Techniques and Technology Article

Detectability and Response Rates of Ferruginous Pygmy-Owls

AARON D. FLESCH,[1] *School of Natural Resources, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85721, USA*
ROBERT J. STEIDL, *School of Natural Resources, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85721, USA*

ABSTRACT Survey techniques that are both reliable and efficient are necessary to accurately estimate population parameters, especially for rare species. Cactus ferruginous pygmy-owls (*Glaucidium brasilianum cactorum*; hereafter pygmy-owls) have declined in southwestern North America and are surveyed often to comply with federal law. We studied owl responses to broadcasted calls to quantify how detectability and response rates (owls/station/transect) vary with environmental, spatial, temporal, and weather-related factors. We surveyed owls along 392 transects (1,113 km) throughout Sonora, Mexico, including a subset of 14 transects (47.2 km) that we surveyed repeatedly to assess factors that affected response rates. We challenged 17 adults and 23 juveniles that were radiomarked, adults attending 50 occupied nests, and adults attending 6 groups of radiomarked juveniles to respond to broadcasted calls to assess factors that affected detectability. Across Sonora, response time averaged 2.6 ± 0.1 minutes ($\bar{x} \pm$ SE, $n = 520$), with 99 ± 0.4% of owls detected in $\leq$8 minutes; response distance averaged 251 ± 7 m, with 91 ± 1% of owls detected at $\leq$400 m. Response time decreased by an average of 4 ± 2% and response distance decreased by 12 ± 3 m with each half-month period from early courtship through brooding ($P \leq 0.035$). Response time averaged 39 ± 24% faster during morning than midday at occupied nests. Detectability was 1.0 ± 0.0 when surveyors were 100 m from occupied nests and decreased to 0.78 ± 0.10 when surveyors were 500 m from occupied nests. Detectability was higher during incubation, brooding, and natal dispersal (0.89 ± 0.05–1.0 ± 0.0) than during fledgling-dependency (0.50 ± 0.20–0.67 ± 0.19). Response rates of males did not vary from early courtship to brooding ($P = 0.84$), yet those of females decreased systematically to zero across the same period ($P < 0.001$). Because detectability of pygmy-owls remains consistently high during nesting, response rates generated from carefully designed surveys can provide reliable estimates of occupancy and abundance. (JOURNAL OF WILDLIFE MANAGEMENT 71(3):981–990; 2007)

DOI: 10.2193/2006-081

KEY WORDS broadcast, cactus ferruginous pygmy-owl, detectability, detection probability, *Glaucidium brasilianum cactorum*, response distance, response rate, response time, Sonora, tape playback surveys.

Increasing the efficiency of strategies for surveying wildlife populations can improve the precision of parameter estimates and the power and reliability of research and monitoring programs (Thompson et al. 1998, Steidl and Thomas 2001, Pollock et al. 2002). All survey methods benefit from a clear understanding of the factors that influence visual or aural detections of animals and true detection probabilities. Survey strategies based on indices can provide a reliable framework for assessing changes in populations when indices closely track changes in population parameters (Yoccoz et al. 2001, Williams et al. 2002). Detection probability, also referred to as detectability or responsiveness, is the probability of detecting an individual provided it is present during sampling (Boulinier et al. 1998), whereas response or detection rate is an index based on the raw number of individuals detected per unit effort.

Broadcasting vocalizations of conspecifics increases detections compared to nonelicited surveys for many species of owls (McGarigal and Fraser 1985, Mosher et al. 1990, Gerhardt 1991), yet the relationship between detectability and response rates is not well understood and may vary with environmental, temporal, spatial, surveyor- or weather-related factors (Fuller and Mosher 1987, Morrell et al. 1991, Hardy and Morrison 2000, Conway and Simon 2003, Seavy 2004). Understanding factors that influence estimates of population parameters are fundamental to developing reliable survey techniques because, when detectability is <1.0, uncorrected estimates may bias information (Pollock et al. 2002, Tyre et al. 2003).

Reliable survey strategies are particularly important for rare or endangered species where small changes in population attributes may be especially consequential. Cactus ferruginous pygmy-owls (*Glaucidium brasilianum cactorum*; hereafter pygmy-owls) are rare in Arizona, USA, and are surveyed regularly for compliance with federal law as some of the areas they occupy are proposed for urban development (United States Fish and Wildlife Service [USFWS] 1997). Consequently, estimating occupancy and abundance of pygmy-owls and assessing whether management and recovery objectives are being met (USFWS 2003) necessitates survey strategies that are reliable and efficient. Although broadcasting vocalizations of pygmy-owls during surveys increases response rates >3 times over nonelicited surveys (Proudfoot and Beasom 1996), almost no information exists on factors that influence detectability (Proudfoot et al. 2002). Therefore, our objectives were to quantify variation in detectability and response rates of pygmy-owls, suggest improvements to strategies for surveying pygmy-owls (USFWS 2000*a*, *b*), and to consider implications for estimating and monitoring population parameters for pygmy-owls and other similar species.

STUDY AREA

We surveyed pygmy-owls throughout Sonora, Mexico (26–32° N, 109–115° W), which was bordered by Arizona to the north, Sinaloa, Mexico to the south, Chihuahua, Mexico to the east, and the Gulf of California to the west. We

---

[1] *E-mail flesch@ag.arizona.edu*

excluded areas above 1,200 m and the extreme northwest and northeast where pygmy-owls have never been observed (van Rossem 1945, Russell and Monson 1998). Sonora encompassed a broad range of environments from arid desert in the northwest to tropical deciduous forest in the southeast (Rzedowski 1978), with 4 major vegetation communities dominating lowlands: Sonoran Desert, Semi-desert Grassland, Sinaloan Thornscrub, and Sinaloan Deciduous Forest (Brown 1982). Sonoran Desert dominated much of western Sonora and was characterized by uplands of open shrubs and sub-shrubs with short trees and cacti, often including large columnar species such as saguaros (*Carnegiea gigantea*) that are especially common in the Arizona Upland Subdivision (Shreve 1951). Semi-desert Grassland was dominated by mesquite (*Prosopis velutina*) and replaced desertscrub at higher elevations mainly east, north, and within the Sonoran Desert. Sinaloan Thornscrub occupied a large area on the Coastal Plain and in foothills of the Sierra Madre Occidental in southern and central Sonora and was dominated by dense, drought-deciduous, often thorny trees, shrubs, and succulents that often formed a closed canopy 2–8 m tall (Brown 1982). Shrubs of the north transitioned to trees further south and formed Sinaloan Deciduous Forest in southeast Sonora where canopy height in uplands can exceed 12 m (Gentry 1982).

METHODS

Design

We quantified responses of owls to broadcasted calls by counting owls that responded during surveys (response rates), measuring the time it took for owls to respond (response time), estimating the distance between locations where owls responded initially and survey stations (response distance), and by determining the ratio of owl responses to total broadcast trials (detectability) for radiomarked owls known to be in the vicinity of broadcast stations and for owls assumed to be attending occupied nests. Systematic daily or seasonal variation in response time may indicate times when owls respond too slowly to be surveyed efficiently; systematic variation in response distance may indicate evidence of differential movements in response to broadcasts that would bias abundance estimates based on distance-sampling methods. We used 3 types of surveys to quantify factors that influenced owl responses: 1) statewide surveys to quantify factors that influenced response rates, response times, and response distances along transects throughout Sonora; 2) repeat surveys to assess seasonal variation in response rates, response times, and response distances by surveying the same set of transects repeatedly; and 3) challenge surveys to quantify the effects of environmental, spatial, and temporal factors as well as nest outcome (success or failure) on detectability to provide a basis to link response rates (the index) with true abundance (the parameter).

Statewide surveys.—We generated a stratified random sample of locations throughout lowland Sonora allocated proportional to the areal coverage of each of 4 major vegetation communities. Within 20 km of these 145 points, we established up to 4 survey transects, one in each of 4 possible topographic formations (valley bottoms, lower bajadas, upper bajadas, and mountain canyons) along the closest accessible drainage that was >2 m wide and within 1 km of a road. We placed a series of 3–12 stations spaced 350–400 m apart along transects or 550–600 m apart after initial detection of an owl. We increased spacing after we detected each pygmy-owl to reduce the probability of counting the same owl more than once and to avoid pulling owls along transects. We surveyed each of 392 transects once between 15 January and 31 May 2000 and 2001.

Repeat surveys.—We repeatedly surveyed a subsample of 14 transects within the Arizona Upland Subdivision of the Sonoran Desert and Semidesert Grassland where we had detected $\geq$1 pygmy-owl during statewide surveys. We surveyed these transects in winter (9–12 Jan), spring (13 Apr–29 May), and autumn (10–19 Nov) 2001; surveys in winter began before courtship behavior was initiated and those in spring coincided with nesting. From 2001 to 2005, average dates for clutch completion, initation of brooding, and fledging in northern Sonora were 22 April, 15 May, and 12 June, respectively, with 75% of nests initiated within a 4-day period each year from 2001 to 2004 or within a 6-day period in 2005 (A. D. Flesch, University of Arizona, unpublished data).

Challenge surveys.—We used 3 techniques to quantify detectability. First, we challenged 17 adult males and 23 juveniles (12 M, 11 F) that were radiomarked to respond to broadcasted calls from a distance of approximately 300 m from between one day and 35 days after initiation of natal dispersal (late Jul–mid-Sep). Second, we challenged 6 pairs of adults, whose locations we knew because they were guarding radiomarked fledglings, to respond from a distance of 300 m during early (within 1 week of fledging) and middle (5 weeks after fledging) fledgling dependency. We did not challenge owls during late fledgling dependency because broadcasts at this time may influence timing of natal dispersal. Third, we challenged adults assumed to be attending 50 occupied nests to respond from distances of 100 m, 300 m, or 500 m (selected at random) from nests during incubation and brooding (19 Apr–14 Jun 2005). Because presence of a nest does not ensure that adult owls are actually present, we considered only those nests that contained eggs or live young immediately after surveys. We then monitored nests to determine success ($\geq$1 young within a week of fledging) or failure to evaluate the effects of nest outcome on detectability.

To ensure that detectability of our sample of owls was representative of the population at large, we selected a random sample of areas where we had found nests between 2001 and 2004 and in 2005 surveyed one station within 300 m of former nest locations. If we failed to detect a pygmy-owl, we then surveyed a second station also located within 300 m of former nests but in a direction opposite the first station and oriented parallel to the main drainage in the area. This arrangement likely provided adequate coverage because mean distance between nests in the same nest areas ($n = 53$) averaged 143 ± 25 m (range 0–640 m) among years and nests were associated with drainages (A. D. Flesch, unpublished data). In each area where a pygmy-owl responded, we searched for nests by observing owls, by searching for sign (pellets, scat, and prey remains), and by confirming nesting with a small pole-mounted video camera. We found nests at 88% of 58 occupied areas we searched. Because false-negative results during initial surveys could have positively biased estimates of detectability by resulting in us sampling a more detectable subset of the population, we also resurveyed former nest sites where we failed to detect a pygmy-owl during initial surveys an additional 1–3 times during the nesting period.

Owl Surveys

We alternated listening and broadcasting recorded territorial calls every 30–45 seconds and listened during the first and last 30 seconds at each station. We surveyed stations for 8 minutes or until 1 minute after we detected an owl and we often remained near stations for up to 12 minutes to write field notes. We surveyed from 1 hour before to 3 hours after sunrise during statewide and repeat surveys, from 1 hour before sunrise to 1 hour after sunset during challenge surveys at occupied nests, and during mornings, evenings (after sunset), or nights within 2 days of the full moon during challenge surveys of radiomarked owls. We did not survey during steady rain or when wind speed exceeded 20 km per hour (Beaufort scale ≥ 3). For each owl, we recorded response time in minutes, estimated direction and distance to initial point of detection with a rangefinder, and noted sex and age (ad or juv) of owls based on vocalization patterns (Proudfoot and Johnson 2000). To estimate numbers of owls along each transect, we used distance and direction of responses to distinguish among owls that did not respond simultaneously. During repeat and challenge surveys the same surveyor visited the same stations whenever possible to minimize the potential for bias.

Environmental Measurements

At each survey station we characterized weather, topographic conditions, and vegetation within 400 m of survey stations and for statewide surveys we averaged measurements by transect. We estimated vegetation volume visually in areas of both riparian and upland vegetation by summing volumes in 5 horizontal strata above ground (0–1 m, 1–3 m, 3–6 m, 6–12 m, and >12 m) that were each estimated to the nearest 10% when values were between 20% and 80% and to the nearest 5% otherwise. We gauged the abundance of 2 types of potential cavity substrates by calculating the percentage of stations on each transect where saguaros (>3 m tall) and large trees (>6 m tall) were present. We ranked dominance of vegetation formations (woodland, desertscrub, thornscrub, riparian scrub, savannah, grassland, and agriculture) by visually estimating percent cover at each station in both upland and riparian areas. We estimated mean vegetation height visually to nearest m in upland and riparian areas. We determined transitions between riparian and upland vegetation areas based on patterns of structural and floristic contrast and measured width of riparian areas perpendicular to drainage orientation with use of rangefinders. We recorded elevation from 1:50,000 topographic maps, latitude and longitude using a Global Positioning System, estimated percent cloud cover to the nearest 10%, and classified wind speed with the Beaufort scale. We used topographic formation to describe topographic complexity and slope as they are highly correlated (Flesch 2003*a*).

For challenge surveys at nests, we categorized potential vegetation obstruction between survey stations and nests as dense (woodland), moderate (combination of woodland and savannah or desertscrub), or low (savannah or desertscrub). To eliminate confounding by topographic formation during challenge surveys, we only surveyed areas with <5% slope between survey stations and nests or owls.

Data Analyses

Statewide surveys.—To assess the amount of time needed to detect potentially responsive pygmy-owls, we calculated the proportion of individuals that responded within each successive minute of each survey. To assess appropriate spacing of survey stations, we calculated the proportion of pygmy-owls that responded within each successive 100-m-radial distance around survey stations. We considered the effects of time-of-morning and season (late Jan–late May) on response time and response distance by dividing the morning into 4 1-hour periods and the season into 9 half-month periods that corresponded with courtship and nest phases. To determine if response time varied with time-of-morning and season, we used log-linear regression for Poisson counts adjusted for extra-Poisson variation (Ramsey and Schafer 2002); for response distance we used multiple linear regression. We considered wind speed, cloud cover, topographic formation, vegetation structure, elevation, latitude, longitude, year, and surveyor as covariates in all analyses. We also considered response distance as a covariate when assessing variation in response time. We first fit models that included all covariates and sequentially eliminated those that did not contribute appreciably to model fit ($P > 0.05$) then assessed the effects of time-of-morning and season on response time and response distance (Ramsey and Schafer 2002). We also assessed whether response time or response distance varied with sex and with sex × time interactions. We report least-square means adjusted for other model parameters.

Systematic seasonal variation in response rates may indicate differences in the proportion of owls responding to broadcasts rather than differences in owl abundance once adjusted for environmental factors that explain abundance. Therefore, when assessing whether response rates of male and female pygmy-owls varied seasonally, we included the first 3 principal components derived from environmental factors associated with abundance as covariates in a multiple linear regression. These factors included abundance of large columnar cacti, width of riparian vegetation areas, drainage density, woodland cover, vegetation height in uplands, and vegetation volume from 3 m to 6 m above ground in riparian

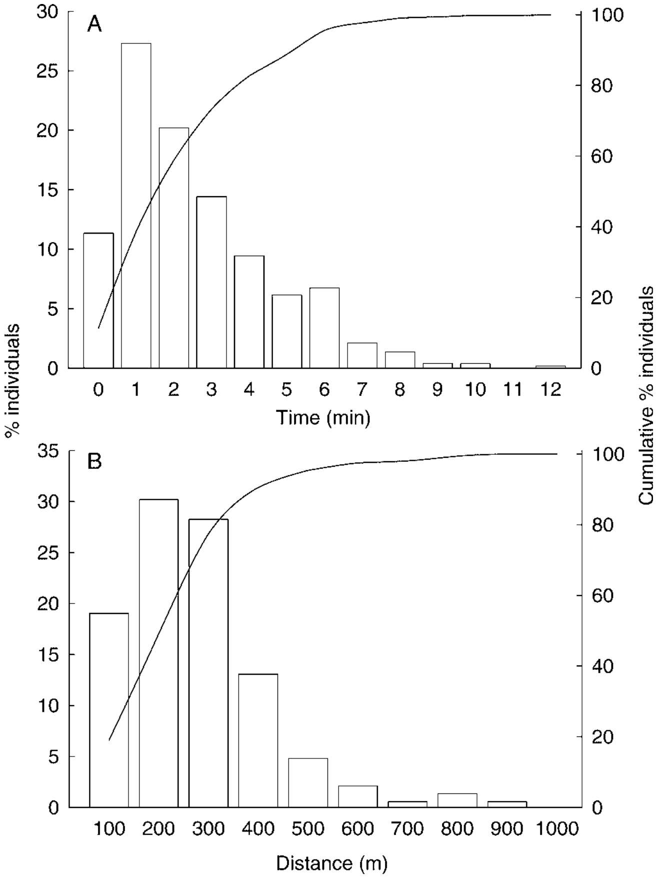

Figure 1. Percent and cumulative percent of ferruginous pygmy-owls ($n = 520$) that responded with each successive minute (A) and in each 100-m-radial interval (B) from broadcast surveys stations (n = 2,812) along transects we surveyed from 15 January to 31 May 2000 and 2001 in Sonora, Mexico. The zero bar represents owls we detected before broadcasts.

areas and from 6 m to 12 m in upland areas that explained 68% of total variation in abundance (Flesch 2003*a*).

Repeat surveys.—To assess seasonal variation in response rates, response time, and response distance, we used a mixed model, repeated-measures analysis of variance followed by linear contrasts. We considered season as a fixed effect and transect as a random effect because they represented a sample from the population of all potential transects. To adjust for autocorrelation among repeated counts along transects, we used an autoregressive covariance matrix (Littell et al. 1996). We did not adjust for potential surveyor effects because the same stations were usually surveyed by the same surveyor.

Challenge surveys.—To assess factors that influenced detectability of pygmy-owls attending occupied nests, we used logistic regression and the model-selection procedure described above. We considered distance between nests and survey stations (100 m, 300 m, or 500 m), time-of-day (early = 1–3 hr after sunrise, late = 2 hr before to 1 hr after sunset, midday = all other times) and nest phase (incubation or brooding) as explanatory variables and vegetation density (low, moderate, or dense) and nest outcome (success or failure) as covariates. To guide appropriate spacing of survey stations, we used the final logistic regression model to predict detectability for each survey event and regressed these predictions against distance from the survey station. To describe temporal variation in detectability, we compared estimates during incubation and brooding obtained at 300 m from nests to those during fledging dependency and natal dispersal obtained at 300 m from radiomarked owls.

To assess temporal variation in response time of nesting owls, we used log-linear regression for Poisson counts adjusted for extra-Poisson variation and the model-selection procedure described above. We considered time-of-day and nest phase as explanatory factors and vegetation density, distance, and nest outcome as covariates.

RESULTS

Statewide Surveys

We detected 438 males, 72 females, and 10 pygmy-owls of undetermined sex at 2,812 stations along 392 transects (1,113 km). Transect length averaged 2,719 ± 40 m ($\bar{x}$ ± SE) with 7.2 ± 0.1 stations per transect spaced an average of 440 ± 3 m apart. Relatively few owls responded before solicitation (11 ± 1% of 520) and we initially detected fewer visually (0.2 ± 0.2%).

Response time.—Response time averaged 2.6 ± 0.1 minutes ($n = 520$, range = 0–12 min) and was similar for males (2.5 ± 0.1 min) and females (2.7 ± 0.2 min). Most owls (83 ± 2%) responded in ≤ 4 minutes, with 99 ± 0.4% responding in ≤ 8 minutes (Fig. 1A). Response time varied seasonally, decreasing by an average of 4 ± 2% ($P = 0.018$) with each half-month period from early courtship in late January to brooding in late May (Table 1) with similar patterns for both males and females ($P = 0.60$ for season × sex interaction). Pygmy-owls responded most rapidly during late courtship in late March (1.7 ± 0.1 min) and during brooding in late May (1.4 ± 0.2 min), ≥ 0.6 ± 0.2 minutes faster than during egg laying in early April (2.3 ± 0.1 min; Fig. 2). Importantly, response time did not vary with time-of-morning ($P = 0.30$) and averaged <2.9 ± 0.3 minutes during each hour of the morning survey period.

Response time varied with longitude, response distance, and among topographic formations and surveyors (Table 1) but not with wind speed, cloud cover, vegetation structure, elevation, latitude, or among vegetation formations or years ($P \geq 0.17$). Response time increased by 14 ± 2% with each 100-m increase in response distance and was 29 ± 14% faster in canyons than in valley bottoms. Response time also decreased somewhat ($P = 0.060$) as the number of pygmy-owls detected along transects increased, resulting in an 18 ± 11% increase in response time from lowest to highest levels of response rates. Response time varied among surveyors ($P = 0.002$); although some surveyors detected owls faster than overall mean response time (2.6 min), none took systematically longer to detect owls.

Response distance.—Response distance averaged 251 ± 7 m ($n = 520$, range 10–900 m) and was similar for males (250 ± 7 m) and females (254 ± 18 m). Most owls (78 ± 2%) responded within 300 m, with 91 ± 1% responding within 400 m of surveyors (Fig. 1B). Response distance

Table 1. Factors that explained variation in initial response time of ferruginous pygmy-owls (n = 498) detected along transects we surveyed between 15 January and 31 May 2000 and 2001 in Sonora, Mexico.

Factor (units)	Parameter estimate[a,b]	SE	χ^2	P
Response distance (100 m)	0.13	0.020	41.07	<0.001
Latitude (10 km)	0.008	0.003	5.54	0.019
Topographic formation				0.003
Canyons[c]	−0.35	0.13	7.32	0.007
Lower bajadas[c]	0.12	0.092	1.75	0.19
Upper bajadas[c]	−0.039	0.097	0.17	0.68
Season (half month)[d]	−0.044	0.019	5.57	0.018
Time of morning (1 hr)	0.038	0.037	1.09	0.30

[a] Parameter estimates and P-values are from log-linear regression for Poisson counts adjusted for surveyor effects ($P = 0.002$).

[b] The inverse natural log of parameter estimates equals the % change in response time with each 1-unit increase for continuous factors or presence for nominal factors.

[c] Reference level equals valley bottom topographic formation.

[d] Nine half-month periods from 15 Jan to 31 May.

Table 2. Factors that explained variation in initial response distance of ferruginous pygmy-owls (n = 469) detected along transects we surveyed between 15 January and 31 May 2000 and 2001 in Sonora, Mexico.

Factor (units)	Parameter estimate[a]	SE	t	P
Riparian vegetation volume (%)	−0.74	0.24	3.05	0.002
Yr	−72.6	15.0	4.84	<0.001
Season (half month)[b]	−12.1	3.4	3.62	<0.001
Time of morning (1 hr)	−7.8	6.9	1.13	0.26

[a] Parameter estimates and P-values are from multiple linear regression.

[b] Nine half-month periods from 15 Jan to 31 May.

varied seasonally ($P < 0.001$), decreasing by 12 ± 3 m with each half-month period from early courtship to brooding and did not vary with time-of-morning ($P = 0.26$; Table 2). Response distances were lower during late courtship in late March (210 ± 17 m) and especially during early incubation in late April (140 ± 25 m) than during egg laying in early April (297 ± 24 m). Response distance declined as volume of vegetation in riparian areas increased ($P = 0.002$) and did not vary among surveyors ($P = 0.29$).

Response rates.—Response rates varied from early courtship to brooding for females ($t_{373} = 3.96$, $P < 0.001$) but not for males ($t_{373} = 0.41$, $P = 0.84$) after adjusting for among-transect variation in environmental factors that explained abundance (Fig. 3). Response rates of females declined from an average of 0.6 ± 0.2 owls per 10 stations during early courtship to near zero during brooding, a decline of 0.07 ± 0.02 owls per 10 stations with each half-month period across the survey season. Only 4 ± 2% ($n = 3$ of 72) of females were detected after 15 April when egg laying typically begins and none were detected after 4 May.

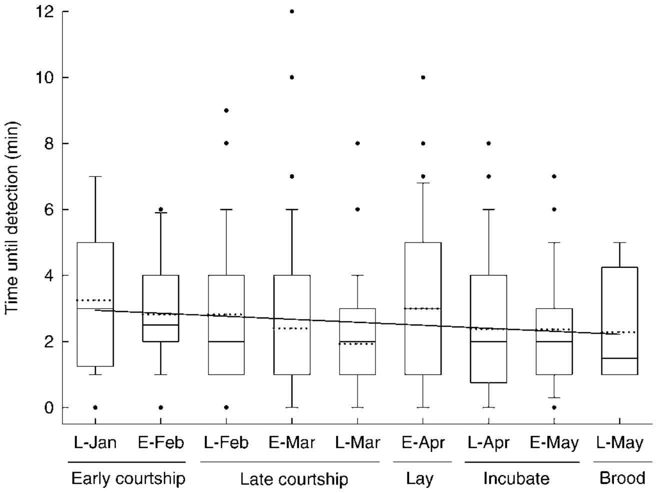

Figure 2. Response time of ferruginous pygmy-owls (n = 520) during broadcast surveys within 9 half-month periods (L = late, E = early) from 15 January to 31 May 2000 and 2001 in Sonora, Mexico. For most pygmy-owls in Sonora, incubation is during April and brooding is during May. Solid line indicates decreasing linear trend in response time across seasons ($P = 0.018$). In boxes, the dotted line indicates the mean, solid line indicates median, lower and upper boundaries indicate 25th and 75th percentiles, respectively, whiskers indicate 10th and 90th percentiles, and points indicate observations <10th and >90th percentiles.

Repeat Surveys

We detected 94 adult males, 39 adult females, and 7 juveniles along 14 transects (n = 99 stations) surveyed in winter, spring, and autumn. Transect length averaged 3,369 ± 152 m, with 7.1 ± 0.2 stations per transect spaced an average of 500 ± 17 m apart. Relatively few owls responded before solicitation (6 ± 2% of 143) and none were initially detected visually.

Response time and distance.—Response time averaged 3.2 ± 0.2 minutes ($n = 140$, range = 0–11 min) and did not vary among seasons for all sexes and ages of owls combined. Response distance averaged 246 ± 11 m (range = 15–700 m) and was 25% (73 ± 35 m) greater in spring than in winter for all sexes and ages of owls combined (Table 3). Adult males responded 1.8 ± 0.7 minutes faster and from 87 ± 27 m farther away in spring than in winter ($t_{26} \geq 2.21$, $P \leq 0.039$); response time and distance did not vary among seasons for adult females. Adult males responded from 121 ± 62 m farther away than females in spring ($t_{17} = 1.94$, $P = 0.069$).

Response rates.—We detected ≥1 pygmy-owl on 100% of transects in spring and autumn and on 86 ± 9% ($n = 12$ of 14) of transects in winter. Response rates were 29 ± 20% lower in winter than at other times ($t_{26} = 1.86$, $P = 0.075$) for all sexes and ages of owls combined (Table 3). Response rates varied among seasons for adult males, adult females, and juvenile owls ($P \leq 0.079$; Table 3). For adult males, response rates were nearly 2 times higher in spring than in winter ($t_{26} = 1.94$, $P = 0.063$), yet we detected ≥1 male in all seasons along 64 ± 13% (n = 9 of 14) of transects. Response rates of adult females were similar in winter and autumn and nearly 3 times lower in spring (Table 3). Juveniles were only detected in autumn when they comprised 7 ± 2% of respondents.

Challenge Surveys

Radiomarked owls.—Detectability of adults was 0.50 ± 0.20 ($n = 3$ of 6) early and 0.67 ± 0.19 ($n = 4$ of 6) midway through fledgling dependency, and only adult males responded. In contrast, detectability was 1.0 for adult males

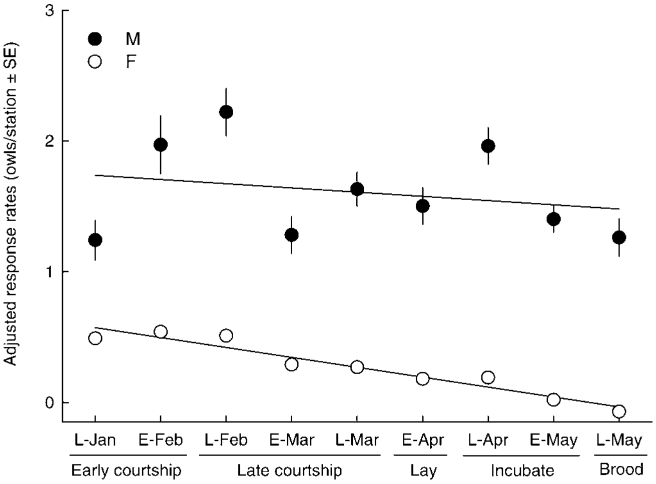

Figure 3. Adjusted response rates (no./station) of male ($n = 438$) and female ($n = 72$) ferruginous pygmy-owls during broadcast surveys within 9 half-month periods (L = late, E = early) from 15 January to 31 May 2000 and 2001 in Sonora, Mexico. Adjustment represents variation remaining after we removed that explained by environmental factors. Solid lines indicate decreasing linear trend in response rates across time for females ($P < 0.001$) and males ($P = 0.84$).

($n = 17$ of 17) and 0.91 ± 0.06 for juveniles ($n = 21$ of 23) during or soon after natal dispersal. For juveniles, 88 ± 9% of males ($n = 10$ of 12) and 100% of females ($n = 11$ of 11) responded to broadcasts. Juvenile males that did not respond were unpaired and had settled in or adjacent to areas already occupied by a territorial male pygmy-owl.

Occupied nests.—We performed 67 challenge surveys at 50 occupied nests, 23 (34%) during incubation and 44 (66%) during brooding; 86 ± 5% of these nests were successful. Overall, owls responded within 8 minutes during 90 ± 4% of surveys, only males responded during 88 ± 4% of surveys, only females during 4 ± 2% of surveys, and both females and males during 8 ± 3% of surveys. In all cases where both sexes responded, survey stations were 100 m from nests and females always responded before males. At 15 former nest sites occupied in previous years where we failed to detect a pygmy-owl during initial surveys, we never detected a pygmy-owl during subsequent surveys ($n = 43$), suggesting that false-negative results are rare.

The overall rate of owl responses to challenge surveys was high and decreased as distance between nests and surveyors increased ($P = 0.007$). At a distance of 100 m, 100% of owls responded ($n = 23$ of 23); at 300 m, 89 ± 7% responded ($n = 23$ of 26); at 500 m, 78 ± 10% responded ($n = 14$ of 18). Odds of detecting a pygmy-owl between 100 m and 500 m of an occupied nest decreased by 15 ± 7% with each 20-m increase in survey distance and were 60 ± 42% lower for nests that eventually failed. We predicted detectability to be $>0.99 \pm 0.02$ at 100 m, 0.93 ± 0.02 at 300 m, and 0.77 ± 0.02 at 500 m from nests after considering the effects of survey distance and nest outcome. Detectability was 0.92 ± 0.04 at nests that eventually succeeded compared to 0.71 ± 0.17 at nests that eventually failed ($P = 0.011$). Detectability did not vary appreciably with time of day, nest phase, or vegetation density ($P \geq 0.13$). Although sample sizes were too small for reliable analyses, detectability tended to be higher in mornings (100% of 12) than in midday and evenings (87 ± 5% of 55) and at low and moderate (94 ± 3% of 52) than at high (73 ± 13% of 11) vegetation density.

Response time averaged 2.1 ± 0.2 minutes ($n = 60$, range = 0–8) with 75 ± 6% of owls responding in ≤2 minutes and 98 ± 2% responding in ≤6 minutes, an estimate similar to that during statewide surveys of 2.6 ± 0.1 minutes. Response distance averaged 206 ± 15 m (range = 20–500 m) with 90 ± 4% of owls responding within 400 m of stations. Response time averaged 39 ± 24% faster during mornings than midday ($P = 0.023$) and did not vary between nest phases (Table 4). Response time increased by 21 ± 5% with each 100-m increase in distance from nests, an estimate similar to that during statewide surveys of 14 ± 2%. Response time was 63 ± 26% faster at nests that were

Table 3. Response rates, response time, and response distance for adult male ($n = 94$), adult female ($n = 39$), and juvenile ($n = 7$) ferruginous pygmy-owls along 14 transects we surveyed ($n = 99$ stations) during 3 seasons in northern Sonora, Mexico, 2001.

Factor (units)	Winter		Spring		Autumn				
Age – sex	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	df	F^a	P
Response rates (owls/station)									
All owls	0.35	0.08	0.47	0.08	0.51	0.08	2, 26	1.73	0.20
Ad M	0.21	0.07	0.41	0.07	0.32	0.07	2, 26	2.81	0.079
Ad F	0.14	0.03	0.058	0.03	0.19	0.03	2, 26	6.93	0.004
All juv	0.00	0.00	0.00	0.00	0.07	0.02	2, 26	4.80	0.017
Response time (min)									
All owls	3.3	0.4	2.7	0.4	3.4	0.4	2, 24	1.36	0.28
Ad M	5.0	0.8	3.2	0.7	3.9	0.7	2, 20	2.48	0.11
Ad F	2.6	0.6	2.5	0.8	3.1	0.6	2, 11	0.35	0.72
Response distance (m)									
All owls	214.5	25.3	287.1	23.5	258.4	23.5	2, 24	3.12	0.063
Ad M	223.0	32.5	310.3	27.8	289.4	29.9	2, 20	2.83	0.083
Ad F	202.9	33.3	189.1	43.7	188.8	29.0	2, 11	0.06	0.94

[a] Test statistics and P-values are from mixed-model, repeated-measures analysis of variance.

Table 4. Factors that explained variation in response time of ferruginous pygmy-owls during challenge surveys ($n = 60$) at 50 occupied nests between 19 April and 14 June 2005 in northern Sonora, Mexico.

Factor (units)	Parameter estimate[a,b]	SE	χ^2	P
Challenge distance (100 m)	0.19	0.05	13.59	<0.001
Nest outcome (failure)	0.49	0.23	4.03	0.045
Time of day[c]			5.87	0.053
Early	−0.49	0.22	5.21	0.023
Late	−0.17	0.26	0.44	0.51
Nest phase (incubation)	−0.0027	0.18	0.00	0.99

[a] Parameter estimates and P-values are from log-linear regression for Poisson counts.

[b] The inverse natural log of parameter estimates equals the percent change in response time with each 1-unit increase for continuous factors or presence for nominal factors.

[c] Reference level equals midday surveys.

eventually successful ($P = 0.045$) and did not vary with vegetation density ($P = 0.22$).

DISCUSSION

Adult male cactus ferruginous pygmy-owls always responded to conspecific calls broadcasted during the nesting season by surveyors that were 100 m from occupied nests and during or soon after natal dispersal when surveyors were 300 m from owls. As the distance between owls and surveyors increased, detectability of nesting owls decreased similarly to that observed for northern goshawks (*Accipiter gentilis*; Kennedy and Stahlecker 1993, Watson et al. 1999, Roberson et al. 2005) and likely other diurnal raptors. Although detectability of pygmy-owls was somewhat higher during mornings than at other times of day, within-day differences in detectability were less than for other raptors (Kimmel and Yahner 1990, McLeod and Andersen 1998, Conway and Simon 2003). Compared to detectability of other owls (range = 0.13–0.76; Debus 1995, Conway and Simon 2003, Olson et al. 2005, Wintle et al. 2005), detectability of pygmy-owls is exceptionally high.

Seasonal changes in territorial behavior likely explain much of the variation we observed in detectability of pygmy-owls (Selmi and Boulinier 2003, Kéry et al. 2005). Detectability of adult males was high when nesting, low during fledgling dependency, and high again during or soon after natal dispersal. This contrasts somewhat with temperate-zone hawks, where detectability is typically lower during nesting and higher immediately before or after nesting or during fledgling dependency (Kennedy and Stahlecker 1993, McLeod and Andersen 1998, Roberson et al. 2005). Response rates of temperate-zone owls peaked either just before or early during nesting (Ganey 1990, Morrell et al. 1991, Clark and Anderson 1997) or during natal dispersal (Lundberg 1980, Ritchison et al. 1988) and were often lower during fledgling dependency. Detectability of pygmy-owls and other raptors likely increase just before and during natal dispersal because of increased frequency of territorial interactions that result from an influx of dispersing juveniles recently recruited into the population.

Response times of pygmy-owls declined slowly and systematically across the courtship and nesting periods (Fig. 2), yet within this general decline, response times were faster during late courtship than immediately before and during egg laying. Similarly, response distances declined systematically across the courtship and nesting periods yet were lowest during late courtship and early incubation, suggesting that owls made responsive movements toward broadcasts. Seasonal changes in territorial behavior likely explain much of the variation we observed in response time and response distance of pygmy-owls.

Although we did not assess detectability before nesting, response rates of male pygmy-owls did not vary systematically between early courtship and brooding (Fig. 3), suggesting that detectability did not vary appreciably during these times. In contrast, response rates of females declined to zero early in the nesting period, suggesting a decline in detectability. Further, we detected many fewer females during all seasons, indicating that females were much less responsive than males.

From transects surveyed repeatedly in winter, spring, and autumn, we found that response rates were lowest in winter, with more males detected in spring and more females detected in autumn. Because pygmy-owls are permanent residents (Johnsgard 1988), some males may have been present in winter and either did not respond or were too far from surveyors to be detected. In winter, home ranges of owls can be larger than during nesting (Mazur et al. 1998, van Riper and van Wagtendonk 2006), potentially explaining the lower response rates we observed. In winter and autumn, females often responded with continuous bouts of territorial calls rather than contact, solicitation, or alarm calls heard during nesting, suggesting that some females defend territories during these seasons perhaps to reduce overlap with males (Belthoff et al. 1993).

During morning surveys from early courtship through brooding, pygmy-owls that responded to conspecific calls did so quickly, with 99% responding in ≤ 8 minutes. The few males that were slower to respond did so less aggressively and often from areas with no apparent nesting structures, suggesting that they may not have been nesting. Although spontaneous calling by pygmy-owls is typically crepuscular (Gilman 1909, Stillwell and Stillwell 1954), pygmy-owls at occupied nests responded to broadcasts throughout the day although more slowly and for shorter durations during midday.

Vegetation screening can reduce detection rates of birds (Emlen 1971, Oelke 1981). We found that response times of pygmy-owls did not vary across a broad gradient of vegetation structure, from open desertscrub to closed tropical deciduous forest. In contrast, topography did influence response times, with owls responding faster in canyons where greater vertical and lower horizontal structure may have focused broadcasts and enhanced listening conditions. Faster responses from owls in areas with higher owl abundance suggest that density of conspecifics can influence calling behavior (Penteriani et al. 2002), yet this pattern might be partially explained by owls hearing broadcasts or other responding owls at stations surveyed earlier.

Shorter response distances in areas with greater vegetation volume may have been an artifact of greater owl abundance in woodlands (Flesch 2003*a*, *b*) rather than sound being attenuated by vegetation. Responses by pygmy-owls began to decline at distances >300 m (Fig. 1B), yet because owls typically move toward broadcasts (Debus 1995), some owls detected at these distances likely originated from farther away. Declines in responses with increasing distance are a function of 1) true declines in responses to broadcasts, 2) arrangement of environmental features such as vegetation and land forms, and 3) reduced ability of surveyors to detect owls at great distances.

Implications for Surveys

The best survey techniques have a high and consistent probability of detecting the target species and low sampling error (Thompson et al. 1998). For ferruginous pygmy-owls, broadcasting territorial calls is a reliable and efficient means of estimating occupancy and abundance during some seasons because detectability approaches 1.0 and owls respond rapidly and predictably across a wide range of distances, vegetation communities, and times of day. Surveys beginning early in courtship and continuing through brooding will reliably index occupancy and abundance of territorial male pygmy-owls. Although surveys during autumn have been recommended for reducing disturbance during nesting (Proudfoot and Beasom 1996), we found that radiomarked pygmy-owls returned to normal activities soon after responding to broadcasts. Further, the rates of nest failure we observed when challenging owls at occupied nests were similar to rates observed in other years (A. D. Flesch, unpublished data) suggesting no adverse influence of broadcasts during nesting. Additionally, autumn surveys often included responses by newly fledged recruits some of whom may not have yet established territories and occupied areas not used for nesting. Therefore, surveys during autumn may overestimate abundance of breeding adult males, the most reliable index of abundance.

Reliably estimating changes in abundance across time using uncorrected counts can only be accomplished when detectability is constant during the survey period (Yoccoz et al. 2001, Bart et al. 2004). Consequently, most studies estimate detectability using capture–recapture, distance, or double-sampling methods (Buckland et al. 1993, Nichols et al. 2000, Williams et al. 2002) so that variation in detectability can be used to correct counts. Without this adjustment, undetected individuals may confound studies of wildlife–habitat relationships (Tyre et al. 2003, Gu and Swihart 2004), population trends (Pollock et al. 2002), or metapopulations (Moilanen 2002). For species with consistently high detectability, such as pygmy-owls, uncorrected counts can provide reliable indices of occupancy and abundance when surveys are done during periods when variation in detectability is low. For example, when based on careful survey design, uncorrected counts can be used to monitor population trends of pygmy-owls (Flesch and Steidl 2006) and other species with similar detectability because counts reliably track changes in abundance over time.

When estimating density using distance-sampling methods, predetection movements by animals that are induced by surveyors will bias density estimates (Buckland et al. 1993) unless accounted for explicitly (e.g., Palka and Hammond 2001). If responsive movements vary seasonally due to changes in territorial behavior, then bias of estimates may vary in a complex way. The systematic seasonal variation we observed in response distances of pygmy-owls suggests that they are often not detected at their initial locations. Therefore, surveys designed to estimate density based on distance-sampling methods should be concentrated over narrow time periods or timing should be considered a covariate when modeling the detection function (Buckland et al. 2004). For species where detectability is consistently high, such as pygmy-owls, the ratio of number of territorial individuals counted relative to survey effort may provide less biased estimates of abundance than those based on distance-sampling methods when responsive movements vary.

MANAGEMENT IMPLICATIONS

Although we studied pygmy-owls in Sonora, our results likely apply well to Arizona because pygmy-owls are distributed continuously across portions of the Sonora–Arizona border region where owls occupy similar ecological settings. Despite high detectability, careful design is necessary to efficiently and reliably survey pygmy-owl populations. Spacing between survey stations should be based on survey objectives because it presents a trade-off between detecting all potentially responsive individuals and limiting the potential for double-counting. If the primary objective is to estimate occupancy of pygmy-owls with high reliability, such as required for compliance with federal laws, we suggest spacing survey stations at 175–200 m intervals. If the primary objective is to estimate abundance of pygmy-owls, we recommend spacing stations at 400 m intervals, which should facilitate detection of >95% of territorial males. Increasing spacing to 600 m following an initial detection will further reduce the potential for double-counting, though not appreciably increase the rate of nondetections because linear distances between neighboring nests on the same transects averaged 1,064 ± 73 m ($n = 39$; A. D. Flesch, unpublished data).

To survey when detectability is high and to allow pygmy-owls sufficient time to respond, we recommend surveying stations for 8 minutes between 1 hour before and 3 hours after local sunrise from early courtship through brooding. Increasing to 12 minutes can ensure detection of virtually all potentially responsive pygmy-owls, which can be essential for meeting some objectives. Although morning surveys seem most effective, surveys during midday and evening are almost equally effective and are appropriate for some objectives. Because pygmy-owls often respond rapidly after broadcasts, we recommend alternating broadcast and listening periods every 30–45 seconds and listening during the last 30–60 seconds at each station. Recommendations for 90 seconds of listening after each broadcast (USFWS 2000*a*) are inefficient unless noise or wind disturbance are present.

Although a single survey seems adequate to estimate occupancy and abundance of pygmy-owls during courtship, nesting, and natal dispersal, completing ≥2 surveys will increase reliability. The current recommended protocol for surveying pygmy-owls for compliance with federal laws (USFWS 2000*a*) suggests 3 surveys between 1 January and 30 June with ≥1 survey between 15 February and 15 April. Instead, we recommend 2 surveys between late January and late May with ≥1 survey between mid-March and late April and a third survey in late summer or early autumn during or immediately after natal dispersal. Further, timing surveys just before nesting will allow detection of individuals that do not nest or that fail early in the season.

ACKNOWLEDGMENTS

We thank G. Valencia, A. Villareal, E. Swarthout, G. Greene, S. Jacobs, S. Lowery, R. Hunt, R. van Ommeren, and R. Wilcox for assisting with surveys and E. Lopez of Instituto del Medio Ambiente y Desarrollo Sustenable del Estado de Sonora and J. Garcia of Centro de Investigacion en Alimentacion y Desarrollo for logistical support. For financial support, we thank F. Baucom and M. Wrigley of the USFWS, M. Maiefski, and J. Pein of the Arizona Department of Transportation, L. Norris of the United States National Park Service, and T. Wootten of T&E, Inc. Finally, we thank the people and landowners of Sonora, Mexico for welcoming us on their lands during this research.

LITERATURE CITED

Bart, J., S. Droege, P. Geissler, B. Peterjohn, and C. J. Ralph. 2004. Density estimation in wildlife surveys. Wildlife Society Bulletin 34:1242–1247.

Belthoff, J. R., E. J. Sparks, and G. Ritchison. 1993. Home ranges of adult and juvenile eastern screech-owls: size, seasonal variation and extent of overlap. Journal of Raptor Research 27:8–15.

Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines, and K. H. Pollock. Estimating species richness: the importance of heterogeneity in species detectability. Ecology 79:1018–1028.

Brown, D. E., editor. 1982. Biotic communities of the American Southwest: United States and Mexico. Desert Plants 4:1–342.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, editors. 2004. Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.

Buckland, S. T., K. P. Burnham, D. R. Anderson, and J. L. Laake. 1993. Density estimation using distance sampling. Chapman and Hall, London, United Kingdom.

Clark, K. A, and S. H. Anderson. 1997. Temporal, climatic, and lunar affecting owl vocalizations of western Wyoming. Journal of Raptor Research 31:358–363.

Conway, C. J., and J. C. Simon. 2003. Comparison of detection probability associated with burrowing owl survey methods. Journal of Wildlife Management 67:501–511.

Debus, S. J. S. 1995. Surveys of large forest owls in northern New South Wales: methodology, calling behavior and owl responses. Corella 19:38–50.

Emlen, J. T. 1971. Population densities of birds derived from transect counts. Auk 88:323–342.

Flesch, A. D. 2003*a*. Distribution, abundance, and habitat of cactus ferruginous pygmy-owls in Sonora, Mexico. Thesis, University of Arizona, Tucson, USA.

Flesch, A. D. 2003*b*. Perch-site selection and spatial use by cactus ferruginous pygmy-owls in south-central Arizona. Journal of Raptor Research 37:151–157.

Flesch, A. D., and R. J. Steidl. 2006. Population trends and implications for monitoring cactus ferruginous pygmy-owls in northern Mexico. Journal of Wildlife Management 70:867–871.

Fuller, M. R., and J. A. Mosher. 1987. Raptor survey techniques. Pages 37–65 *in* B. A. Giron Pendleton, B. A. Milsap, K. W. Cline, and D. M. Bird, editors. Raptor management techniques manual. National Wildlife Foundation Scientific and Technical Series Number 10, Washington, D.C., USA.

Ganey, J. L. 1990. Calling behavior of spotted owls in northern Arizona. Condor 92:485–490.

Gentry, H. S. 1982. Sinaloan deciduous forest. Desert Plants 4:73–77.

Gerhardt, R. P. 1991. Response of mottled owls to broadcast of conspecific call. Journal of Field Ornithology 62:239–244.

Gilman, M. F. 1909. Some owls along the Gila River of Arizona. Condor 11:145–150.

Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of nondetection of species occurrence on wildlife-habitat models. Biological Conservation 116:195–203.

Hardy, P. C., and M. L. Morrison. 2000. Factors affecting detection of elf owls and western screech owls. Wildlife Society Bulletin 28:333–342.

Johnsgard, P. A. 1988. North American owls: biology and natural history. Smithsonian Institution Press, Washington, D.C., USA.

Kennedy, P. L., and D. W. Stahlecker. 1993. Responsiveness of nesting northern goshawks to taped broadcasts of 3 conspecific calls. Journal of Wildlife Management 57:249–257.

Kéry, M., J. A. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated counts using binomial mixture models. Ecological Applications 15:1450–1461.

Kimmel, J. T., and R. H. Yahner. 1990. Response of northern goshawks to taped conspecific and great-horned owl calls. Journal of Raptor Research 24:107–112.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS systems for mixed models. SAS Institute, Cary, North Carolina, USA.

Lundberg, A. 1980. Vocalizations and courtship feeding of the Ural owl *Strix uralensis*. Ornis Scandinavia 11:65–70.

Mazur, K. M., S. D. Frith, and P. C. James. 1998. Barred owl home range and habitat selection in the boreal forest of central Saskatchewan. Auk 115:746–754.

McGarigal, K., and J. D. Fraser. 1985. Barred owl responses to recorded vocalizations. Condor 87:552–553.

McLeod, M. A., and D. E. Andersen. 1998. Red-shouldered hawk broadcast surveys: factors affecting detection of responses and population trends. Journal of Wildlife Management 62:1385–1397.

Moilanen, A. 2002. Implications of empirical data quality for metapopulation model parameter estimation and application. Oikos 96:516–530.

Morrell, T. E., R. H. Yahner, and W. L. Harkness. 1991. Factors affecting detection of great horned owls by using broadcast vocalizations. Wildlife Society Bulletin 19:481–488.

Mosher, J. A., M. R. Fuller, and M. Kopeny. 1990. Surveying woodland raptors by broadcast of conspecific vocalizations. Journal of Field Ornithology 61:453–461.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408.

Oelke, H. 1981. Limitations of estimating bird populations because of vegetation structure and composition. Studies in Avian Biology 6:316–321.

Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. Journal of Wildlife Management 69:918–932.

Palka, D. L., and P. S. Hammond. 2001. Accounting for responsive movements in line-transect estimates of abundance. Canadian Journal of Fisheries and Aquatic Sciences 58:777–787.

Penteriani, V., M. Gallardo, and H. Cazassus. 2002. Conspecific density biases passive auditory surveys. Journal of Field Ornithology 73:387–391.

Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13:105–119.

Proudfoot, G. A., and S. L. Beasom. 1996. Responsiveness of cactus ferruginous pygmy-owls to broadcasted conspecific calls. Wildlife Society Bulletin 24:294–297.

Proudfoot, G. A., S. L. Beasom, F. Chavez-Ramirez, and J. L. Mays. 2002. Response distance of ferruginous pygmy-owls to broadcasted conspecific calls. Journal of Raptor Research 36:170–175.

Proudfoot, G. A., and R. R. Johnson. 2000. Ferruginous pygmy-owl (*Glaucidium brasilianum*). Account 498 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in methods of data analysis. Wadsworth, Pacific Grove, California, USA.

Ritchison, G., P. M. Cavanagh, J. R. Belthoff, and E. J. Sparks. 1988. The singing behavior of eastern screech-owls: seasonal timing and response to playback of conspecific song. Condor 90:648–652.

Roberson, A. M., D. E. Andersen, and P. L. Kennedy. 2005. Do breeding phase and detection distance influence the effective area surveyed for northern goshawks? Journal of Wildlife Management 69:1240–1250.

Russell, S. M., and G. Monson. 1998. The birds of Sonora. University of Arizona Press, Tucson, USA.

Rzedowski, J. 1978. La vegetacion de Mexico. Limusa-Wiley, Mexico City, Mexico. [In Spanish.]

Seavy, N. E. 2004. Environmental correlates of African wood-owl calling activity in Kibale National Park, Uganda. Journal of Raptor Research 38: 208–213.

Selmi, S., and T. Boulinier. 2003. Does time of season influence bird species number determined from point-count data? A capture–recapture approach. Journal of Field Ornithology 74:349–356.

Shreve, F. 1951. Vegetation of the Sonoran desert. Carnegie Institute of Washington, Publication Number 591, Washington, D.C., USA.

Steidl, R. J., and L. Thomas. 2001. Power analysis and experimental design. Pages 14–36 *in* S. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Second edition. Oxford University Press, New York, New York, USA.

Stillwell, J., and N. Stillwell. 1954. Notes on the call of ferruginous pygmy-owl. Wilson Bulletin 66:152.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego, California, USA.

Tyre, A. J., B. Tenhumberg, S. A. Field, H. P. Possingham, D. Niejalke, and K. Parris. 2003. Improving precision and reducing bias in biological surveys by estimating false negative error rates in presence–absence data. Ecological Applications 13:1790–1801.

United States Fish and Wildlife Service [USFWS]. 1997. Endangered and threatened wildlife and plants: determination of endangered species status for the cactus ferruginous pygmy-owl in Arizona; Final Rule, March 10, 1997. Federal Register 62:10730–10747.

United States Fish and Wildlife Service [USFWS]. 2000*a*. Cactus ferruginous pygmy-owl survey protocol. Arizona Ecological Services Field Office, Phoenix, Arizona. <http://www.fws.gov/ifw2es/Documents/R2ES/FINAL_REV_PROTOCOL.pdf>. Accessed 30 Jan 2006.

United States Fish and Wildlife Service [USFWS]. 2000*b*. Notice of availability; recommended guidance for private landowners concerning the cactus ferruginous pygmy-owl; and the cactus ferruginous pygmy-owl survey protocol. Federal Register 65:14999–15000.

United States Fish and Wildlife Service [USFWS]. 2003. Cactus ferruginous pygmy-owl (*Glaucidium brasilianum cactorum*) draft recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.

van Riper, C., III, and J. van Wagtendonk. 2006. Home range characteristics of great gray owls in Yosemite National Park. Journal of Raptor Research 40:130–141.

van Rossem, A. J. 1945. A distributional survey of the birds of Sonora, Mexico. Occasional Papers Museum of Zoology, Louisiana State University 21:1–379.

Watson, J. W., D. W. Hays, and D. J. Pierce. 1999. Efficacy of northern goshawk broadcast surveys in Washington state. Journal of Wildlife Management 63:98–106.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Wintle, B. A., R. P. Kavanagh, M. A. McCarthy, and M. A. Burgman. 2005. The magnitude and management consequences of false negative observation error in surveys of arboreal marsupials and large forest owls. Journal of Wildlife Management 69:905–917.

Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution 16:446–453.

Associate Editor: Bechard.