). Three control calls (2 female, 1 male) were classified as unknown.

DISCUSSION

Like call patterns observed in other owl species (Delpont et al. 2002, Grava et al. 2008, Odom and Mennill 2010, Odom et al. 2013), female Spotted Owl location calls tend to be higher pitched than male calls (Ligon 1926, Forsman et al. 1984, Ganey 1990). However, we found that using a simple frequency threshold is unlikely to result in efficient sex classification due to overlap in the distribution of several acoustic metrics between sexes. Previous quantitative investigations of owl vocalizations have suggested that metrics related to pitch may be less useful than temporal variables (e.g., call-note duration) for distinguishing individuals within a species (Odom et al. 2013, Zhou et al. 2020). Our top-ranked logistic regression models included variables relating to both pitch (e.g., mean fundamental

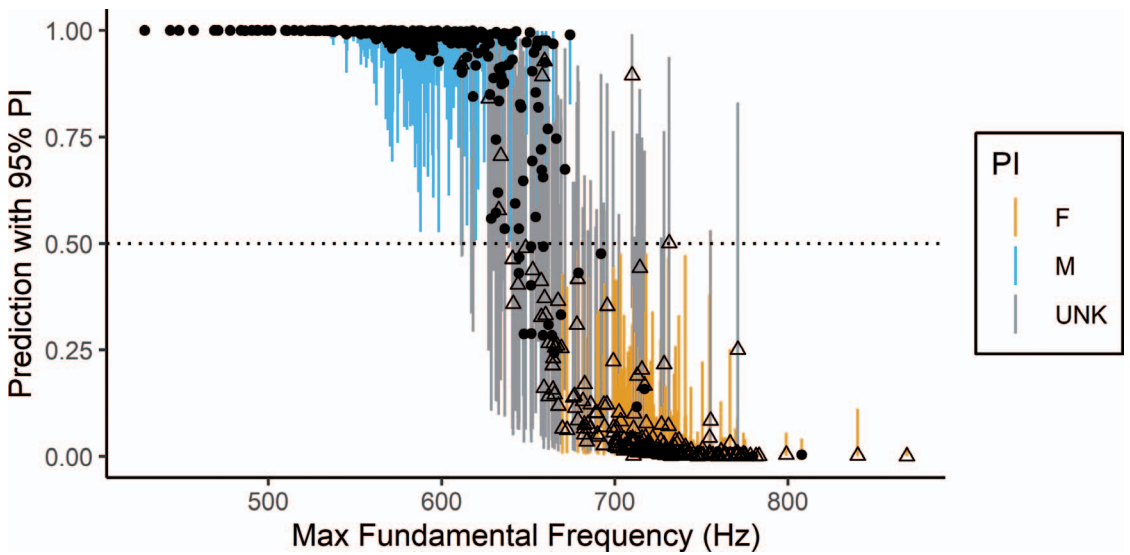


Figure 3. Training-set mean predictions and 95% prediction intervals (PI) generated using the top-ranked logistic-regression model from the middle-two-note segment of the Northern Spotted Owl four-note location call plotted along maximum fundamental frequency. Samples that were classified as male or female by our manual reviewers are shown as black dots and triangles, respectively with model 95% PI colored according to classification as male (M), female (F) or unknown (UNK). Calls were collected in 2017 with autonomous acoustic recorder units in western Oregon and Washington, USA.

frequency) and time (e.g., signal median time). However, the maximum fundamental frequency and average fundamental frequency of the four-note location call segments were more strongly related to sex classification than temporal metrics, based on ranking of single-variable logistic regression models (Supplemental Material Table S6, S8). The fundamental frequency is the lowest harmonic, or frequency component, of an acoustic signal (Klapuri 2003). The maximum and minimum fundamental frequencies are the highest and lowest values of the fundamental frequency of a signal, and the mean fundamental frequency is the average value of the fundamental frequency over the entire signal (Araya-Salas and Smith-Vidaurre 2017). Our top predictive model, which had an overall accuracy rate of 99%, classified 18% of test set calls as unknowns based on the 95% PI, suggesting there is some overlap between acoustic call metrics between sexes. Additionally, we were able to correctly classify the sex of most of our control samples taken from outside of our sampling region. We believe that our method, which incorporates prediction intervals, will allow for automated sex classification and will be an important contribution to broad-scale passive acous-

tic monitoring focused on Northern Spotted Owl populations.

We tested two segments of the four-note location call for differences between male and female calls. Although the top-ranked logistic regression models for both call segments performed similarly well ( $A_{all} = 98\text{--}99\%$ ), there were stronger differences in temporal metrics for the full-call segment. There is likely greater variability in temporal aspects of the first and fourth note, which are not present in the middle-two-note segment. Rognan et al. (2009) chose to omit the introductory note in their Great Gray Owl (*Strix nebulosa*) vocalization study due to its variability, which made deriving accurate metrics difficult. Our analyses indicate that both the full-call and middle-two-note segments of the four-note location call of Northern Spotted Owls can be used to distinguish sex in this species with accuracy comparable to human experts.

Although our primary objective was to establish methods for classifying female and male Northern Spotted Owls using the four-note location call, we also collected data describing their diverse vocal repertoire. The four-note location call was the only call type we detected in hexagons overlapping territories occupied by single (unpaired) Northern

Spotted Owls. Nest calls were detected in hexagons overlapping territories designated as both nesting and non-nesting by our demographic survey crews; this could be an indication that declining detection probabilities lead to the demographic survey missing a nesting attempt or that non-nesting pairs make these nest calls. Mangan et al. (2019) found that when Barred Owls were present it was more difficult for demographic surveys to detect Northern Spotted Owl nesting attempts. The rates of detected call-types from hexagons overlapping nesting and non-nesting pairs and single Northern Spotted Owls suggested that ratios of call types within sample locations may also be useful to make inferences about the presence and breeding status of a pair. Additionally, territorial calls, such as the four-note location call, are more commonly given by male owls, so it is often assumed that females call less frequently. However, females may more often utilize call types not considered in analyses of territorial vocalizations (Terry et al. 2005). Further analyses exploring contact call duets, as described by Forsman et al. (1984) and by Ganey (1990) for Mexican Spotted Owls, could improve understanding of the calling behavior of female and male Northern Spotted Owls.

Passive acoustic monitoring is fundamentally transforming the spatial and temporal scale of avian research and population monitoring (Shonfield and Bayne 2017, Wood et al. 2020, Lesmeister et al. 2021), and ushering in an era of next-generation natural history (Tosa et al. 2021). Like other remote sensing technologies, the magnitude of data produced with passive acoustic monitoring makes automation of data processing and interpretation vital for timely and efficient analysis. Ruff et al. (2020) developed a deep convolutional neural network model that automates the identification of potential Northern Spotted Owl four-note location calls in ARU monitoring data. Our top-ranked sex classification model can be used to expand the data processing workflow of Ruff et al. (2021) to further classify identified four-note location calls based on sex (or unknown). These advancements have greatly improved insights into Northern Spotted Owl territory social status using passive methods. Further research directly comparing social status of owls inferred from passive acoustic monitoring to results obtained from traditional mark-resight methods would improve both interpretation of passive acoustic monitoring results and connectivity with historical data. This could allow monitoring programs to

infer not only Spotted Owl presence at a survey site, but also demographic status, based solely on passive acoustic monitoring.

SUPPLEMENTAL MATERIAL (available online). Table S1: Descriptions of spectrogram analysis metrics used to describe Northern Spotted Owl vocalizations derived from autonomous acoustic monitoring units in western Oregon and Washington, USA, 2017. Table S2: Mean acoustic metric values with bootstrapped 95% confidence intervals from a random subset of the first-note segment of the Northern Spotted Owl four-note location call collected with autonomous acoustic monitoring units in western Oregon and Washington, USA, 2017. Table S3: Mean acoustic metric values with bootstrapped 95% confidence intervals from a random subset of male and female fourth-note segment of the Northern Spotted Owl four-note location call. Table S4: Spearman's correlation matrix for acoustic metrics summarizing the full-call segment of the Northern Spotted Owl four-note location call. Table S5: Spearman's correlation matrix for acoustic metrics summarizing the middle-two-note segment of the Northern Spotted Owl four-note location call. Table S6: Full model selection ranking of the mixed logistic regression model set for distinguishing male and female full-call segment of the Northern Spotted Owl four-note location call. Table S7: Metric mean and bootstrapped 95% confidence interval lower (lcl) and upper limits (ucl) from linear mixed-effect models of a fixed effect of sex and random effect of hexagon. Table S8: Model selection ranking of the mixed logistic-regression model set for distinguishing male and female middle-two-note call segments of the Northern Spotted Owl four-note location call.

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