

FACTORS INFLUENCING THE DETECTABILITY OF FOREST OWLS IN SOUTHEASTERN ALASKA

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Abstract. Patch-occupancy models offer a realistic approach to monitoring populations of nocturnal owls. However, because most owls are relatively rare, increasing the probability of detecting an owl at an occupied site will make estimates of occupancy more precise. We investigated the influence of temporal, biological, and environmental factors on rates of detection of forest owls in southeastern Alaska, 2005–2006. Following MacKenzie et al. (2006), we modeled probabilities of detection of the Northern Saw-whet Owl (*Aegolius acadicus*), Western Screech-Owl (*Megascops kennicottii*), and Barred Owl (*Strix varia*). We conducted 479 point counts over 100 days and detected owls 147 times. Sound broadcast increased detections 21–86% over silent surveys. During peak detection (9 April–8 May), probabilities (SE) of detection were 0.39 (0.13) for the Western Screech, 0.44 (0.16) for the Saw-whet, and 0.54 (0.25) for the Barred. For the Barred and Saw-whet, estimated occupancy probabilities (ψ) were constant (i.e., did not vary with covariates), but for the Western Screech, ψ was a function of whether large owls had been detected at a site, with estimated ψ about 66% lower at sites with large owls. For the Western Screech detection probability increased after sunset. For the Barred, the pattern of detection probability was non-linear in relation to time after sunset, being high near sunset and late at night. For the Saw-whet detection probabilities were most influenced by weather covariates, primarily precipitation and wind. We provide recommendations on allocating survey effort and increasing probabilities of detection of these three owls in southeastern Alaska.

Key words: Barred Owl, detection probability, Northern Saw-whet Owl, occupancy, point count, Western Screech-Owl.

Factores que Influyen la Detectabilidad de Lechuzas en el Sudeste de Alaska

Resumen. Los modelos de ocupación de parches ofrecen una aproximación realista para monitorear poblaciones de lechuzas nocturnas. Sin embargo, la mayoría de las especies de lechuzas son relativamente raras, por lo que aumentar la probabilidad de detectar una lechuza en un sitio ocupado hará que los estimados de ocupación sean más precisos. Investigamos la influencia de factores temporales, biológicos y ambientales sobre las tasas de detección de lechuzas de bosque en el sur de Alaska, entre 2005 y 2006. Siguiendo a MacKenzie et al. (2006), modelamos las probabilidades de detección de *Aegolius acadicus*, *Megascops kennicottii* y *Strix varia*. Realizamos 479 conteos en puntos en un periodo de 100 días y detectamos lechuzas 147 veces. La reproducción de llamadas de lechuzas aumentó las detecciones en un 21–86% con relación a los muestreos silenciosos. Durante el periodo de mayor detección (9 abril–8 mayo), las probabilidades de detección (EE) fueron 0.39 (0.13) para *M. kennicottii*, 0.44 (0.16) para *A. acadicus* y 0.54 (0.25) para *S. varia*. Para *A. acadicus* y *S. varia*, las probabilidades de ocupación (ψ) fueron constantes (i.e., no variaron con las covariables), pero para *M. kennicottii* ψ dependió de la detección previa de especies de lechuza de gran tamaño en el sitio, con una ψ estimada que fue 66% más baja en sitios con lechuzas de gran tamaño. Para *M. kennicottii*, la probabilidad de detección aumentó después de la puesta del sol. Para *S. varia*, el patrón de detectabilidad no fue lineal con relación al tiempo transcurrido desde la puesta del sol, siendo alta cerca de la puesta del sol y tarde en la noche. Para *A. acadicus*, las probabilidades de detección estuvieron más influenciadas por las covariables relacionadas al clima, principalmente precipitación y viento. Brindamos recomendaciones de asignación de esfuerzos en los muestreos para aumentar las probabilidades de detección de estas tres especies de lechuzas en el sudeste de Alaska.

INTRODUCTION

With the exception of a few species of conservation concern, little is known about the distribution, abundance, and population trend of nocturnal owls in North America (Takats et al.

2001). Because of their general rarity, elusive behavior, and nocturnal habits, most owls are poorly monitored by existing multi-species surveys (e.g., Breeding Bird Survey, Raptor Migration Monitoring; Takats et al. 2001). Therefore, for monitoring of populations of nocturnal owls, specific surveys are

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required, but effective survey methods vary geographically and by species. Point-count surveys are the most common method for monitoring the relative abundance, distribution, and habitat of breeding owls (Andersen 2007). For nocturnal owls, however, point-count surveys are susceptible to incomplete detectability or false absences (i.e., failure to detect an owl when present), which if not accounted for, can lead to biased estimates and misleading inferences (Thompson et al. 1998, Williams et al. 2002, MacKenzie et al. 2006).

Several methods of population or density estimation approximate and adjust for detection probabilities <1 (Reynolds et al. 1980, Seber 1982, Buckland et al. 2001, Farnsworth et al. 2002, Williams et al. 2002), but these methods were not developed, nor are they practical, for nocturnal species, such as most owls, whose densities are relatively low. Distance sampling is not reliable because darkness and the ventriloquial quality of many owls' vocalizations hinder accurate estimation of distance. Capture–recapture methods are inefficient because of the difficulty in acquiring a sample size adequate relative to effort and models based on resighting of individuals are unreasonable because of the near impossibility of resighting marked individuals at night. Patch-occupancy models, which estimate the proportion of the area occupied rather than density or population size, offer the most realistic approach to long-term monitoring of nocturnal owls (Ganey et al. 2004, Olson et al. 2005); these models rely on repeated surveys to determine a species' presence and estimate detection probabilities (MacKenzie et al. 2004). For monitoring territorial species that occur at low densities (e.g., most owls), estimated probability of occupancy is a reasonable surrogate for population density because changes in population size likely will be reflected by changes in occupancy. Designing a study to estimate occupancy that accounts for imperfect detection involves a tradeoff between efficiency and robustness. In general, if occupancy is low, effort should be devoted to surveying more sites and to increasing the probability of detecting an owl if the site is occupied (MacKenzie et al. 2004). Identifying and quantifying factors that affect detection rates will result in improved estimates of detection probabilities and therefore more precise estimates of patch occupancy (Hardy and Morrison 2000, Williams et al. 2002, MacKenzie et al. 2006); efficiency in the field also might be improved by focusing surveys during periods when the probability of detection is higher.

Rates of detection of owls are influenced by the survey technique and various environmental, biological, and temporal factors (Hardy and Morrison 2000, Andersen 2007). Broadcast recordings of owl vocalizations increase rates of detection of most target species and can elicit or discourage responses from nontarget species (Fuller and Mosher 1987, Hardy and Morrison 2000). Environmental factors such as wind, precipitation, surrounding landscape features, and temperature can affect rates of owls' calling as well as the ability of surveyors to detect owls (Fuller and Mosher 1987, Andersen 2007).

Time of year and annual variation in phenology can affect calling rates, which, at least for some species, are positively correlated with prey abundance (Lundberg 1980, Palmer 1987) and whether the bird is paired or breeding (Martin 1974, Bondrup-Nielsen 1984). Similarly, rates of owl calls vary significantly through the night (Palmer 1987).

In this study, we investigated the influence of temporal, biological, and environmental factors on the probability of detection of forest owls in southeastern Alaska, 2005–2006. Our overall objective was to establish an efficient survey protocol for monitoring occupancy of forest owls. We targeted three species of which we expected an adequate number of detections and are relevant to forest management in southeastern Alaska: the Northern Saw-whet Owl (*Aegolius acadicus*), a migratory species that breeds but does not overwinter in southeastern Alaska, the Western Screech-Owl (*Megascops kennicottii*), a year-round resident, and the Barred Owl (*Strix varia*), a resident species that recently colonized southeastern Alaska and has raised conservation concerns for smaller owls in other areas it has colonized recently (COSEWIC 2002, Olson et al. 2005, Elliot 2006). Our specific objectives were to (1) estimate probabilities of detection of each target species with broadcast vocalizations, repeated surveys, and radio-telemetry (for the Western Screech-Owl only) and (2) investigate the influence of temporal, lunar, weather, and biological factors on owl occupancy and probability of detection.

METHODS

STUDY AREA

We conducted this study in southeastern Alaska, near Juneau (58° 18' N, 134° 25' W) and Petersburg (56° 48' N, 132° 56' W). We chose this area because its road system is relatively extensive and accessible most of the year and its landscapes are representative of the region. Southeastern Alaska is sparsely populated and characterized by steep, rugged topography, coastal fjords, and large tracts of temperate rainforest. It comprises over 2000 islands of the Alexander Archipelago and a narrow stretch of mainland separated from the remainder of North America by the vast Coastal Mountain Range (Alaback 1982). The region is roughly 700 km long and averages 190 km wide. The majority (81%) of the land is managed by the U.S. Forest Service (Tongass National Forest). The region has a cool, wet maritime climate with between 75 and 500 cm of precipitation distributed evenly through the year (Harris et al. 1974). The landscape of southeastern Alaska is naturally fragmented by mountainous terrain, wetlands, and various fine-scale disturbances (e.g., wind-throw). Commercial timber harvesting, most often by extensive, broad-scale clearcutting, is widespread. The forest is dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), and the understory consists primarily of blueberry (*Vaccinium* spp.), devil's club (*Oplomanax horridus*), and salmonberry (*Rubus* spp.).

FIELD METHODS

We conducted point-count surveys along roads from 28 February to 7 June 2005. We selected transects on the basis of accessibility during the winter and the likelihood of encountering and detecting owls (e.g., forested habitat, minimal or no traffic, little noise disturbance). Poor access and logistical constraints precluded equal survey effort across all forest types and elevations, but we attempted to maximize the diversity of habitats surveyed, given the access limitations. We established five transects: two near Juneau and three near Petersburg. Each transect consisted of 10 count points ($n = 50$ total) spaced 1.6 km apart to avoid detecting one individual at multiple points. We alternated the direction in which we surveyed each transect to avoid temporal bias. We divided the survey season into ten 10-day periods and, therefore, each transect was surveyed 10 times (some survey stations were not always accessible) during the breeding season of the three target species (Cannings 1993, Mazur and James 2000, Cannings and Angell 2001).

SURVEY PROTOCOL

The same two observers counted owls at each point. Each survey consisted of a 2-min settling segment, a 4-min segment of silent listening, and then a broadcast of the male's territorial songs (Mazur and James 2000, Cannings and Angell 2001). We broadcasted the songs of the Western Screech-Owl and Barred Owl with a hand-held megaphone (PA Genie Amplifier APM-760, Fanon Courier, Irvine, CA) and a portable compact-disk player (CD Walkman D-NS505, Sony). We always broadcast for the Western Screech-Owl first to avoid attracting the larger species by playing the territorial call of the Barred Owl. We did not specifically broadcast for the Northern Saw-whet Owl because, on the basis of surveys along the coast of British Columbia, we expected this species to respond to one of the other species' calls (D. Cannings, pers. comm.). In this study, we assumed this pattern to hold in the similar coastal forests of southeastern Alaska. Using a digital sound-level meter, we adjusted the volume to be 100–110 db at 1 m in front of the speaker (Fuller and Mosher 1987). We broadcast Western Screech-Owl and Barred Owl songs for 30 sec while rotating the megaphone 360°, then counted for 1 min in silence. This cycle was repeated once, so that each of these two species' broadcast series was 30 sec broadcast, 60 sec silence, 30 sec broadcast, 60 sec silence. The broadcast rotation began with the Western Screech-Owl and ended with the Barred Owl, and there was 1 min of silent listening between the series of each species' broadcast. The count ended with 1 min of silent listening. In total, we spent approximately 12 min at each count station.

Surveys began at least 30 min after sunset (determined by the U.S. Naval Observatory; <http://tycho.usno.navy.mil/srss.html>) and were completed within 6 hr. Nocturnal owls

are most responsive and closer to daytime roosts or nests during this time (Johnson et al. 1981). At the beginning of each count, we recorded time, ambient air temperature (°C), moon phase, precipitation, percent snow cover, percent cloud cover, wind speed (km hr^{-1}), and a categorical variable describing external noise (e.g., barking dogs, ocean surf). We recorded air temperature and wind speed and direction with a hand-held weather monitor (Kestrel 3000 Pocket Weather Station; Forestry Supply, Inc.). We also tallied the number of cars that passed during the silent and broadcast components separately. If an owl was detected, we recorded species, number, direction, estimated distance (m), and elapsed time to detection. Although estimating the distance and direction to singing owls was challenging, the attempt assisted us in determining whether detections of the same species were of different birds. We did not survey during inclement weather (i.e., heavy rain, winds $>20 \text{ km hr}^{-1}$).

RADIO-MARKED BIRDS

Using mist nets with an audio lure and decoy mouse, we captured eight Western Screech-Owls in Petersburg from 17 March to 11 May 2006 (Lewis and Kissling 2009). We equipped three females and five males with backpack-mounted radio transmitters (model TW-4, Biotrack, Ltd.) with Teflon ribbon. To estimate probability of detection, we located radio-marked birds at night by triangulating their position with a hand-held receiver and two-element "H" antenna (Telonics, Inc., Mesa, AZ). Immediately after successful triangulation, we followed the point-count survey protocol described previously. If a bird was detected (either during a silent count or by its response to broadcast), we recorded the elapsed time, type of detection (aural, visual, both), type of call (bouncing ball, double trill, bark or bill snap, or begging whinny; Cannings and Angell 2001, Herting and Belthoff 2001), and whether the detected bird was the radio-marked bird. We stopped the survey as soon as a bird responded to minimize disruption of its breeding.

STATISTICAL ANALYSES

We used the presence or "absence" of an owl at each surveyed point to address our objectives. Because nondetection does not confirm absence of a species unless detection is perfect, we employed occupancy modeling to account for variation in both spatial sampling and detectability (MacKenzie et al. 2006). These procedures improve inferences in studies monitoring populations of rare species, such as most owls, that are likely detected imperfectly.

At each point surveyed, we estimated occupancy probability (ψ) and detection probability (p) and investigated the influence of covariates on these probabilities for the three target species in PRESENCE (Hines 2006). We included models that allowed both ψ and p to be functions of covariates. To model ψ , we considered three categorical variables. We

included “lg-owl” to indicate whether a large owl such as the Barred or Great Horned (*Bubo virginianus*) was ever detected at a survey station, “transect” to describe each survey transect, and “area” to distinguish the Juneau (mainland southeastern Alaska) and Petersburg (island southeastern Alaska) study areas. For modeling p , we considered 18 temporal, environmental, and biological variables. Temporal variables included “period,” identifying the survey periods of equal length (1–10), and “hours,” representing the time (hr) after sunset. Environmental variables consisted of temperature (°C; “temp”), the proportion of ground covered by snow within a 50-m radius (“ground”), wind speed (km hr⁻¹; “wind”), four indicator variables to describe varying levels of precipitation (“fog,” “all-precip,” “heavy-precip,” and “snow”), three variables to incorporate ambient light (“cloud,” “moon,” and “light”), and three indicator variables to describe increasing intensity of noise (“noise234,” “noise34,” and “noise4”). The only biological variable we considered to model p was whether a large owl was detected at the survey station during the current survey (“big-owl”). Because the amount of ambient light was dependent on several factors, we included “cloud” as the proportion of the sky covered by clouds, “moon” as the proportion of moonlight relative to the maximum possible at full moon (obtained from <http://aa.usno.navy.mil/data/docs/MoonFraction.php>), and “light” as the theoretical amount of moonlight available reduced for that obscured by clouds and computed as $(1 - \text{cloud}) \times \text{moon}$. “All-precip” included drizzle, showers, and rain; “heavy-precip” included only showers and rain. Following Takats et al. (2001), we scaled ambient noise from 0 (quiet) to 4 (noisy) and modeled it as noise ≥ 2 , noise ≥ 3 , and noise = 4;. We modeled the number of cars passing during a survey separately because this type of noise was acute and rarely lasted the entire count (as opposed to, for example, stream noise). We categorized these variables as 1 or 2 cars (“cars12”) or ≥ 3 cars (“cars3”) passing. Period, hours, temp, snow, wind, cloud, moon, and light were continuous variables; we included quadratic terms for period and hours because we suspected that the relationship between detection probability and these variables might not be linear. For the cumulative indicator variables (i.e., precipitation, noise, cars), no more than one variable of each type was included in a single model (e.g., if noise234 was in the model, neither noise34 nor noise4 was used in that model).

To select a final model for each species of owl, we began by fitting models, using each variable singly to predict ψ or p ; we also fit a model with ψ constant across sites and p constant across surveys and a model with p period-specific. We assessed the models’ fit with AIC and related model weights (Burnham and Anderson 2002). Once the single-variable models had been fit, we fit a more complex model containing a combination of the best-supported variables, on the basis of model weights and the precision of the estimated coefficients, from the single-variable model. From this base model, we

added additional variables, examining each model’s weight after each addition. We continued to add variables until all reasonably supported variables not in the model had been considered. The final model was the one that ranked with the highest weight.

To assess the efficacy of broadcast surveys, we fit multi-method occupancy models that estimated detection probability separately for the initial segment of silent listening and the following segment of broadcast (Hines 2006). If an owl was detected during both segments, it was included in both estimates. For these models we did not include covariates because they could affect method-specific detection probabilities differently and therefore could lead to a large and complex set of models. Therefore, our method-specific estimates should be viewed as averages over the range of the other covariates. To determine whether broadcast surveys influenced detection probabilities, particularly of the smaller owls, negatively, we considered the initial detection or response of each owl in relation to the segment of the broadcast recording (i.e., during the silent segment, Western Screech-Owl song, or Barred Owl song).

We calculated detection probabilities for the Western Screech-Owl on the basis of radio-marked individuals only. We used the program Location of a Signal (Ecological Software Systems, <http://www.ecostats.com>) to estimate the location of owls on the basis of directional azimuths obtained from locations known before the survey. We measured the distance from the survey location to the owl’s estimated location in a GIS (ArcView, version 3.3, ESRI, Redlands, CA). We averaged distances for radio-marked birds that responded to the broadcast and those that did not respond.

RESULTS

We conducted 479 point counts and recorded 147 detections of six species of owls. We tallied detections of 62 Northern Saw-whet Owls, 37 Western Screech-Owls, 38 Barred Owls, seven Great Horned Owls, two Northern Pygmy-Owls (*Glaucidium gnoma*), and one Boreal Owl (*Aegolius funereus*). We detected the greatest number of owls during the seventh survey period (29 April–8 May; Fig. 1). Overall, 44% of detections from 9 April to 8 May, a result driven primarily by increased detections of the Northern Saw-whet Owl during this 30-day period (Fig. 1), and 59% of the detections were recorded from 30 March to 18 May. Throughout the survey, detections of the Northern Saw-whet Owl were more variable than those of the Barred Owl or Western Screech-Owl (Fig. 1).

MODELING OCCUPANCY AND DETECTION PROBABILITY

We evaluated between 30 and 36 models for each species (Table 1). The best models contained 0 or 1 covariates for ψ and 1–5 covariates for p ; for the Western Screech-Owl and Barred Owl we present estimates from two models with

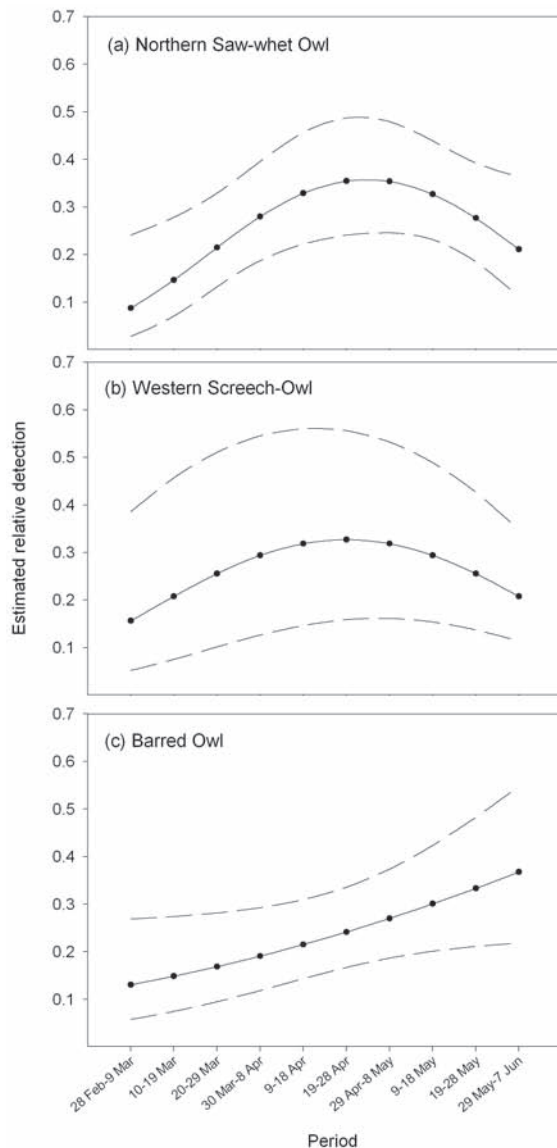


FIGURE 1. Modeled detection probabilities and 95% CI based on parameter estimates of the survey period selected in final models for the (a) Northern Saw-whet Owl, (b) Western Screech-Owl, and (c) Barred Owl.

very similar weights (Tables 1 and 2). Neither route- nor area-specific estimates of ψ were supported for any species. For both the Barred Owl and Northern Saw-whet Owl, the models estimated occupancy probability (ψ) to be constant, but for the Western Screech-Owl, ψ was best modeled as a function of whether large owls were ever detected at a survey station, with estimated ψ about 66% lower for stations with large owls (Table 3). During the peak survey period (9 April–8 May), the average estimate of occupancy (SE, CV) of the Northern Saw-whet Owl was 0.58 (0.08, 14%), that of the Western Screech-Owl was 0.48 (0.09, 20%), and that of the Barred Owl was 0.28 (0.07, 24%).

For both the Western Screech-Owl and Northern Saw-whet Owl, estimated p peaked in survey periods 5–7 (9 April–8 May; Fig. 1). For the Western Screech-Owl, the probability of detection increased after sunset (Fig. 2a). Precipitation (drizzle, showers, or rain) decreased the probability of detection of both the Barred Owl and Northern Saw-whet Owl; the pattern for the Barred Owl was relatively weak, and for the Northern Saw-whet Owl the coefficient and its standard error indicated estimation problems (Table 2). Further examination of the data showed no overlap of detections with precipitation. That is, none of the 57 detections of Northern Saw-whet Owl was made during the 62 surveys (of 482) when precipitation other than snow was recorded. So, although we cannot produce a precise estimate, the data strongly suggest that precipitation greatly reduces detections of the Northern Saw-whet Owl. Wind caused similar declines in p for both the Western Screech-Owl and Northern Saw-whet Owl (Fig. 2b). For Northern Saw-whet Owl, estimated p increased with increasing light (i.e., cloud-adjusted moonlight; Fig. 2c). Noise ≥ 3 negatively affected p for the Western Screech-Owl and Northern Saw-whet Owl with reductions of about two-thirds (Table 3).

Silent versus broadcast surveys. During the segment of silence, the average elapsed time until detection of an owl was 1 min 5 sec, and 74% of these detections were made within 2 min from the start of the survey. For all three species, detection probabilities were greater during the broadcast segment than during the silent segment (Table 4). This increase was largest for the Western Screech-Owl, the odds of detecting an owl being 16.0 (95% CI: 3.8–66.8) times higher during broadcasts than during silent listening. The odds of a Northern Saw-whet or Barred Owl being detected during broadcasts were 3.2 (1.3–7.93) and 3.0 (1.1–8.3) times higher than during the silent segment.

Across all species, initial detections during the silent (48%; 71 of 147) and broadcast (52%; 76 of 147) segments were similar, but this proportion also varied considerably by species (Fig. 3). Northern Saw-whet Owls were most often first detected during the silent segment (66% of the time; $n = 62$), whereas 89% of Western Screech-Owls ($n = 37$) were first detected during the broadcast segment. First detections of Barred Owls during silent (47%; 18 of 38) and broadcast (53%; 20 of 38) segments were similar. Of those initially recorded during the broadcast segment, the majority of Northern Saw-whet Owl (67%; 14 of 21) and Western Screech-Owl (64%; 21 of 33) detections were made during the Western Screech-Owl song; similarly, the majority (85%) of Barred Owls responded during the Barred Owl song. Although few smaller owls (i.e., Northern Saw-whet and Western Screech-Owls) initially responded during the Barred Owl song (19%; 19 of 99), only 45% of smaller owls that were already singing prior to the Barred Owl recording stopped singing.

Radio-marked birds. We made 42 surveys for eight radio-marked Western Screech-Owls from 4 April to 31 May 2006.

TABLE 1. Candidate models considered for estimating probabilities of occupancy and detection of three species of forest owls, southeastern Alaska, 2005. Models are ranked by AIC weights (w_i). Only those models with strong support ($\Delta AIC \leq 2$) are shown; the null is included for comparison.

Species	Model no.	Model	ΔAIC	w_i	K^a
Barred Owl	1	$\psi(\cdot), p(\text{period})$	0	0.103	3
	2	$\psi(\cdot), p(\text{period} + \text{all-precip})$	0.36	0.086	4
	3	$\psi(\cdot), p(\text{period} + \text{period}^2)$	0.66	0.074	4
	4	$\psi(\cdot), p(\text{all-precip})$	0.89	0.066	3
	5	$\psi(\cdot), p(\text{temp})$	0.89	0.066	3
	6	$\psi(\cdot), p(\text{period} + \text{period}^2 + \text{all-precip})$	1.47	0.049	5
	7	$\psi(\text{area}), p(\text{period})$	1.68	0.044	4
	8	$\psi(\cdot), p(\text{period}^2)$	1.69	0.044	3
	9	$\psi(\cdot), p(\text{period} + \text{temp})$	1.87	0.040	4
	Null	$\psi(\cdot), p(\cdot)$	2.12	0.036	2
Western Screech-Owl	1	$\psi(\text{big-owl}), p(\text{noise34} + \text{hours} + \text{period}^2)$	0	0.107	6
	2	$\psi(\text{big-owl}), p(\text{noise34} + \text{hours} + \text{period}^2 + \text{wind})$	0.14	0.102	7
	3	$\psi(\text{big-owl}), p(\text{noise34} + \text{hours})$	0.56	0.083	5
	4	$\psi(\text{big-owl}), p(\text{noise34} + \text{wind} + \text{hours})$	0.63	0.080	6
	5	$\psi(\text{big-owl}), p(\text{noise34} + \text{wind})$	0.74	0.076	5
	6	$\psi(\text{big-owl}), p(\text{noise34})$	0.98	0.067	4
	7	$\psi(\text{big-owl}), p(\text{noise34} + \text{hours} + \text{period}^2 + \text{cars3})$	1.04	0.065	7
	8	$\psi(\text{big-owl}), p(\text{noise34} + \text{hours} + \text{period}^2 + \text{hours2})$	1.31	0.057	7
	9	$\psi(\text{big-owl}), p(\text{noise34} + \text{hours} + \text{period}^2 + \text{period})$	1.84	0.044	7
	10	$\psi(\text{big-owl}), p(\text{noise34} + \text{hours} + \text{period}^2 + \text{moon})$	1.94	0.042	7
Null	$\psi(\cdot), p(\cdot)$	7.47	0.003	2	
Northern Saw-whet Owl	1	$\psi(\cdot), p(\text{period} + \text{period}^2 + \text{wind} + \text{light} + \text{all-precip})$	0	0.956	7
	Null	$\psi(\cdot), p(\cdot)$	25.14	0.000	3

^aNumber of parameters.

TABLE 2. Final models predicting probabilities of occupancy and detection of the Barred Owl, Western Screech-Owl, and Northern Saw-whet Owl, southeastern Alaska, 2005.

Species	Response	Variables	Coefficients	SE
Barred Owl (model 1)	ψ	intercept	-0.94	0.34
	p	intercept	-1.14	0.24
		period	0.15	0.08
Barred Owl (model 2)	ψ	intercept	-0.92	0.34
	p	intercept	-1.07	0.24
		period	0.12	0.08
		all-precip	-1.22	1.09
Western Screech-Owl (model 1)	ψ	intercept	0.50	0.51
	p	big-owl	-1.81	0.82
		intercept	-1.29	0.32
		noise34	-1.48	0.77
		hours	0.20	0.13
Western Screech-Owl (model 2)	ψ	period ²	-0.04	0.03
	p	intercept	0.59	0.55
		big-owl	-1.87	0.84
		intercept	-1.15	0.34
		noise34	-1.46	0.77
		hours	0.19	0.13
		period ²	-0.04	0.03
Northern Saw-whet Owl	ψ	wind	-0.32	0.24
	p	intercept	0.33	0.34
		intercept	-0.73	0.31
		period	0.06	0.06
		period ²	-0.06	0.03
		wind	-0.41	0.21
		light	0.75	0.48
	all-precip	-27.51	315 807.9	

TABLE 3. Estimates of probability of occupancy and detection of the Barred Owl, Western Screech-Owl, and Northern Saw-whet Owl as a function of categorical predictor variables included in final models, southeastern Alaska, 2005.

Species	Response	Variables included	Estimate	95% CI
Barred Owl (model 2)	ψ	all	0.28	0.17–0.43
	p	no precipitation	0.42	0.21–0.66
Western Screech-Owl (model 1)	ψ	all-precip	0.17	0.02–0.71
		without big-owls	0.62	0.38–0.82
	p	with big-owls	0.21	0.07–0.50
		quiet (noise ≤ 1)	0.33	0.17–0.53
Northern Saw-whet Owl	ψ	noise34	0.10	0.02–0.38
		all	0.58	0.42–0.73

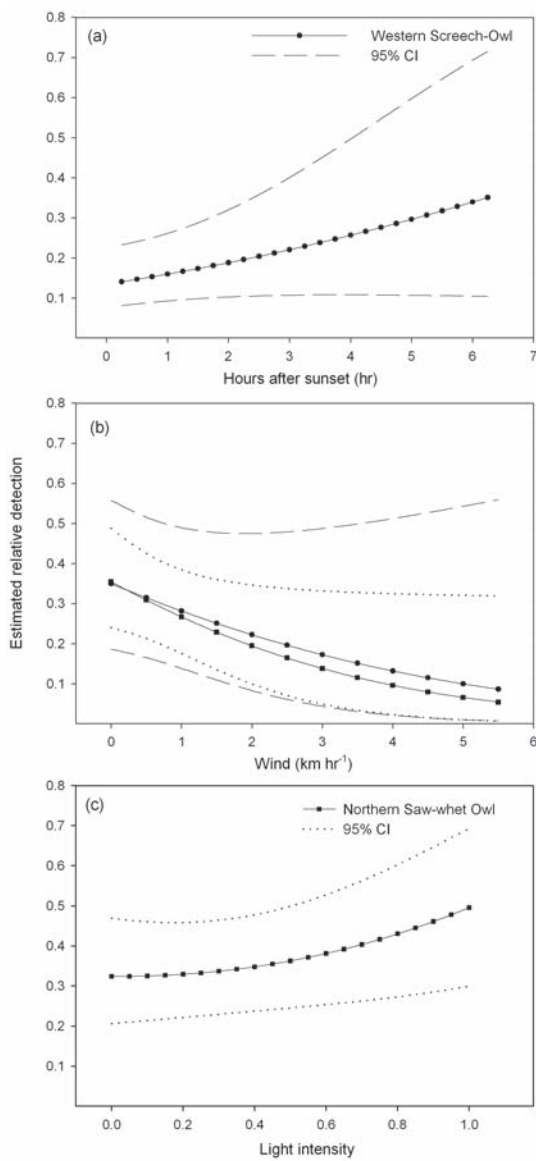


FIGURE 2. Modeled detection probabilities based on parameter estimates of (a) hours after sunset, (b) wind, and (c) light intensity selected in the final models for the Northern Saw-whet Owl and Western Screech-Owl. Legends are consistent across all three graphs.

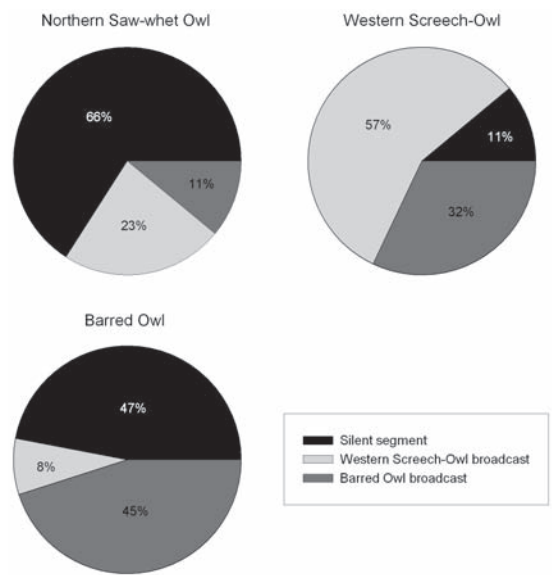


FIGURE 3. Proportion of initial detections by survey segment for the Northern Saw-whet Owl ($n = 62$), Western Screech-Owl ($n = 37$), and Barred Owl ($n = 38$), southeastern Alaska, 2005.

During these surveys, we detected five Western Screech-Owls, one Saw-whet Owl, and one Barred Owl. The detectability of the Western Screech-Owls was extremely low (12%; 5 of 42); furthermore, only three of five detections were of radio-tagged birds (2 males, 1 female). During the 15 surveys from 9 April to 8 May, only one Western Screech-Owl responded, and it was not radio-marked. The distance between the count point and location of the radio-marked owls prior

TABLE 4. Method-specific (silent listening vs. broadcast) detection probabilities (95% CI), conditional on occupancy, for three species of owls, southeastern Alaska, 2005.

Species	Silent	Broadcast
Barred Owl	0.09 (0.03–0.23)	0.60 (0.20–0.90)
Western Screech-Owl	0.44 (0.27–0.63)	0.71 (0.46–0.87)
Northern Saw-whet Owl	0.61 (0.47–0.74)	0.83 (0.68–0.92)

to the broadcast averaged 382 m ($n = 3$, $SE = 125$, range 239–468) for those that responded and 489 m ($n = 39$, $SE = 390$, range 143–1616) that were present but did not respond.

DISCUSSION

We examined many factors that affected probabilities of detection of the Northern Saw-whet Owl, Western Screech-Owl, and Barred Owl. If an owl occupied a site, its detection depended on three factors: (1) availability, (2) cue production, and (3) detectability. Availability is whether, during the survey, the owl was close enough to the count point to be detected if it called; cue production is whether an owl that was available vocalized during the survey; detectability is whether an owl that was available and vocalized during the survey was heard by the surveyor. Each of the variables used to model p were related to one or more of these detection factors.

AVAILABILITY

For resident species (i.e., the Barred Owl and Western Screech-Owl), availability was a function of where the owl was in its home range at the time of a survey, relative to the location of the survey point; in general, large or irregularly shaped home ranges lower availability. The Barred Owl and Western Screech-Owl remain year round in a home range that includes their nest site, and the site fidelity of both species is strong (Mazur and James 2000, Cannings and Angell 2001). We began surveys in late February when we expected courtship behavior and calling of both species to be centered on or near the nest. However, we did not know the configuration of the owls' home ranges or locations of their nests with respect to our survey points. In addition, the home ranges of nonmigratory owls typically are larger in the nonbreeding season than during the breeding season (Mazur and James 2000). If an owl's movements within its home range were independent of the timing and location of our surveys, the intercept term of the p portion of the model accounted for a reduction of detections because of availability.

For the Northern Saw-whet Owl, a migratory species, availability has a different connotation. A site might have been "occupied" by the species, but, as migration proceeded and territories were established, the occupants might have been different individuals during different surveys. Although the Northern Saw-whet Owl breeds in southeastern Alaska, the timing of its migration and nesting is unknown. One of the critical assumptions for estimating probabilities of occupancy and detection from these models is that sites were "closed" to changes in occupancy over the survey season (MacKenzie et al. 2006). Given the Northern Saw-whet Owl's migratory behavior, we were concerned about drawing incorrect inferences about the factors that influenced either occupancy or detection. However, assuming that Saw-whet Owls moved in and out of these sites at random, we considered a lack of detections when no owls were present to be a component of availability,

comparable to a resident owl's being at the far side of its home range (Kendall 1999, MacKenzie et al. 2006). Therefore the interpretation for the Northern Saw-whet Owl is slightly different because the occupancy estimate instead represents the proportion of sites "used" rather than continuously "occupied" (MacKenzie et al. 2006).

CUE PRODUCTION

In this study, we primarily investigated variables that explained variation in cue production. In general, survey method (Table 4) and date (Fig. 1) had the most consistent effect on probabilities of detection of all three target species, but variables influenced species differently (Table 2). The peak period for detecting the target species was 9 April–8 May (30 days), with an extended peak period of 30 March–18 May (50 days; Fig. 1). In modeling detection probabilities, we included survey period in the final model for all three species (Table 2).

Our results confirm the effectiveness of conspecific broadcasts in increasing rates of detection of the Western Screech-Owl and Barred Owl over those during silent surveys (Table 4). The majority of initial detections of both species were during broadcast of their respective call; however, a relatively large proportion (37%) of Western Screech-Owls was also recorded during the Barred Owl song (Fig. 3). We believe that these birds were not responding to the Barred Owl recording but instead had a slow response time to the Western Screech-Owl recording. Unlike the song of the Barred Owl, which can be heard from great distances, that of the Western Screech-Owl can be relatively difficult to hear, requiring the bird to be close to the survey station in order for the surveyor to detect it (pers. obs.). We never detected both species during the same count segment, and, in fact, occupancy of the Western Screech-Owl was negatively associated with that of larger owls (Table 2). Therefore, it is unlikely that the Western Screech-Owl's delayed response affects detection probabilities or occupancy estimates under the survey protocol we used in this study. However, these results suggest that the broadcast calls should be played in sequence from smallest to largest owls. Although one could argue that broadcasting the calls in random order would be more statistically valid, our results demonstrate that the presence of larger owls negatively affects the probability of detection of smaller owls. It is illogical to think that the reverse would be true, but we did not test this possibility explicitly. As expected, Northern Saw-whet Owls were most often detected during the silent segment of the survey, prior to broadcast of calls of larger owls. To maximize spatial coverage and overcome logistical constraints (e.g., limited darkness), we did not broadcast specifically for the Northern Saw-whet Owl, which may have increased its probability of being detected. However, we do not believe this additional effort would have changed our results drastically, particularly because the probability of a Northern Saw-whet Owl being detected during silent and broadcast surveys was relatively high

(0.61 and 0.83, respectively; Table 4) compared to that of the other two species.

Hours after sunset affected the Western Screech-Owl's cue production. This species vocalized more as time after sunset increased (Fig. 2a). Courtship feeding by the Western Screech-Owl is common, and males feed females during egg laying, incubation, and brooding (Cannings and Angell 2001). Therefore, a male may hunt more actively immediately following sunset in order to deliver food to the female as quickly as possible, likely strengthening the pair bond. In this species, territory defense may be secondary to nest attendance.

The probability of detection of the Northern Saw-whet Owl was positively associated with the amount of ambient light at night (Fig. 2c). Migration of this species may be suppressed by a full moon or high amounts of light (Cannings 1993), possibly to avoid predation from larger owls. However, Palmer (1987) concluded that a full moon may proximally stimulate the seasonal onset of the Northern Saw-whet Owl's singing, which is used almost exclusively to attract mates for breeding (Cannings 1993).

Some variables (e.g., precipitation, wind) may affect cue production, detectability, or both, but this possibility would be difficult to determine if a reduction of detections was due to fewer vocalizing owls or the observer's failure to hear those that were vocalizing. High winds and precipitation inhibit singing by Northern Saw-whet Owls (Palmer 1987). Our results confirm that probabilities of detection of the Northern Saw-whet Owl and Western Screech-Owl are negatively affected by these weather variables (Table 2, Fig. 2b). Even moderate winds ($<3 \text{ km hr}^{-1}$) had a negative effect on probabilities of detection of both species. During the study, we did not survey in constant high winds, but at some stations we occasionally did in strong gusty winds. Similarly, our data also strongly suggest that precipitation reduced the probability of detection of the Barred Owl and greatly reduced that of the Northern Saw-whet Owl (Table 2); we did not detect any Saw-whet Owls during even light precipitation, which is common in southeastern Alaska. The negative effects of wind and precipitation on probabilities of detection of these smaller owls can be eliminated, or at least reduced, if surveys avoid inclement weather strictly.

DETECTABILITY

It is difficult to ascertain which detection factors, cue production or detectability, were affected by some of the variables we considered. We attempted to reduce heterogeneity in detectability by not conducting surveys under marginal or unacceptable conditions, but these conditions may have suppressed cue production. Conversely, the noise and car variables most likely affected detectability, but reduced cue production cannot be completely ruled out. Significant noise decreased the probability of detection of a Western Screech-Owl from 33% to 10% (Table 3). This species is strongly associated with

riparian habitats (Kissling and Lewis 2009), so this result was likely driven by an interaction between preferred habitat and detection rates. Stream noise also varied through the survey season because of snow melt; locations of stations in riparian areas should be selected to minimize stream noise, particularly as the season progresses.

RECOMMENDATIONS

Point-count surveys for nocturnal owls can produce reliable estimates of occupancy provided that the study's objectives are clear and that the survey's design and protocol are robust (MacKenzie et al. 2006). We present information necessary for developing a survey protocol efficient for monitoring occupancy of three species of forest owls in southeastern Alaska. This approach could be repeated in other areas where surveys for multiple species of owls are desirable. We recommend the use of broadcast calls to improve detection probability, especially for the Western Screech-Owl. If this is the primary target species, we suggest eliminating the broadcast of the Barred Owl (or other larger owls) from the survey protocol or increasing the silent listening time between the broadcast of the songs of the Western Screech-Owl and Barred Owl. To produce an occupancy estimate for southeastern Alaska with a CV of 20–25%, we recommend three surveys ($k = 3$) at 180–200 stations each season (MacKenzie and Royle 2005). We believe that, despite the limitations in the scope of inference, roadside surveys constitute the most reasonable approach to monitoring owl populations in this region, where few roads exist and even fewer are maintained year round. For other areas, we recommend preliminary surveys, such as those described here, to investigate variables that may affect owl occupancy and detectability and to design the most robust survey possible.

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