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DISTRIBUTION AND HABITAT ASSOCIATIONS OF NORTHERN PYGMY-OWLS IN OREGON

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ABSTRACT.—We conducted acoustic lure surveys of Northern Pygmy-Owls (*Glaucidium gnoma*) on 224 transects that were systematically placed in forested areas in Oregon. Our objectives were to determine if pygmy-owls were associated with particular forest types, regions, or with large trees. We also examined temporal variation in numbers of owls located. We detected pygmy-owls at 161 of 224 transects. The mean number of owls detected per linear km on individual transects was 0.21 (SE = 0.01, range of means = 0–1.07, $N = 224$). Mean detections per transect were highest in the Western Cascades, intermediate in the Coast Ranges, Klamath Mountains, Eastern Cascades, and Blue Mountains, and lowest in the Willamette Valley and High Desert Ecoregions. The mean number of owls detected per transect was highest in mesic Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine forests (*Pinus ponderosa*), intermediate in conifer/hardwood and mixed-conifer forests, and lowest in alpine conifers, deciduous hardwoods, and western juniper (*Juniperus occidentalis*) woodlands. Also, the mean number of owls located per transect increased with the average diameter ranking of the dominant overstory trees. The mean number of owls detected per transect declined in July, and there was evidence of a decrease in the number of owls detected per survey station with increasing time after sunrise. Our data suggested that removal of large trees may have reduced numbers of Northern Pygmy-Owls, but this finding needs to be viewed in the context that our surveys also show that this species is a widely-distributed and fairly common forest bird in Oregon.

KEY WORDS: *Northern Pygmy-Owl*; *Glaucidium gnoma*; *acoustic lure survey*; *forest management*; *Oregon*; *population monitoring*; *transect sampling*.

DISTRIBUCIÓN Y ASOCIACIONES DE HÁBITAT DE *GLAUCIDIUM GNOMA* EN OREGON

RESUMEN.—Realizamos censos acústicos de *Glaucidium gnoma* reproduciendo vocalizaciones previamente grabadas en 224 transectos ubicados sistemáticamente en áreas boscosas en Oregon. Nuestro objetivo fue determinar si los individuos de esta especie se encuentran asociados con tipos particulares de bosque, con regiones particulares o con árboles grandes. También examinamos la variación temporal en el número de individuos localizados. Detectamos individuos de esta especie en 161 de los 224 transectos. El número

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promedio de individuos detectados por kilómetro por transecto fue 0.21 (EE = 0.01, rango de promedios = 0–1.07, $N = 224$). El promedio de detecciones por transecto fue máximo en las Western Cascades, intermedio en Klamath Mountains, Eastern Cascades y Blue Mountains, y mínimo en las ecoregiones del valle de Willamette y High Desert. El número promedio de individuos detectados por transecto fue máximo en bosques húmedos dominados por *Pseudotsuga menziesii* y en bosques de *Pinus ponderosa*, intermedio en bosques de coníferas y maderas duras y en bosques mixtos de coníferas, y mínimo en bosques de coníferas alpinos, bosques caducifolios de maderas duras y rodales de *Juniperus occidentalis*. Además, el número promedio de individuos detectado por transecto incrementó con el promedio del rango de diámetros de los árboles dominantes de los estratos superiores del bosque. El número promedio de individuos detectados por transecto disminuyó en julio, y el número de individuos detectados por estación de muestreo disminuyó con en el tiempo transcurrido desde el amanecer. Nuestros datos sugieren que la remoción de árboles grandes podría haber reducido el número de individuos de *G. gnoma*, pero este hallazgo debe examinarse teniendo en cuenta que nuestros censos también muestran que esta especie está ampliamente distribuida y es relativamente común en los bosques de Oregon.

[Traducción del equipo editorial]

Although the Northern Pygmy-Owl (*Glaucidium gnoma*) is a commonly encountered resident of forest areas in western North America (e.g., Bent 1938, Holt and Petersen 2000), little is known about its relative abundance in different regions or forest types. Some authors have suggested that Northern Pygmy-Owls are associated with mature forests (Hume and Boyer 1991, Thomas et al. 1993) and others have suggested that populations of this species may be declining (Marcot 1995). The presumed association between Northern Pygmy-Owls and older forests is largely based on the fact that pygmy-owls nest primarily in woodpecker cavities (Voous 1988), which tend to be in large trees or snags (Thomas 1979, Bull 1986, Lundquist and Mariani 1991, Nelson 1991). However, the Northern Pygmy-Owl is a food generalist (e.g., Bent 1938, Holt and Leroux 1996, Giese 1999, Holt and Petersen 2000, Giese and Forsman 2003), and Reynolds et al. (1988) suggested that it might be less affected by tree harvest than some owl species because it occupies a variety of forest vegetation types (see also Hayward and Garton 1988, Voous 1988, Marcot 1995).

In Oregon, Northern Pygmy-Owls are regularly observed in a diverse array of habitats and at all seasons of the year, but their nests are rarely found and there is no quantitative information on their abundance in different regions or forest types. In 1996–97, we conducted a systematic survey of Northern Pygmy-Owls in Oregon to determine if they differed in abundance among forest types or ecoregions. We also examined diameters of dominant overstory trees at survey stations in order to test the hypothesis that the abundance of pygmy-owls was correlated with the presence of large trees (i.e., older forests). Another objective was to design a repeatable survey protocol for Northern Pygmy-

Owls that could be used to detect population trends.

STUDY AREA

The study area included all forested areas in Oregon (Fig. 1). Topography varied from relatively flat river valleys and lava plains to steep mountainous terrain. Elevation of study sites ranged from 10–2200 m. Forests in the study area were largely dominated by conifers and included a broad array of age-classes and structural types, ranging from relatively uniform stands of young trees on recently harvested or burned areas to very old forests (250–750 yr old) characterized by large overstory trees, multilayered canopies, and high within-stand variability in tree size (Franklin and Dyness 1973, Franklin and Spies 1984). This mosaic of vegetation types was the result of a long history of wildfires, windstorms, forest management, grazing, and development.

For our analysis we subdivided the study area into eight ecoregions based on the map produced by Omernik (1987), who based his classification on major differences in vegetation, soils, and climate (Fig. 1). Forests in the Coast Range and Western Cascades ecoregions were primarily dominated by mesic conifer forest in which Douglas-fir (*Pseudotsuga menziesii*), was intermixed with variable amounts of western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Forests in the Klamath Mountains Ecoregion were dominated by conifer/hardwood forests of Douglas-fir intermixed with evergreen hardwoods, including tanoak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), and Pacific madrone (*Arbutus menziesii*), or by mixed-conifer forests of Douglas-fir, grand fir (*Abies grandis*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and incense-cedar (*Caloce-*

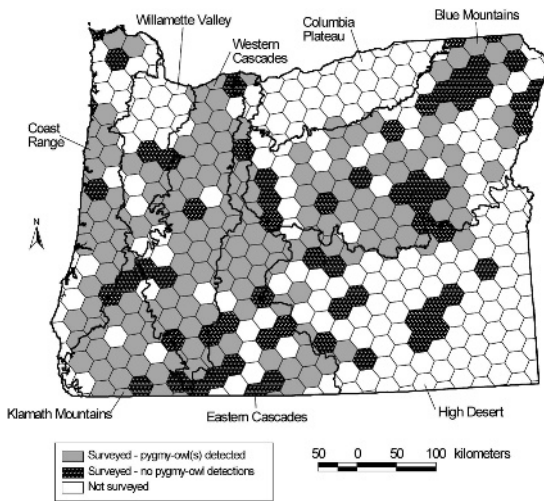


Figure 1. Sampling hexagons and ecoregions used to stratify surveys of Northern Pygmy-Owls in Oregon, 1996–97. Hexagonal grid adapted from White et al. (1992). Ecoregions adapted from Omernik (1987) and U.S. Environmental Protection Agency (1996).

drus decurrens). The Willamette Valley Ecoregion in western Oregon was dominated by urban and agricultural areas, but deciduous forests dominated by black cottonwood (*Populus trichocarpa*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*) were common along streams throughout the valley. The Eastern Cascades and Blue Mountain ecoregions were characterized by ponderosa pine forests at mid-elevations, western juniper (*Juniperus occidentalis*) woodlands at lower elevations, and mixed-conifer forests at higher elevations. The High Desert Ecoregion of southeast Oregon was dominated by shrub-steppe vegetation, but also included extensive areas of western juniper woodland. Western juniper typically occurred in a savanna setting, but in a few areas it also formed closed-canopy forests.

METHODS

To estimate the relative abundance of pygmy-owls, we conducted acoustic lure surveys on point transects and recorded unlimited distance counts of owls at each survey station (Ralph 1981). Each transect consisted of 15 survey stations along a road, spaced at straight-line intervals of 0.8 km. Our predictions were that mean numbers of individuals detected per transect would differ among forest types and ecoregions and increase with the diameter of overstory trees. To account for variation in numbers of owls detected due to our methodology, we also examined relationships between the number of owls detected per transect and the time and day of the year of the survey. Of

the total transects surveyed, 92% were done by us or by wildlife biologists or wildlife technicians who worked for state or federal agencies, and 8% were surveyed by experienced birdwatchers, who were recommended by local biologists. We provided all surveyors with detailed written and oral instructions, field forms, and a cassette tape of pygmy-owl vocalizations. We also talked with all observers to make sure that they could discriminate between the calls of pygmy-owls and the other birds that could be encountered during surveys. Pygmy-owl calls are very distinctive and are difficult to confuse with any other species, except for imitations given by jays. All surveyors were instructed to attempt to visually locate owls if there was any question regarding the correct identity of the owl or the type of forest that the owl was in. In 69 cases in which this was done, the vocal identification was correct in every case.

The study area was divided into 434 hexagonal sampling polygons, 275 of which included forest areas that were extensive enough to accommodate survey transects (Fig. 1, White et al. 1992). Our objective was to conduct one transect in each of the 275 forested hexagons, but because of logistical problems and time constraints, we conducted surveys in 248 hexagons. Of these, 24 were dropped from the analysis because of survey irregularities or adverse weather conditions, so the sample available for analysis was 224 surveys, distributed as follows: Coast Ranges (34), Western Cascades (37), Klamath Mountains (17), Eastern Cascades (42), Blue Mountains (66), Willamette Valley (8), and High Desert (20); Fig. 1. Survey irregularities that led to routes being dropped from the sample included forms with incomplete data, improper spacing of survey stations, or surveys that were not discontinued under inclement weather conditions.

The initial survey station in each hexagon was placed on a road as close as possible to a randomly selected Universal Transmercator grid intersection. If the random starting point fell in non-forest, the starting point was moved to the nearest forest. Our definition of non-forest included areas that were permanently deforested (towns, fields, farms, shrub-steppes), but did not include clear-cuts, which were only temporarily deforested. To avoid subjective decisions about which roads to use for transects, surveyors were instructed to proceed as much as possible in a northerly direction from the initial survey station when laying out transects. In some cases, survey transects were broken into 2–3 sections separated by areas of non-forest or by sections of road that were closed. In 28 polygons in which forests were not extensive enough to include 15 survey stations, we conducted partial transects with 5–14 stations. As long as access was possible, transects were laid out regardless of land ownership. Once started, transects could continue into adjacent sampling hexagons, as long as they did not overlap other transects.

We conducted surveys between 6 April and 31 July in 1996 and 1997. At each station, we listened for owls for 1 min before starting to play pygmy-owl calls. Then, we alternated between 30-sec intervals of calling and 30-sec intervals of passive listening for 9 more min. We used a megaphone attached to a cassette player to broadcast the territorial call of a male Northern Pygmy-Owl. We aimed the megaphone in all directions to maximize coverage. Calls were broadcast at high volume and were audible to humans 0.3–0.5 km away, depending on terrain and

ambient noise. Surveys were started within ± 1 hr of sunrise and were completed before noon. Surveyors were instructed to avoid doing surveys in windy or rainy conditions and to discontinue a survey if marginal weather conditions (moderate wind or rain) occurred at >3 stations on a transect.

When a pygmy-owl responded, we recorded the time of initial detection and plotted the location on a 7.5 min USGS topographic map. Visual contact was not required, and auditory detections were often plotted by triangulation, or by obtaining a compass bearing and estimating the distance to the owl. In most cases, observers were able to see the forest stands from which owls were calling and used these visual references to assign the response location to a particular forest type and diameter rank. We used a variety of clues to estimate the number of owls responding, including spacing, timing and direction of responses, visual sightings, and number of owls responding simultaneously. Detections were assumed to be repeat responses if they came from the direction of a previously-located owl, unless there was evidence to the contrary. In cases of confusion, we often drove back to a previous location to determine if an owl was still calling at that location or had followed us. We did not use fixed criteria for time or distance between responses to estimate the number of owls responding because we felt that would result in more errors than a method that was based on all available clues.

Surveyors assigned each transect to one of seven forest types based on the forest type at the majority of survey stations (mesic douglas-fir, deciduous hardwoods, alpine conifers, mixed-conifer, conifer/hardwoods, ponderosa pine, western juniper). Trees that were immediately adjacent to each survey station were classified into one or more diameter ranks based on an ocular estimate of the mean diameter-at-breast-height of the overstory trees, as follows: 1 = 0–11 cm, 2 = 12–29 cm, 3 = 30–49 cm, 4 = 50–99 cm, 5 = ≥ 100 cm. Observers were instructed to measure a few trees along each transect in order to calibrate their ocular estimates of tree size and reduce observer variability. If the forest included more than one size class of overstory trees, then the observer recorded multiple rank scores for the stand. However, for analyses, we used only the highest rank score for each stand. We did not use a cutoff for the number of trees that had to be present to assign a particular rank score, but in all but a few cases, dominant rank scores were based on trees that comprised a large part of the forest canopy, as opposed to just a few trees scattered through the stand. Diameter ranks were used to compute a mean diameter rank score for each transect.

We used Poisson log-linear regression (Ramsey and Schafer 1997) to examine relationships between a set of explanatory variables and the number of owls detected per transect. Explanatory variables were year, ecoregion, forest type, mean diameter rank of the largest overstory trees, number of survey stations per transect (log transformed), day of the year (1 January = day 1), and mean time of the survey relative to sunrise. We used quasi-likelihood analysis to account for any extra-Poisson variation (Ramsey and Schafer 1997). This was necessary because the deviance divided by the degrees of freedom for the regression model was 1.7, suggesting overdispersion. Significance levels of coefficients were determined with χ^2 tests, and

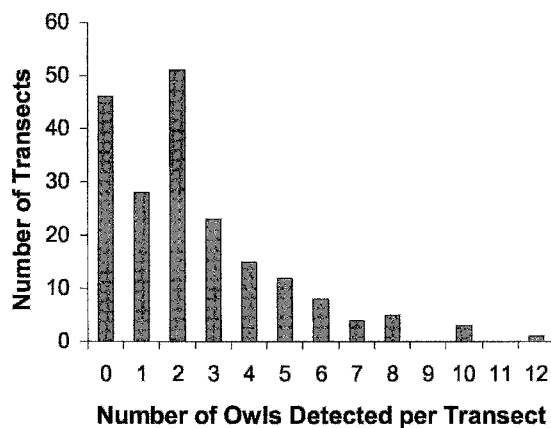


Figure 2. Distribution of Northern Pygmy-Owl survey transects relative to the number of owls detected per transect in Oregon, 1996–97. Counts were limited to 196 transects with 15 calling stations.

95% confidence intervals for parameters were based on likelihood ratios.

We tested ecoregion predictions in a model that included forest type, despite the fact that ecoregions are largely defined by vegetation types, because we wanted to determine whether there were any ecoregion patterns not accounted for by forest type. To evaluate relationships between owls and forest type without the confounding effects of ecoregion, we used a reduced model that did not include the ecoregion variable.

To examine the null hypothesis that time of day did not influence the number of owls detected per transect we used a composite variable (mean survey time), which was simply the mean of the starting times for all stations on a transect. We also used one-way analysis of variance to test the null hypothesis that the mean number of owls responding per survey station did not differ among the eight 1-hr time intervals from 1 hr before sunrise through 7 hr after sunrise. Results, reported as mean \pm SE, were considered significant if $P < 0.05$.

RESULTS

We detected pygmy-owls on 161 (72%) of 224 transects (Fig. 1). A total of 495 owls were detected. The mean number of owls detected per transect was 2.24 ± 0.15 (range = 0–12) for all 224 transects, and 2.43 ± 0.17 for 196 transects with 15 stations (range = 0–12; Fig. 2). The mean number of owls detected per survey station was 0.15 ± 0.01 (range of means = 0–0.80, $N = 224$), and the mean number of owls detected per linear km in individual transects was 0.21 ± 0.01 (range of means = 0–1.07, $N = 224$). The mean number of owls detected per hr of survey was 0.91 ± 0.06 ($N = 224$, range of means = 0–4.8). Most owls (86%) were detected by call only, but 14% were detected visually as well as by

Table 1. Regression coefficients ($\hat{\beta}$) and test results from Poisson log-linear regression analysis of the number of Northern Pygmy-Owls detected per acoustic lure survey transect in Oregon, 1996–97. Analysis based on a sample of 224 transects, including 196 transects with 15 survey stations and 28 transects with 5–14 stations.

MODEL ATTRIBUTES	$\hat{\beta}$	95% CI		χ^2	df	P
		LOWER	UPPER			
Full model (with ecoregion)						
Log no. of survey stations	1.553	-0.025	3.131	3.720	1	0.054
Day of the year	-0.004	-0.009	0.000	2.989	1	0.084
Mean time-after-sunrise	-0.107	-0.252	0.037	2.132	1	0.144
Year	-0.168	-0.520	0.184	0.873	1	0.350
Mean diameter rank	0.466	0.266	0.667	20.724	1	<0.001
Forest type ^a						
Mesic Douglas-fir	0.194	-0.652	1.040	0.202	1	0.653
Mixed-conifer	0.007	-0.866	0.880	0.000	1	0.987
Conifer/hardwood	0.120	-0.859	1.099	0.060	1	0.809
Ponderosa pine	0.664	-0.031	1.358	3.506	1	0.061
Alpine conifer	-0.339	-1.357	0.679	0.425	1	0.515
Deciduous hardwoods	-0.440	-1.506	0.627	0.653	1	0.419
Ecoregion ^b						
Blue Mountains	1.336	0.126	2.546	4.681	1	0.031
Coast Range	1.975	0.659	3.291	8.655	1	0.003
East Cascades	1.566	0.339	2.792	6.260	1	0.012
Klamath Mountains	2.007	0.680	3.334	8.789	1	0.003
Willamette Valley	1.796	0.128	3.464	4.454	1	0.035
Western Cascades	1.997	0.694	3.299	9.022	1	0.003
Reduced model (without ecoregion)						
Log no. of survey stations	1.865	0.169	3.560	4.648	1	0.031
Day of the year	-0.005	-0.009	0.000	4.413	1	0.036
Mean time-after-sunrise	-0.122	-0.268	0.023	2.710	1	0.099
Mean diameter rank	0.441	0.244	0.637	19.311	1	<0.001
Forest type ^a						
Mesic Douglas-fir	1.082	0.369	1.794	8.862	1	0.003
Mixed-conifer	0.549	-0.312	1.411	1.565	1	0.211
Conifer/hardwood	0.956	0.075	1.837	4.52	1	0.034
Ponderosa pine	1.069	0.382	1.756	9.289	1	0.002
Alpine forest	0.341	-0.647	1.328	0.261	1	0.610
Deciduous hardwoods	0.246	-0.698	1.191	0.465	1	0.499

^a Juniper forest was used as reference type.

^b High Desert was used as reference type.

call. At stations where detections occurred, the mean time from initiation of survey to initial detection was 5.9 ± 0.17 min ($N = 159$ transects). The percentages of owls that were first detected in each 1-min interval of the 10-min survey period were 9.6, 7.3, 10.6, 10.8, 12.0, 13.0, 8.7, 7.1, 7.9, and 13.0%, respectively. The estimated mean distance from the survey station to the location of initial owl response was 325 ± 18.1 m (range = 5–1450 m, $N = 159$ transects).

The regression model provided no evidence of a year effect on the number of owls detected per transect (Table 1). Models with and without eco-

region indicated that the number of owl detections increased with the number of survey stations; this effect, which was expected, was strongest in the model that did not include ecoregion (Table 1).

The full regression model indicated that the number of pygmy-owls detected per transect differed among ecoregions, but not among forest types (Table 1). Mean detections per transect were highest in the Western Cascades, intermediate in the Coast Ranges, Klamath Mountains, Eastern Cascades, and Blue Mountains, and lowest in the Willamette Valley and High Desert ecoregions (Fig. 3). More subtle ecoregion patterns were

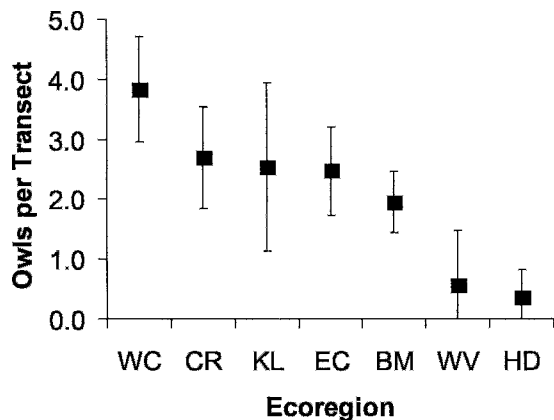


Figure 3. Mean number ($\pm 95\%$ CI) of Northern Pygmy-Owls detected per 15-station survey transect in different ecoregions in Oregon, 1996–97. Ecoregions were: Western Cascades (WC), Coast Ranges (CR), Klamath Mountains (KL), Eastern Cascades (EC), Blue Mountains (BM), Willamette Valley (WV), and High Desert (HD).

suggested by some of the data, but samples were too small to test them. For example, four transects in western juniper forests in the Blue Mountains had a high mean number of owls detected per survey station (0.20 ± 0.05) whereas the mean number of owls detected per survey station in 16 transects in western juniper forests in the High Desert Ecoregion was low (0.01 ± 0.03).

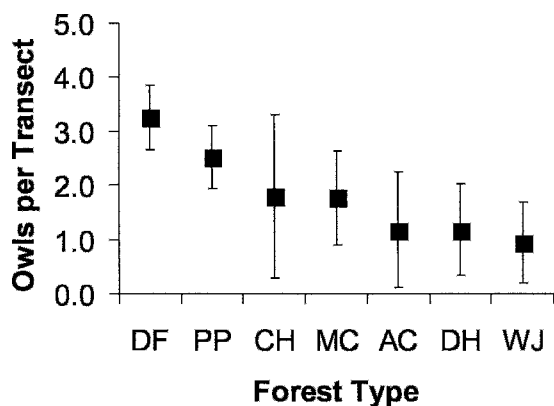


Figure 4. Mean number ($\pm 95\%$ CI) of Northern Pygmy-Owls detected per 15-station survey transect in different forest types in Oregon, 1996–97. Forest types were: mesic Douglas-fir (DF), ponderosa pine (PP), conifer/hardwoods (CH), mixed-conifer (MC), alpine conifers (AC), deciduous hardwoods (DH), and western juniper (WJ).

In contrast to the full model, the reduced regression model that did not include ecoregions, indicated that the number of owls detected per transect differed among forest types, with higher numbers of owls located in mesic Douglas-fir and ponderosa pine forests, intermediate numbers in conifer/hardwood and mixed-conifer forests and the lowest numbers in alpine conifers, deciduous hardwoods, and western juniper forests (Table 1; Fig. 4).

The number of owls detected per transect increased with the mean diameter rank of overstory trees at survey stations (Table 1). The number of detections was highly variable among transects within the same ecoregions and forest types, regardless of tree diameter rank scores. For example, on 14 transects with 15 stations in mesic Douglas-fir stands with mean diameter rank ≥ 3 in the Coast Ranges Ecoregion, the number of owls detected ranged from 0–12 ($\bar{x} = 3.0 \pm 0.2$). Unusually high numbers of detections also occurred on a few transects in other ecoregions and forest types. For example, 10 owls each were detected on a mesic Douglas-fir transect in the Western Cascades, a Douglas-fir transect in the Klamath Mountains, and a ponderosa pine transect in the Eastern Cascades (all three transects had 15 survey stations).

In the full and reduced regression models, there was only marginal evidence that the number of owls detected per transect was negatively correlated with mean time of survey (Table 1). However, the comparison of mean numbers of detections per station in different 1-hr time intervals indicated highly significant differences among intervals ($F_{7,1144} = 3.928$, $P < 0.001$), with the number of detections being highest during the 1-hr intervals immediately before and after sunrise and gradually declining with increasing time after sunrise (Fig. 5).

There was some evidence from both the full and reduced models that the number of owls located per transect declined with increasing day of the year (Table 1). Further investigation revealed that the average number of owls detected per transect did not differ among April, May, or June, but the July mean was 45% lower than the means for all earlier mo (95% CI = 24–61%; $F_{1,206} = 13.60$, $P < 0.001$; Fig. 6).

DISCUSSION

In our surveys, Northern Pygmy-Owls were fairly common in most forested regions of Oregon, with the exception of deciduous forests in the Willamette Valley Ecoregion and western juniper forests in the

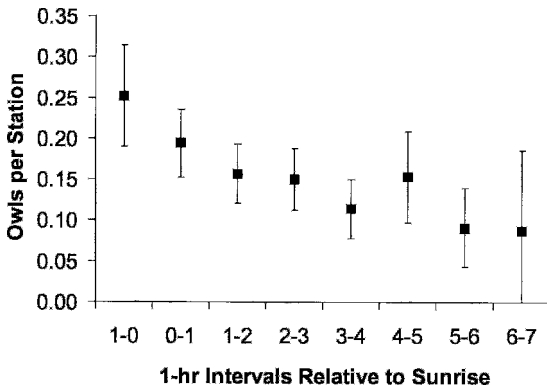


Figure 5. Mean number ($\pm 95\%$ CI) of Northern Pygmy-Owls detected per survey station during different 1-hr time intervals on acoustic lure survey transects in Oregon, 1996–97. First interval started 1 hr before sunrise and last interval ended 7 hr after sunrise.

High Desert Ecoregion. This suggests that pygmy-owls in Oregon are limited primarily to forests dominated by conifers or mixed associations of conifers and hardwoods, but are otherwise habitat generalists that occur in a broad range of plant associations, as suggested by Hayward and Garton (1988), Reynolds et al. (1988), and Holt and Petersen (2000). However, numbers of pygmy-owls detected varied substantially among and within general forest types and overstory tree size ranks, suggesting that factors other than forest type and size of overstory trees have an important influence on the abundance and distribution of Northern Pygmy-Owls. This variation could have been due to chance fluctuations in local abundance of pygmy-

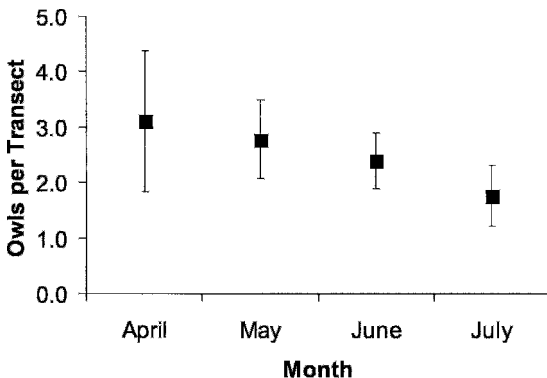


Figure 6. Mean number ($\pm 95\%$ CI) of Northern Pygmy-Owls detected per 15-station survey transect in different months in Oregon, 1996–97.

owls or to factors unrelated to our explanatory variables, such as local variation in prey abundance. Population densities of Eurasian Pygmy-Owls (*Glaucidium passerinum*) fluctuate substantially in some areas, depending on vole (*Clethrionomys* spp., *Microtus* spp.) population cycles (Cramp 1985).

Variation in numbers of pygmy-owls detected in the same forest type, but in different ecoregions, could have been due to any number of factors, including differences among regions with respect to climate, abundance or availability of prey, or structural characteristics of forests. It is also possible that variation in the number of owls detected within the same forest type in different regions could have been due to large-scale random or cyclic fluctuations in owl abundance or responsiveness that could not be detected in our brief study (Kellner et al. 1992).

In our analysis, the ecoregion variable probably acted as a surrogate for many vegetation or landscape attributes that we did not measure. For example, the low numbers of pygmy-owls detected in western juniper forests in the High Desert Ecoregion may have been due to the fact that dense juniper forests in that region tended to occur on small mountain ranges isolated by large expanses of shrub-steppe vegetation. In comparison, western juniper forests in the Blue Mountains Ecoregion often intergraded with extensive areas of mixed-conifer or ponderosa pine forest and appeared to have moderately high numbers of pygmy-owls.

One potential bias in our study that needs to be considered in assessing the results relates to our visual assignment of diameter rankings of dominant trees to evaluate habitat associations of owls. This visual interpretation could have reduced the precision of our estimates (Ralph 1981) or produced estimates that were not an unbiased measure of average conditions in the areas surveyed. In an acoustic lure survey, analyses of habitat associations can be confounded if owls move toward the observer before responding or before they are detected (Giese 1999, Proudfoot and Beasom 1996). However, if there are strong patterns of habitat association, those patterns should become obvious with large sample size, regardless of variation caused by owl movements. Thus, we think the positive association between pygmy-owls and large trees in our study is real, and is not unexpected, considering that radiotelemetry studies have found that Northern Pygmy-Owls select older forest for foraging and that they often nest in cavities in large trees (Giese and Forsman 2003).

Documented use of young forest and recent clearcuts by pygmy-owls (Giese and Forsman 2003), in combination with our detections of pygmy-owls in many stands of fairly small trees (diameter ranks <4) suggest that this species may be fairly tolerant of management practices that produce mixtures of old and young forest interspersed with openings. However, Giese and Forsman (2003) also found that nests were predominantly located in old forest and that old forests were disproportionately used for foraging. Therefore, there may be a limit below which replacement of older forests with younger forests would cause pygmy-owl populations to decline. Experimental tests of this hypothesis will be difficult to carry out, but additional studies of habitat associations and diet may shed some light on these relationships.

The limited information that is available on Northern Pygmy-Owl activity periods indicates that they are largely a crepuscular/diurnal species with a peak period of activity just before and after sunrise (Holman 1926, Voous 1988, Noble 1990, Holt and Petersen 2000, A. Giese pers. comm. 2000). Our results support this hypothesis, at least in terms of the responsiveness of pygmy-owls to an acoustic lure. Seasonal changes in numbers of pygmy-owls detected on our transects were probably due to changes in behavior associated with annual breeding chronology. Pygmy-owls in Oregon establish territories in March and April, when spontaneous calling appears to reach a peak (Bent 1938). After females begin to incubate in April or May (Holt and Norton 1986), breeding males apparently are less likely to call, and may become even more quiet when the young hatch about a month later. By July, when the most dramatic decrease in numbers of detections per transect occurred, pygmy-owls in Oregon were either caring for fledged young or had finished breeding (Holt and Petersen 2000). Although we did not conduct surveys after July, Bent (1938) reported that pygmy-owls were quite vocal during autumn, in conjunction with dispersal after the breeding season. We have observed similar behavior in Oregon.

With careful controls and training of field crews, we believe the survey protocol used in our study could be repeated at regular intervals to evaluate trends in pygmy-owl populations. If acoustic lure surveys are used to estimate trends in pygmy-owl populations, we suggest limiting the survey season to 1 April–30 June, starting surveys 1 hr before sunrise, completing them ≤ 5 hr after sunrise, and

standardizing decibel levels of broadcast calls. We also recommend that additional work be conducted to evaluate variation in detectability of pygmy-owls in different types of landscapes, as counts of pygmy-owls in acoustic lure surveys may not provide comparable indices of local population density if detectability varies depending on such things as topography, vegetation density, and stream noise (Dawson 1981, Schieck 1997). Because of time and money constraints we used ocular estimates of tree size adjacent to calling stations to evaluate habitat associations, which limited the utility of our habitat data for making inferences about habitat associations of pygmy-owls. If we were to repeat the study and had more funding, we would probably utilize GIS habitat maps to evaluate the number of owls located per transect as a function of the mean proportions of different tree age classes or diameter classes within a fixed-radius circle around each calling station.

Although our study provides some insights regarding habitat associations and distribution of the Northern Pygmy-Owl, factors that directly influence pygmy-owl numbers are poorly understood. Additional work on habitat selection, prey abundance, seasonal movements, dispersal, genetics, and population trends is needed to make better predictions regarding the effects of forest management practices on Northern Pygmy-Owls.

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