

AN ABSTRACT OF THE THESIS OF

Dawn M. Sater for the degree of Master of Science in Wildlife Science presented on May 21, 1999. Title: Distribution and Habitat Associations of the Northern Pygmy-owl in Oregon.

Abstract approved: _____

Eric D. Forsman

I conducted acoustic lure surveys of northern pygmy-owls (*Glaucidium gnoma*) on transects that were systematically placed in forested areas throughout the state of Oregon. My objectives were to determine if pygmy-owls were associated with particular forest types, ecoregions, or with large-diameter dominant overstory trees. I also examined temporal variation in response rates. All analyses accounted for decreases in counts of owls with increasing day of the survey season ($P = 0.01$) and with increasing time after sunrise ($P = 0.06$). Counts were highest in Douglas-fir, ponderosa pine and mixed conifer-hardwood forests, intermediate in mixed conifer, deciduous and high elevation forests, and lowest in western juniper ($P = 0.0003$). Even after accounting for forest type, numbers of owls detected varied among ecoregions ($P = 0.002$). Counts of owls increased with the average diameter ranking of dominant overstory trees ($P = 0.0001$). Also, diameters of dominant trees were greater at survey points where owls were detected than at survey points where no owls were detected ($P = 0.008$), and greater in the actual stands from which owls responded than around the survey points from which owls were

detected ($P = 0.0001$). My data suggest that widespread decreases in large-diameter trees, or the late-successional forests in which such trees are most abundant, may reduce numbers of northern pygmy-owls. However, this finding needs to be viewed in the context that my surveys also show that the pygmy-owl is a well-distributed and fairly common forest bird in Oregon and is not limited to late-successional forest.

Distribution and Habitat Associations of the Northern Pygmy-owl in Oregon

by

Dawn M. Sater

A THESIS

submitted to

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in partial fulfillment of
the requirements for the
degree of

Master of Science

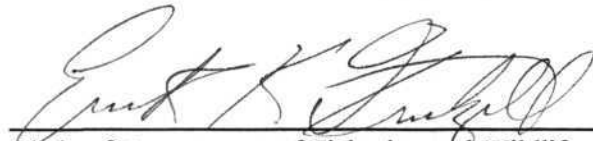
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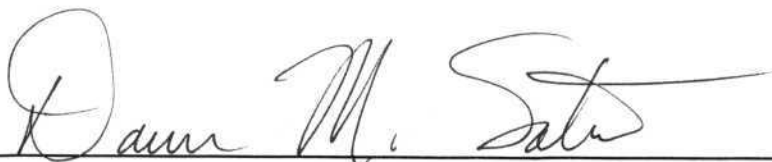


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DISTRIBUTION AND HABITAT ASSOCIATIONS OF THE NORTHERN PYGMY-OWL IN OREGON

INTRODUCTION

Management of late-successional forests on federal lands in the Pacific Northwest has been the subject of heated debate since the early 1970's (Thomas et al. 1993b). In this debate, lists of species thought to be associated with late-successional forests (Thomas et al. 1993a) are often used to imply that harvest of such forests will threaten the persistence of those species. In reality, however, there are few quantitative data on the distribution or habitat use of many species thought to be associated with old forests in the Pacific Northwest. The northern pygmy-owl is a typical example. Some experts believe this species may be associated with mature or old-growth forests (Hume and Boyer 1991, Thomas et al. 1993a), but there have never been any quantitative studies to evaluate its abundance in relation to forest type or structure. The presumed association between pygmy-owls and older forests is largely based on the observation that they 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), and that large trees and snags are generally most abundant in older forests (Carey et al. 1991, U.S. Forest Service and U.S. Bureau of Land Management 1994: 3&4-177).

Although there are no data on population trends of northern pygmy-owls, the closely related Eurasian pygmy-owl (*G. passerinum*) has disappeared or declined in many parts of its range in Europe and the former USSR (Cramp 1985). This decline is thought

to be due to habitat loss and intensive forest management that in many areas has resulted in even-aged forests with simple structure (König 1981, Cramp 1985, Marcot 1995: 23). Declines in numbers and habitat also led to the recent listing of the cactus ferruginous pygmy-owl (*G. brasilianum cactorum*) as an endangered species in Arizona (U.S. Fish and Wildlife Service 1997). Some have suggested that long-term declines in density may also be occurring in the northern pygmy-owl (Marcot 1995: 22).

Because of its presumed association with older forests and the paucity of information on its population status and habitat use, the northern pygmy-owl was listed as a sensitive species by the Oregon Department of Fish and Wildlife (Marshall 1992). However, the pygmy-owl is a food generalist (Bent 1938, Holt and Leroux 1996), 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). All opinions about the conservation status of this species have been based primarily on expert judgement, anecdotal observations, or studies with small samples.

The purpose of this study was to provide quantitative data on northern pygmy-owl habitat associations in Oregon, in order to help land managers anticipate effects of management practices on northern pygmy-owls. I wanted to determine if pygmy-owls were associated with particular forest types, ecoregions (Omernik 1987), or with large-diameter overstory trees. To accomplish this, I conducted acoustic lure surveys for northern pygmy-owls along point transects and recorded unlimited distance counts of owls at each survey point (Ralph 1981). I compared numbers of owls detected among

forest types and ecoregions, and examined the relationship between owl responses and diameters of dominant overstory trees. Another objective was to design a repeatable survey protocol for northern pygmy-owls that could be used to estimate population trends.

My predictions were that numbers of northern pygmy-owls detected per transect would differ among forest types and ecoregions and increase with the diameter of dominant overstory trees. I also tested the hypothesis that pygmy-owl response locations would be associated with large-diameter trees at the local scale. Specifically, at the local scale I tested whether the average diameter ranking of dominant overstory trees would: (1) be higher around survey points from which owls were detected than around survey points from which no owls were detected; and (2) be higher in the forest stands from which owls responded (often some distance from survey points) than around the survey points from which the owls were detected. To account for variation in numbers of northern pygmy-owls detected due to my methodology, I also examined relationships between the numbers of owls detected per transect and the time of day and date of the survey.

METHODS

STUDY AREA

The study area included all forested areas in Oregon. Topography varied from relatively flat river valleys and lava plains to steep mountainous terrain. Elevation of study sites ranged from 10 - 2,200 m. Annual precipitation averages 600 - 3,000 mm in western Oregon and 200 - 1,000 mm in eastern Oregon (U.S. Weather Bureau 1965). Precipitation occurs primarily in winter and increases with elevation, as does average winter snow depth. Summers are warm and dry.

Forests in the study area are largely dominated by conifers and include a broad array of age-classes and structural types, ranging from seedlings on recently planted clear-cuts to multi-layered old-growth forests dominated by trees over 750 years old (Franklin and Dyrness 1973, Franklin and Spies 1986). Broadleaf deciduous trees are limited primarily to riparian zones. Vegetation is typically distributed in a complex mosaic of openings and young forests interspersed with stands of old forest. This mosaic is the result of a long history of wildfires, windstorms, cutting, grazing, and development. Young stands are typically characterized by closed canopies and relatively uniform tree size, whereas mature and old-growth forests are typically characterized by high variation in tree size and numerous gaps in the canopy (Franklin and Spies 1984, 1986). Dominant trees in old forests in western Oregon are typically 50-200 cm dbh and 40-80 m tall.

Trees in eastern Oregon tend to be slightly smaller because of lower precipitation and poorer growing conditions.

Study sites fell within eight ecoregions that have characteristic forest vegetation associations (Franklin and Dyrness 1973; Fig. 1). Forests in the Coast Range and Western Cascades Ecoregions are primarily dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Forests in the Klamath Mountains Ecoregion are dominated by mixtures of Douglas-fir and evergreen hardwoods including tanoak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepsis*) and Pacific madrone (*Arbutus menziesii*), or by mixed conifer associations of Douglas-fir, sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), incense-cedar (*Libocedrus decurrens*) and true firs (*Abies* spp.). The Willamette Valley Ecoregion is a wide, flat basin between the Coast Range and Western Cascades. Forests bordering the valley are typically dominated by mixtures of Douglas-fir, grand fir (*Abies grandis*) and oak woodland (*Quercus* spp). Forested areas within the valley are primarily limited to scattered oak woodland (*Quercus* spp) and riparian corridors dominated by black cottonwood (*Populus trichocarpa*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), willow (*Salix* spp.), or Oregon ash (*Fraxinus latifolia*). The High Cascades Ecoregion, which straddles the crest of the Cascade Range, is dominated by forests of mountain hemlock (*Tsuga mertensiana*), lodgepole pine (*Pinus contorta*) or true firs (*Abies* spp.). The Eastern Cascades and Blue Mountain Ecoregions are characterized by forests of ponderosa pine at mid-elevations, western juniper woodlands at lower elevations, and mixed forests of Douglas-fir, grand fir, ponderosa pine and

subalpine fir (*Abies lasiocarpa*) at higher elevations. The High Desert Ecoregion of southeast Oregon is dominated by shrub-steppe vegetation, but also includes extensive areas of western juniper (*Juniperus occidentalis*) woodland. Western juniper typically occurs in a savanna setting, but in a few areas it also forms closed-canopy forests.

SAMPLING

The study area was divided into 434 hexagonal polygons (White et al. 1992; Fig. 1). Of the 434 polygons, 275 included forest areas that were extensive enough to accommodate survey transects. The initial objective was to conduct a survey transect in each of the 275 forested polygons, but logistics problems and time constraints limited surveys to 224 polygons.

Each transect consisted of 15 survey points along a road, spaced at straight-line intervals of 0.8 km. The initial survey point for each transect was placed on a road as close as possible to a randomly selected Universal Transverse Mercator coordinate in each of the selected polygons. If the random starting point fell in non-forest, the starting point was moved to the nearest forest. 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 location when laying out transects.

In 28 areas where forests were not extensive enough to support 15 survey points, I conducted partial transects that had 5-14 points. In some cases, survey transects were

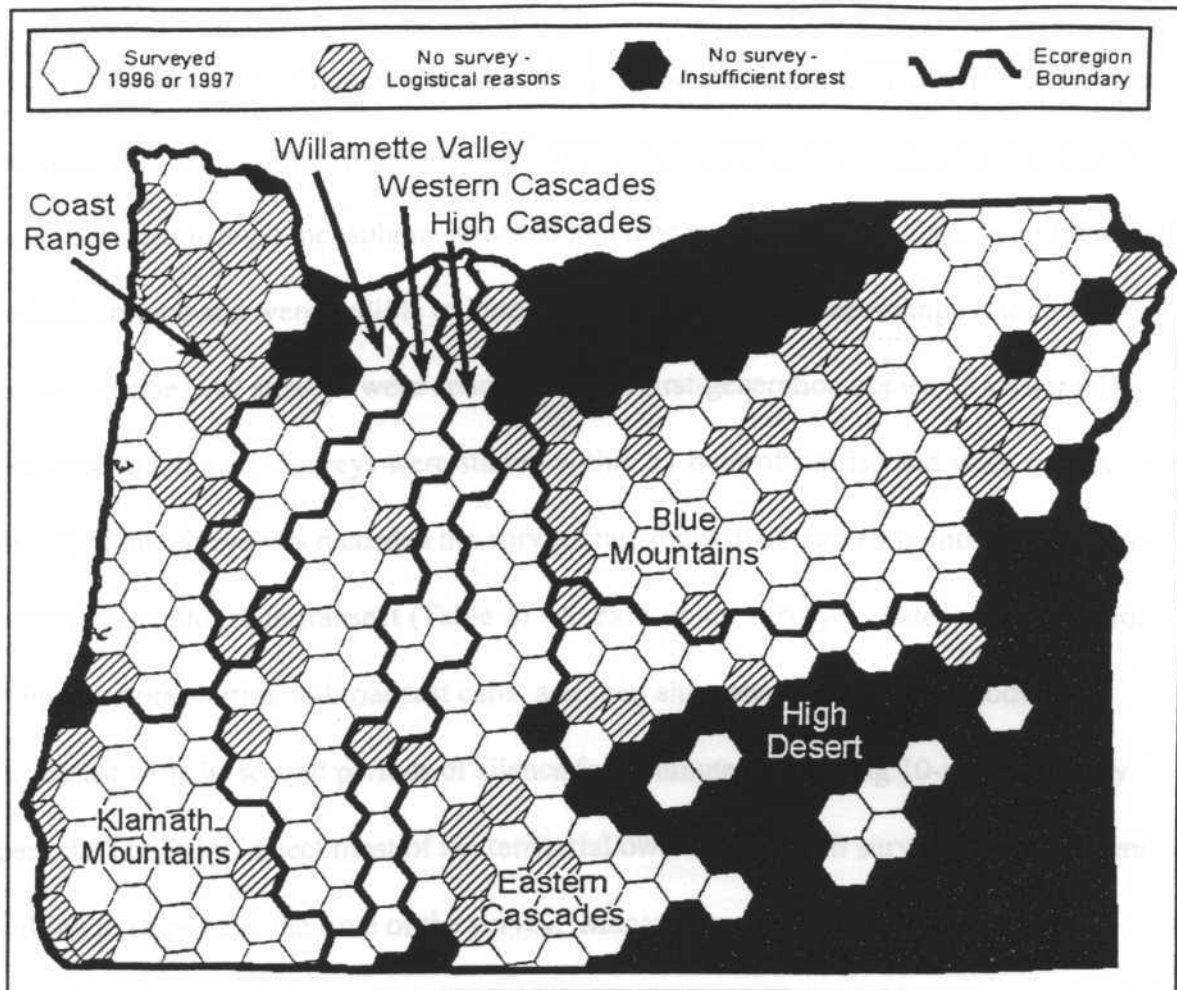


Fig. 1. Map of Oregon showing sampling hexagons (White et al. 1992) and ecoregions (Omernik 1987, U.S. Environmental Protection Agency 1996) that were used to stratify northern pygmy-owl acoustic lure survey transects. Surveys were conducted in 1996-97. Names refer to ecoregions.

broken into 2 or 3 sections that were separated by small areas of non-forest or by sections of road that were not accessible. As long as access was possible, transects were laid out regardless of land ownership. Transects could continue into adjacent sampling polygons once started, as long as they did not overlap other transects.

ACOUSTIC LURE SURVEYS

Surveys were conducted between 6 April and 31 July in 1996 and 1997. At each survey point, the northern pygmy-owl territorial call (a repeated, single-whistle "toot") was broadcast using a megaphone attached to a tape cassette player. Calls were broadcast at high volume and were audible to humans 0.3-0.5 km away, depending on terrain and ambient noise. All surveys were conducted with first-generation copies of master tapes recorded in Oregon. Surveys were started within ± 1 hour of sunrise and were completed before noon. Surveyors recorded the survey start-times at all survey points, which were then averaged for each transect (Table 1). At each point, surveyors listened for owls for 1 minute before starting to broadcast calls, and then alternated 30-second periods of broadcast with 30-second periods of silence for 9 minutes. By using 10-minute survey periods, I hoped to detect most of the territorial owls around each survey point that were willing to respond at the time of the survey. Megaphones were aimed in different directions for each broadcast period to maximize survey coverage. Surveys were generally not conducted during windy and rainy conditions, but up to 3 survey points per transect could be called in marginal weather conditions (moderate wind or light rain).

When an owl responded at any time during a 10-minute survey period, the surveyor recorded the time, and plotted the owl's location on a 7.5" USGS topographic map. Visual contact was not required, and auditory detections were often plotted by triangulation, or by obtaining a compass bearings and estimating distances between survey points and owls. Many owls were detected multiple times and/or from

Table 1 . Variables and variable definitions used in multiple regression and paired *t*-tests to investigate northern pygmy-owl habitat associations and effects of survey methodology on numbers of owls detected on northern pygmy-owl acoustic lure survey transects conducted in Oregon, 1996-97.

Use of variable	Variable definition
Regression	<p>Response variable</p> <p>Number of owls detected on a transect</p> <p>Explanatory variables</p> <ol style="list-style-type: none"> 1. Log of the number of survey points 2. Day of the survey season (1 April = 1) 3. Average time after sunrise for all points on transect (hours) 4. Average diameter ranking of dominant overstory trees <ol style="list-style-type: none"> 1 = <12 cm dbh 2 = ≥ 12 cm and <30 cm dbh 3 = ≥ 30 cm and <50 cm dbh 4 = ≥ 50 cm and <100 cm dbh 5 = ≥ 100 cm dbh 5. Forest type <ul style="list-style-type: none"> Deciduous: Dominated by deciduous trees, occasionally with minor coniferous component Douglas-fir: Usually dominated by Douglas-fir, but western hemlock generally also present, and sometimes dominant High elevation: Dominated by mountain hemlock, lodgepole pine, or true-firs Mixed conifer: Mixed associations of conifers, including Douglas-fir, sugar pine, ponderosa pine, incense-cedar and true-firs Mixed conifer-hardwood: Mixed associations of conifers, with a substantial evergreen hardwood component Ponderosa pine: Predominantly ponderosa pine Western juniper: Usually pure western juniper, but some ponderosa pine occasionally present 6. Ecoregion: After Omernik (1987)
Paired <i>t</i> -tests	<p>Mean number of owls detected per survey point</p> <p>Average diameter ranking of dominant overstory trees around:</p> <ol style="list-style-type: none"> 1. Survey points from which owls were detected 2. Survey points from which no owls were detected 3. Locations from which owls initially responded

more than one survey point, but individuals were counted only once. Surveyors used a variety of clues to estimate the number of owls responding, including spacing, timing and direction of responses. A detection was assumed to be a repeat response if it came from

the direction of a previously located owl, especially if it was heard within the first 1-2 minutes at the next survey point. In ambiguous situations, responses were usually interpreted as repeat detections.

Surveys were completed by 95 different surveyors, who were recruited by telephone. Of the 224 transects surveyed, 65% were surveyed by wildlife biologists, 27% were surveyed by wildlife technicians supervised by wildlife biologists, and 8% were surveyed by volunteers, most of whom were recommended as experienced bird surveyors by local biologists. All surveyors were provided with detailed written instructions, field forms, survey tapes and a contact phone number for inquiries regarding survey protocols.

VEGETATION CLASSIFICATION

Surveyors recorded the species and diameter ranking of dominant overstory trees adjacent to each transect point (Table 1). For each transect, a single forest type was assigned based on the forest type at the highest proportion of survey points (Table 1). Diameter-size rankings at survey points were averaged for each transect (Table 1). I believe averages from survey points were reasonably representative of transect areas, given my coarse vegetation classifications. For each transect with pygmy-owl detections ($n = 161$), an average diameter-size ranking was also calculated separately for forest around survey points from which owls were detected and forest around survey points from which no owls were detected. For a non-random subset of transects with owl detections ($n = 121$), surveyors made an extra effort to obtain diameter-size rankings for

all forest stands from which owls initially responded. These stands often located some distance from survey points, and were located by triangulation or by homing in on owls that were calling. The rankings for owl locations were then averaged for each transect.

Each transect was assigned to the ecoregion into which a majority of its survey points fell. This was determined by comparing digitized survey points with a digital Oregon ecoregion map (Omernik 1987, U.S. Environmental Protection Agency 1996) in a Geographic Information System (ARC/INFO, ESRI, Redlands, California, USA).

STATISTICAL ANALYSES

The analysis was divided into two parts. First, the number of owls detected on a transect was used as a response variable in several regression models that included predetermined sets of explanatory variables (Table 1). I chose explanatory variables based on availability and a knowledge of pygmy-owl ecology, and hoped to explain enough variation in owl counts to reveal patterns relating to my questions of interest. Second, paired *t*-tests were used to make within-transect comparisons. For each transect with owl detections, average diameter-size rankings at certain locations on the transect were compared to average rankings at other locations within the same transect area (Table 1). For all 224 transects, a mean number of owls detected per survey point was calculated for each 1-hour time interval of the surveys relative to sunrise. For example, each transect that was started at sunrise had a mean number of owls detected per survey point for all of the points surveyed between sunrise and 1 hour after sunrise. Time interval

means were compared within transects using paired *t*-tests.

The number of owls detected on a transect was a count, so I used Poisson log-linear regression to examine relationships between the number of owls detected and the explanatory variables (Table 1). The distribution of the number of owls detected per transect appeared more or less Poisson (Figure 2), but there were no identical configurations of explanatory variables to allow a test of the Poisson assumption (Ramsey and Schafer 1997: 646). Quasi-likelihood analysis was used to account for any extra-Poisson variation (Ramsey and Schafer 1997: 612). This was necessitated by the fact that the deviance divided by the degrees of freedom for the full model was 1.6, suggesting overdispersion. Significance levels of coefficients were determined with drop-in-deviance *F*-tests, and confidence intervals for parameters were based on likelihood ratios.

I accounted for variation in effort per transect by including the log of the number of survey points as a regression variable (Ramsey and Schafer 1997: 650). Making the log of the number of survey points an offset did not change results. Using the full model, I tested predictions that the number of owls detected per transect: (1) differed by ecoregion; (2) increased with average diameter-size ranking; (3) decreased with increasing day of the survey season; and (4) decreased with increasing average time-after-sunrise. I tested ecoregion predictions in a model that included forest type, despite the fact that ecoregions are largely defined by vegetation types, because I wanted to determine whether there were any ecoregion patterns not accounted for by forest type. A reduced model without ecoregion was used to test the prediction that number of owls detected per transect differed by forest type, because I was interested in effects of forest type without the

confounding effects of ecoregion. To test whether the number of owls detected per transect increased with average diameter-size ranking within forest types and ecoregions with $n \geq 30$, I evaluated separate regression models for each of these categories using all explanatory variables except forest type and ecoregion. In case pygmy-owls were more likely to respond to calls from neighboring owls than to tape broadcast, which would positively bias counts in areas of high owl density, I repeated the full regression analyses after omitting from the sample any owls that were detected less than 3 survey points from a previously detected owl, including where multiple owls were heard from the same survey point.

Data from surveys in 1996 ($n = 58$) and 1997 ($n = 166$) were pooled for analysis. The possible influence of pooling across years was investigated by including year as an explanatory variable in the full regression model.

I judged my regression models to be adequate for this data set. There did not appear to be any substantial patterns in the data that would make Poisson log-linear regression an inappropriate method. The basic explanatory variables squared and all possible interactions were added to the models, one at a time, but none were significant. Explanatory variables were examined for multicollinearity by performing simple correlations on all pairs of continuous variables, and one-way analysis of variance on continuous variables grouped by categorical variables. There was only a slight correlation between average time after sunrise and average diameter ranking ($r = 0.15$, $P = 0.02$), so all continuous variables were included in the regression analysis. As expected, average tree size differed by forest type and by ecoregion, but all three variables

were included because all were significant in the regression model. Survey variables survey date, average time after sunrise, and the log of the number of survey points also differed somewhat by forest type and ecoregion because the timing and logistics of surveys in different ecoregions and forest types varied somewhat. However, exclusion of any single survey variable did not change results with respect to ecoregion or forest type. Exclusion of forest type, ecoregion, or both actually decreased the significance of average time after sunrise, so again all variables were included. Several outliers slightly changed results when any one of them was excluded from the analysis, but they were included in inferential models because they were legitimate data points with unusual variable values and were not judged to point to model inadequacy.

To compare the mean number of owls detected per transect among categories, indicator variables with values of one or zero were created for each month, forest type and ecoregion. Sets of indicator variables then replaced categorical variables in regression models, with one indicator variable in each set excluded as a reference level. Ninety-five percent confidence intervals around category means were computed relative to the reference level within the context of the regression model, allowing me to account for all other explanatory variables when making comparisons among categories.

For transects with owl detections, I used paired *t*-tests to determine whether the average diameter ranking of trees differed between (1) survey points from which owls were or were not detected and (2) between survey points from which owls were detected and locations from which owls initially responded. The latter analysis was done because the locations where owls initially responded were often some distance away from the

survey points from which the owls were detected. To determine whether the size of these differences varied by any of the survey or habitat variables, differences obtained for each transect were used as response variables in multiple linear regression models that included all explanatory variables (the number of survey points per transect was not log transformed). To examine the effect of time of day on detection rates within transects, I used paired *t*-tests to compare the mean number of owls detected per survey point among 7 1-hour time intervals, defined from 1-hour before sunrise to 6 hours after sunrise. Comparisons between detection rates obtained in different time intervals were made only within the context of the same survey. All means are presented in the format $x \pm SD$.

RESULTS

OWL DETECTIONS

Northern pygmy-owls were detected on 161 (72%) of 224 survey transects. A total of 495 owls were detected. The average number of owls detected per transect was 2.2 ± 2.3 (range = 0 - 12; Fig. 2). As expected, the number of owls detected per transect increased with the number of survey points on each transect ($F_{1,206} = 6.13$, $P = 0.01$; Table 2).

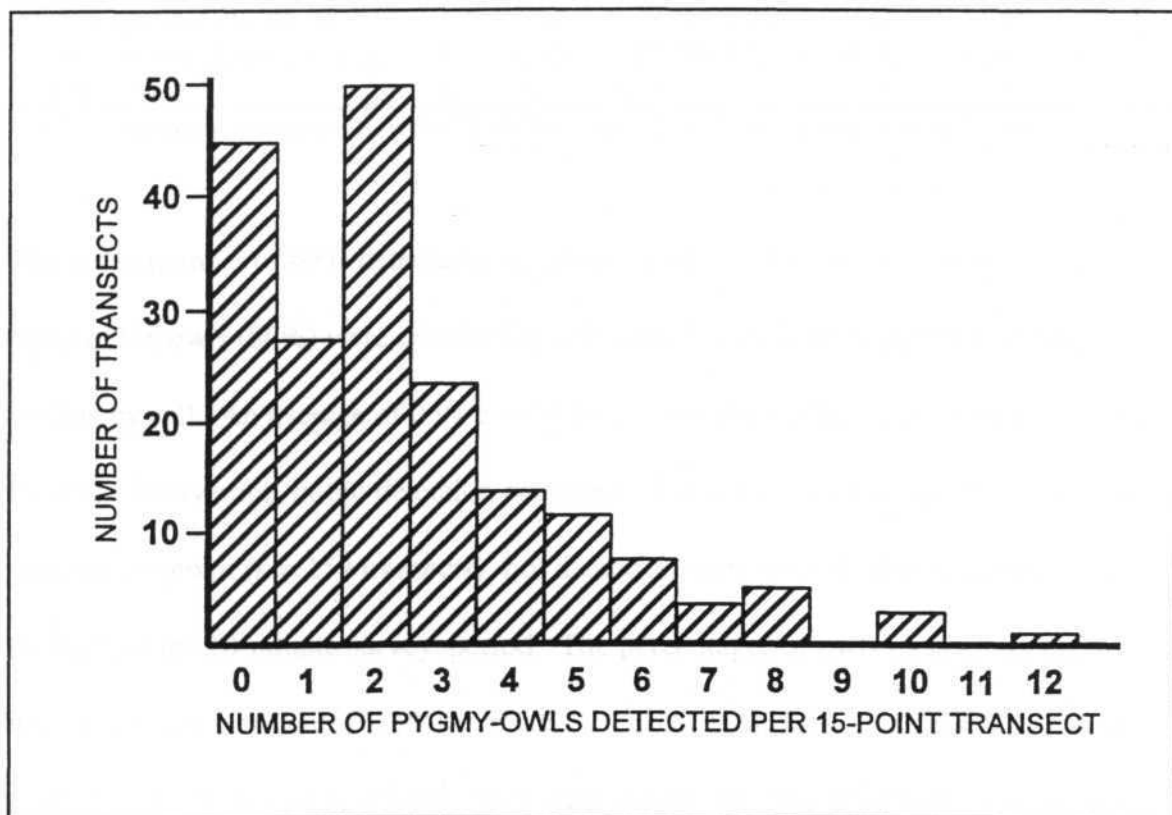


Fig. 2. Distribution of the number of northern pygmy-owls detected per 15-point survey transect in Oregon, 1996-97 ($n = 196$ surveys).

Table 2. Parameter estimates and associated values resulting from Poisson log-linear regression analysis of the numbers of northern pygmy-owls detected per acoustic lure survey transect conducted in Oregon, 1996-97 ($n = 224$). Confidence intervals were based on likelihood ratios.

Variable	df	Parameter estimate ^a	95% CI	F	df	P
Full model (including ecoregion)						
Log number of survey points	1	1.73	0.33 to 3.55	6.13	1,206	0.01
Julian survey date	1	-0.006	-0.01 to -0.001	6.49	1,206	0.01
Average time-after-sunrise	1	-0.14	-0.28 to 0.004	3.62	1,206	0.06
Average tree diameter ranking	1	0.41	0.22 to 0.61	17.78	1,206	0.0001
Forest type	6			2.20	6,206	0.04
Ecoregion	7			3.34	7,206	0.002
Reduced model (w/o ecoregion):						
Log number of survey points	1	1.93	0.42 to 3.92	6.78	1,213	0.01
Day of survey season	1	-0.006	-0.01 to -0.001	6.66	1,213	0.01
Average time-after-sunrise	1	-0.11	-0.26 to 0.03	2.41	1,213	0.12
Average tree diameter ranking	1	0.43	0.23 to 0.63	18.38	1,213	0.0001
Forest type	6			4.45	6,213	0.0003

^a N = 224, including 196 transects with 15 survey points and 28 transects with 5-14 survey points.

The mean number of owls detected per survey point was 0.15 ± 0.16 (range = 0 - 0.80). Most of the owls (86%) were detected by call only, but 14% were detected visually as well as by call. An average of 0.91 ± 0.94 owls were detected per hour of survey (range = 0 - 4.8). On average, initial detection occurred 5.9 ± 2.1 minutes after surveying began at each survey point ($n = 159$ transects), but detection rates were relatively constant throughout the 10-minute survey period. The percentages of owls by first minute detected (listed by minutes 1-10) were 9.6, 7.3, 10.6, 10.8, 12.0, 13.0, 8.7, 7.1, 7.9, and 13.0. The estimated mean distance from survey point to location of initial owl response was 325 ± 228 m (range = 5-1,450, $n = 159$ transects). The skewness of the distribution of detection distances reflects the fact that in certain circumstances pygmy-owls could

easily be heard from over a kilometer away, but owls were generally detected much closer to survey points than this.

HABITAT VARIABLES

The number of owls detected per transect varied among forest types ($F_{6,213} = 4.45$, $P = 0.0003$; Table 2), even after accounting for differences in average diameter rankings of overstory trees. Mean detections per transect were highest in Douglas-fir, ponderosa pine and mixed conifer-hardwood forests, intermediate in mixed conifer, deciduous and high elevation forests, and lowest in western juniper forests (Table 3).

Detections per transect varied among ecoregions ($F_{7,206} = 3.34$, $P = 0.002$; Table 2) in ways not explained by regional variation in forest types or diameter ranking of dominant trees. Mean detections per transect were highest in mountainous ecoregions in western Oregon, namely the Western Cascades, Coast Range, Klamath Mountains and High Cascades. Detections per transect were intermediate in the Eastern Cascades, Blue Mountains and Willamette Valley Ecoregions, and lowest in the High Desert Ecoregion (Table 4). More subtle ecoregion patterns are suggested by comparisons among owl counts categorized by forest type and ecoregion, after standardizing counts for variable transect lengths by dividing by the number of survey points per transect (Table 5). However, sample sizes were too small to allow analysis of these patterns. For example, 4 transects in western juniper forest in the Blue Mountains had a high mean number of owls detected per survey point (0.20 ± 0.05) whereas the mean number of owls detected per

Table 3. Mean number of northern pygmy-owls detected per 15-point acoustic lure survey transect by forest type in Oregon, 1996-97 ($n = 196$). Confidence intervals were based on likelihood ratios within the context of a Poisson log-linear regression model that accounted for differences between forest types with respect to transect lengths, survey dates, survey times of day, and diameter rankings of dominant trees in transect areas.

Forest Type	n	Mean owls detected per 15-point transect	95% confidence interval (***)					
			Douglas-fir	Ponderosa pine	Mixed conifer-hardwood	Mixed conifer	High elevation	Deciduous
Douglas-fir	74	3.3 ± 2.6	*****					
Ponderosa pine	61	2.5 ± 2.3	*****					
Mixed conifer-hardwood	10	1.8 ± 2.1	*****					
Mixed conifer	13	1.8 ± 1.4	*****					
High elevation	11	1.2 ± 1.6	*****					
Deciduous	11	1.2 ± 1.3	*****					
Western juniper	16	0.9 ± 1.3	*****					

survey point in western juniper stands in the High Desert ecoregion was low (0.01 ± 0.03 , $n = 16$). Within ecoregions, forest type still explained variation in numbers of owls detected per transect ($F_{6,206} = 2.20$, $P = 0.04$, from the full regression model including ecoregion; Table 2).

The number of owls detected per transect increased with the average diameter ranking of the dominant overstory trees around survey points (Fig. 3), even after accounting for forest type and ecoregion ($F_{1,206} = 17.78$, $P = 0.0001$; Table 2). This result was similar when I omitted all owls detected less than 3 survey points from a previously detected owl (Table 6). An increase in number of owls detected with increasing tree diameter was evident in most of the independent regression analyses that were done for forest types

Table 4. Mean number of northern pygmy-owls detected per 15-point acoustic lure survey transect by ecoregion in Oregon, 1996-97 ($n = 196$). Confidence intervals were based on likelihood ratios within the context of a Poisson log-linear regression model that accounted for differences between ecoregions with respect to forest types, transect lengths, survey dates, survey times of day, and diameter rankings of dominant trees in transect areas.

Ecoregion	n	Mean owls detected per 15-point transect	95% confidence interval (***)							
			Western Cascades	Coast Range	Klamath Mtns	High Cascades	Eastern Cascades	Blue Mtns	Willamette Valley	High Desert
Western Cascades	35	3.8 ± 2.5	*****							*****
Coast Range	33	2.7 ± 2.4	*****							*****
Klamath Mtns	15	2.5 ± 2.5	*****							
High Cascades	6	1.8 ± 2.2	*****							
Eastern Cascades	36	2.5 ± 2.4	*****							
Blue Mtns	53	2.0 ± 1.8			*****					
Willamette Valley	7	0.6 ± 1.0	*****							
High Desert	11	0.4 ± 0.7								*****

and ecoregions with ≥ 30 transects, including Douglas-fir forests ($F_{1,73} = 5.19$, $P = 0.03$), ponderosa pine forests ($F_{1,64} = 6.84$, $P = 0.01$), and the Eastern Cascades ($F_{1,32} = 9.11$, $P = 0.005$) and Western Cascades ($F_{1,32} = 5.67$, $P = 0.02$) Ecoregions. Exceptions were the Coast Range ($F_{1,29} = 0.42$, $P = 0.52$) and Blue Mountains ($F_{1,61} = 3.03$, $P = 0.09$) Ecoregions.

Within transects the average tree diameter rankings around survey points from which owls were detected (3.00 ± 0.86) were greater than around points from which no owls were detected (2.82 ± 0.66 ; $t_{159} = 2.68$, $P = 0.008$). The magnitude of this difference

Table 5. Numbers of northern pygmy-owls detected per survey point and average diameter rankings of dominant trees for 224 acoustic lure survey transects by forest type and ecoregion. Surveys were conducted in Oregon, 1996-97. Sample includes transects that had 5-15 survey points.

Ecoregion	Forest type															
	Douglas-fir		Ponderosa pine		Western juniper		Higher elevation		Mixed conifer		Conifer-hardwood		Deciduous		All forest types	
	x	SD	x	SD	x	SD	x	SD	x	SD	x	SD	x	SD	x	SD
Blue mountains	(n = 5)		(n = 38)		(n = 4)		(n = 4)		(n = 7)		(n = 3)		(n = 5)		(n = 66)	
Owls per survey point	0.06	0.06	0.15	0.14	0.20	0.05	0.02	0.03	0.10	0.08	0.13	0.07	0.05	0.12	0.12	0.12
Ave. diameter ranking	2.71	0.80	2.83	0.58	2.29	1.02	2.79	0.53	3.49	0.49	2.60	0.23	2.03	0.40	2.79	0.66
Coast Range	(n = 27)								(n = 2)		(n = 3)		(n = 2)		(n = 34)	
Owls per survey point	0.19	0.16							0.03	0.05	0.21	0.24	0.10	0.05	0.18	0.16
Ave. diameter ranking	2.90	0.65							2.00	0.95	2.37	0.47	1.44	0.90	2.72	0.76
Eastern Cascades	(n = 1)		(n = 26)		(n = 3)		(n = 3)		(n = 3)						(n = 36)	
Owls per survey point	0.13		0.19	0.17	0.04	0.08	0.02	0.04	0.20	0.12					0.17	0.16
Ave. diameter ranking	2.73		2.84	0.56	2.45	0.57	2.09	0.14	3.45	0.20					2.79	0.58
High Cascades	(n = 2)						(n = 3)		(n = 1)						(n = 6)	
Owls per survey point	0.27	0.19					0.07	0.07	0.00						0.12	0.15
Ave. diameter ranking	3.54	0.09					2.78	0.79	2.07						2.91	0.75
High Desert			(n = 3)		(n = 16)								(n = 1)		(n = 20)	
Owls per survey point			0.07	0.07	0.01	0.03							0.00		0.02	0.04
Ave. diameter ranking			3.04	0.27	2.50	0.68							2.60		2.59	0.64
Klamath Mountains	(n = 8)		(n = 1)						(n = 1)		(n = 4)		(n = 3)		(n = 17)	
Owls per survey point	0.25	0.20	0.13						0.20		0.08	0.06	0.04	0.04	0.16	0.16
Ave. diameter ranking	2.62	0.46	2.53						3.20		2.87	0.64	2.12	0.63	2.62	0.55
Western Cascades	(n = 34)		(n = 1)				(n = 2)								(n = 37)	
Owls per survey point	0.25	0.18	0.57				0.27	0.09							0.26	0.18
Ave. diameter ranking	3.13	0.56	2.86				4.24	0.23							3.18	0.60
Willamette Valley	(n = 1)										(n = 1)		(n = 6)		(n = 8)	
Owls per survey point	0.00										0.00		0.07	0.07	0.05	0.07
Ave. diameter ranking	2.00										1.13		2.12	0.63	1.99	0.73
All ecoregions	(n = 78)		(n = 69)		(n = 23)		(n = 12)		(n = 14)		(n = 11)		(n = 17)		(n = 224)	
Owls per survey point	0.21	0.17	0.17	0.16	0.05	0.08	0.07	0.10	0.11	0.10	0.12	0.13	0.06	0.08	0.15	0.16
Ave. diameter ranking	2.96	0.62	2.84	0.55	2.46	0.70	2.85	0.84	3.15	0.75	2.50	0.65	2.05	0.62	2.79	0.68

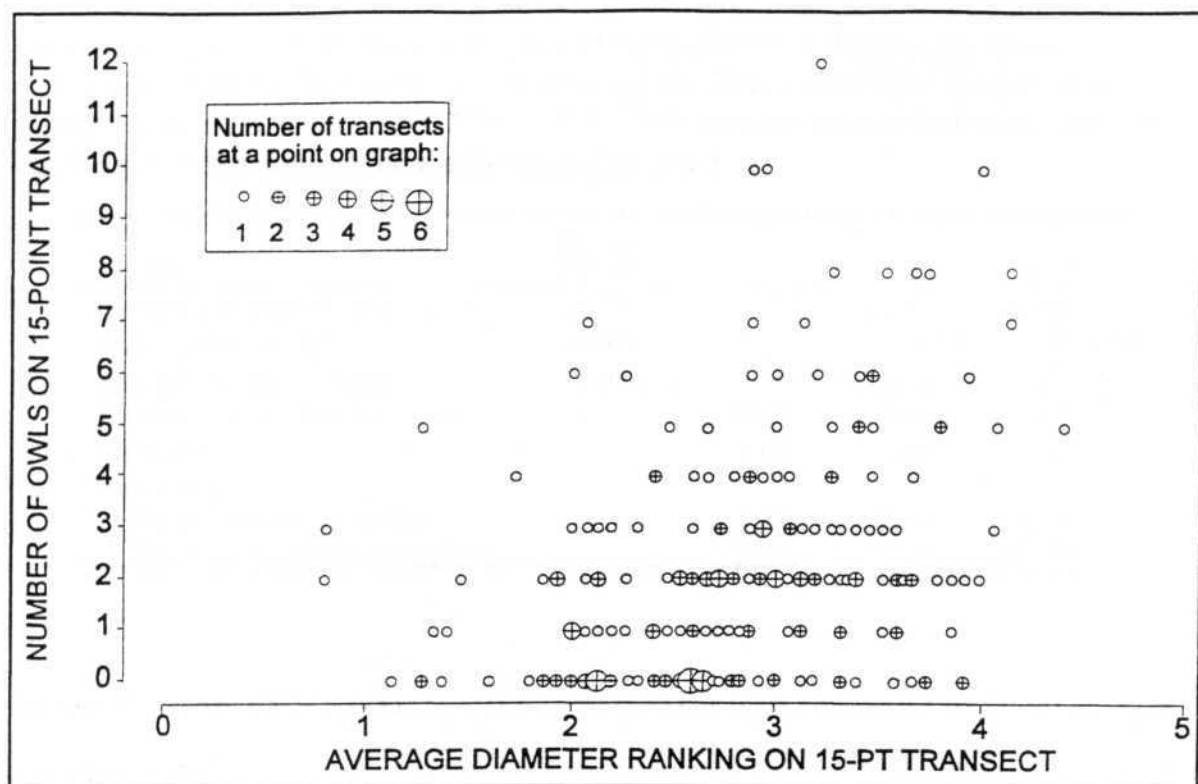


Fig. 3. Number of northern pygmy-owls detected per 15-point acoustic lure survey transect versus average diameter-size ranking of the dominant trees in the area of the transect. Surveys were conducted in Oregon, 1996-97 ($n = 196$).

did not change with any regression variables. Average diameter rankings of dominant trees were larger in forest stands from which owls responded (3.44 ± 0.85) than around survey points from which owls were detected (3.00 ± 0.86 ; $t_{121} = 5.48$, $P = 0.0001$). This relationship differed by ecoregion ($F_{7,90} = 3.62$, $P = 0.002$). When t -tests were conducted separately for all ecoregions with ≥ 30 transects, there was evidence of a difference between rankings in the Western Cascades (mean \pm SE = 1.25 ± 0.18 ; $t_{27} = 6.98$, $P = 0.0001$) and Coast Range (0.52 ± 0.22 ; $t_{18} = 2.38$, $P = 0.03$) Ecoregions, but not in the

Table 6. Parameter estimates and associated values from the Poisson log-linear regression model for the number of northern pygmy-owls detected per acoustic lure survey transect in Oregon, 1996-97 ($n = 224$). This analysis excluded all owls detected less than 3 survey points from a previously detected owl.

Variable	Parameter estimate	F	df	Pr > F
Log of the number of survey points	2.90	13.64	1,206	0.0003
Day of survey season	-0.005	5.61	1,206	0.02
Average time-after-sunrise	-0.08	1.67	1,206	0.20
Average tree-diameter size rating	0.33	13.35	1,206	0.0003
Ecoregion		2.68	7,206	0.01
Forest type				
Full model (with ecoregion)		1.34	6,206	0.24
Reduced model (w/o ecoregion)		3.93	6,213	0.0009

Eastern Cascades (0.07 ± 0.11 ; $t_{18} = 0.61$, $P = 0.55$) or Blue Mountains (0.11 ± 0.43 ; $t_{39} = 0.80$, $P = 0.43$).

Numbers of northern pygmy-owl detections varied substantially among transects in the same ecoregion and forest type, and with similar-sized dominant trees. For example, on 15-point transects in Douglas-fir in the Coast Range Ecoregion with average diameter rankings ≥ 3 ($n = 15$), the mean number of owls detected was 3.1 ± 3.0 (mean \pm SD), but ranged from 0 - 12. Unusually high numbers of detections also occurred on some transects in other ecoregions and forest types. Ten owls were detected on a 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 transects had 15 survey points).

SURVEY VARIABLES

The number of owls detected per transect decreased with increasing survey date ($F_{1,206} = 6.49, P = 0.01$; Table 2). The average number of owls per transect did not differ among April, May or June, but the July average was 45% lower than the average for all earlier months ($F_{1,206} = 13.60, P = 0.0003$; 95% CI = 24-61%; Fig. 4). Regression results were unchanged when July transects were excluded from the analysis, except that there was evidence of a decrease in the number of owls detected per transect with increasing average hours after sunrise of the survey points ($F_{1,159} = 8.82, P = 0.003$).

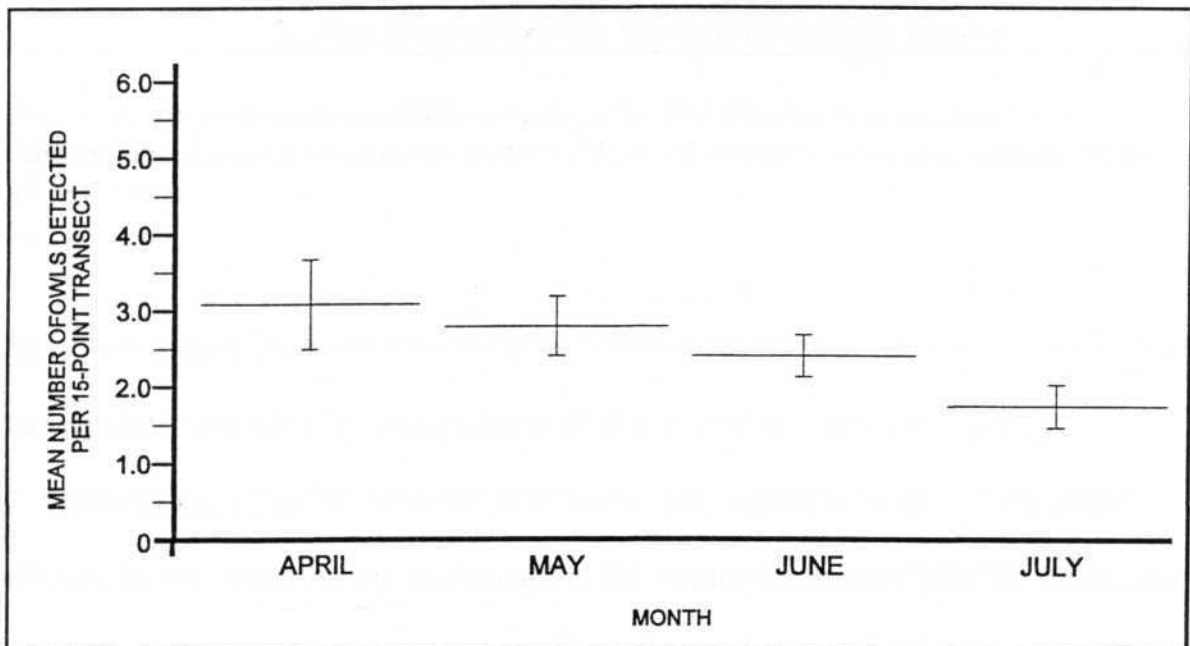


Fig. 4. Mean number (\pm SD) of northern pygmy-owls detected per 15-point acoustic lure survey transect in Oregon, 1996-97, relative to month ($n = 196$).

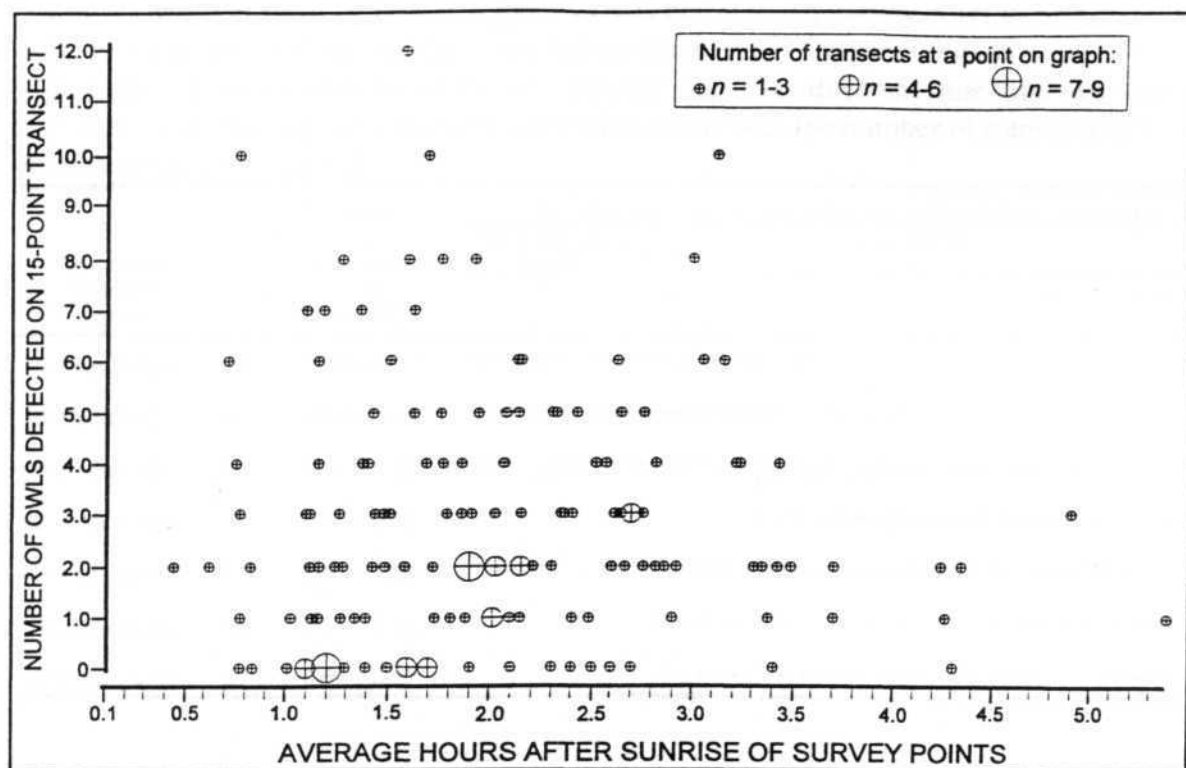


Fig. 5. Number of northern pygmy-owls detected per 15-point acoustic lure survey transect versus average hours after sunrise of survey points for surveys in Oregon, 1996-97 ($n = 196$).

In the full sample, there was only marginal evidence that the number of owls detected per transect decreased with the average hours after sunrise of the survey points ($F_{1,206} = 3.62$, $P = 0.06$; Table 2; Fig. 5). However, within transects, a gradual decrease in the number of owls detected per survey point throughout the morning is evident (Table 7). There was no evidence of a year effect on numbers of owls detected per transect ($F_{1,205} = 1.49$, $P = 0.22$).

Table 7. Mean number of northern pygmy-owls detected per survey point during different time intervals on acoustic lure survey transects in Oregon, 1996-97 ($n = 224$). Confidence intervals were based paired t -tests of means for different time intervals within transects. Sample size for each time interval estimate was the number of transects that included that time interval.

Time interval relative to sunrise	n	Mean number of owls detected survey point (\pm SD)	Means for other time intervals included in 95% confidence interval (***)						
			Hours BEFORE Sunrise		Hours AFTER Sunrise				
			0-1	0-1	1-2	2-3	3-4	4-5	5-6
0-1 hrs before	155	0.25 \pm 0.39	*****						
0-1 hours after	210	0.19 \pm 0.31	*****						
1-2 hours after	215	0.16 \pm 0.26	*****						
2-3 hours after	218	0.15 \pm 0.28	*****						
3-4 hours after	173	0.11 \pm 0.24	*****						
4-5 hours after	107	0.15 \pm 0.29	*****						
5-6 hours after	51	0.09 \pm 0.17	*****						

DISCUSSION

Northern pygmy-owls seemed fairly common and well distributed throughout the forested areas of Oregon. However, numbers of owls detected varied substantially among forest types and ecoregions, suggesting that habitat quality or carrying capacity for northern pygmy-owls may differ among forest types and ecoregions. Also, though pygmy-owls were not strictly limited to mature or old-growth forests, the increase in pygmy-owl abundance with the diameters of dominant trees indicated that this species tends to be associated with older forests in Oregon. These findings lend credence to the concern that harvest of old forests in the Pacific Northwest could be detrimental to northern pygmy-owls, though they also support previous observations that the pygmy-owl is, to a large extent, a habitat generalist (Hayward and Garton 1988, Reynolds et al. 1988). Further study is needed, because counts of pygmy-owls on acoustic lure surveys may not provide unbiased indices of population densities, and high density does not necessarily reflect high habitat quality or high carrying capacity (Hobbs and Hanley 1990, Kellner et al. 1992, Van Horne 1983). Also, the regional differences in owl abundance I found may point to important habitat associations, species interactions, or population dynamics of northern pygmy-owl populations that are not understood.

The only forest types in which northern pygmy-owls were consistently not detected in my study were deciduous forests in the Willamette Valley Ecoregion and western juniper forests in the High Desert Ecoregion. This suggests that pygmy-owls in Oregon are limited primarily to closed-canopy forests dominated by conifers, but are otherwise

habitat generalists that occur in a broad range of plant species associations. Numbers of pygmy-owls detected varied substantially among forest types, so there are probably other factors affecting habitat use by northern pygmy-owls that result in a non-random distribution of the owls. Tree species composition appears to be related to these factors because forest type is correlated with apparent differences in local pygmy-owl abundance, but not itself a primary determinant of habitat occupancy because pygmy-owls occur in almost every forest type.

Differences in numbers of 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, winter snow pack, abundance or availability of prey, or structural characteristics of similar forest types. Regional variation within forest types could have been due to the unconfirmed subspecific divisions in northern pygmy-owls (Gabrielson and Jewett 1940, AOU 1987), or may have reflected large-scale random or cyclic fluctuations in owl abundance or responsiveness that could not be detected in my short study (Kellner et al. 1992). For the most part, ecoregion probably acted in my analysis as a surrogate variable for many habitat characteristics and conditions I did not measure. However, ecoregion might explain why northern pygmy-owls appeared absent from dense, old forests of western juniper on Steens Mtn. in the High Desert Ecoregion, but were fairly common in similar forests in the Blue Mountains Ecoregion. Pygmy-owls may infrequently disperse to Steens Mtn. because it is separated from large tracts of contiguous forest by about 50 km of non-forest shrub-steppe vegetation. Other differences in pygmy-owl numbers among ecoregions could be due to landscape-level

factors such as population dynamics or the relative locations of source and sink habitats (Pulliam and Danielson 1991).

I used visually assigned diameter rankings of dominant trees to incorporate a coarse measure of average dominant tree diameter into my analyses, but this measure has several limitations. First, surveyors classified diameters of trees visible from roads, which may not have been representative of forest in surveyed areas. Second, visual classification of tree diameters probably compromised precision of the measure (Ralph 1981). Finally, diameter classes were broad and defined for ease of classification, so the resulting rankings were not closely or linearly related to average diameters. Because of this, averaged rankings cannot be readily translated back into average diameter classes. For example, a 15-point transect with an average diameter ranking of 3 could have dominant overstory trees that averaged 120 cm at 5 points, 40 cm at 5 points, and 30 cm at 5 points. The actual average diameter of dominant trees on this transect would be 55 cm, which corresponds to the diameter class with a ranking of 4. Averaged rankings may have regularly underestimated the average diameter class of dominant trees on transects where trees at some survey points averaged over 50 cm dbh. This would have caused my analyses to underestimate the strength of the association between high numbers of pygmy-owl detections and large-diameter trees, as well as underestimate the typical average diameter ranking of dominant trees in forest with high numbers of detections. However, I do not know whether this was the case because I did not actually measure tree diameters.

Because of the limitations of diameter ranking as an explanatory variable, I can

conclude only that there was a general increase in numbers of northern pygmy-owls detected with increasing diameter of dominant trees, and that pygmy-owls seemed to respond from forest stands dominated by relatively large-diameter trees on a local scale. I do not know the amount of population density increase per unit increase in tree diameter, or the magnitude of the difference between dominant tree diameters in forest associated with pygmy-owls and in forest where the owls appear to be rare or absent. Further study with more precise measurement of vegetation is needed to clarify these patterns. Also, associations of owl response locations with large diameter trees at the local scale should be interpreted cautiously, as response locations may not always reflect high-use areas within home ranges (Giese 1999). In spite of this, I feel confident that the relationship between pygmy-owls and dominant tree diameter found in this study is not spurious. Northern pygmy-owls were rarely detected on transects with dominant trees that averaged ≤ 30 cm dbh. In areas with larger trees, dominant tree diameter seemed to increase along with the number of owls detected, though owl detections did not necessarily increase with tree diameter. On transects with survey points that had a wide range of average diameter rankings, any pygmy-owl detections generally occurred at survey points with diameter rankings among the highest on the transect. This pattern appeared to hold even in areas with no late-successional forest, where the highest diameter rankings on a transect were no greater than 3. However, pygmy-owl detections did not occur at all survey points with relatively high diameter rankings, probably in part because owls were not always detected, or did not occupy all available habitat.

Our study does not indicate why northern pygmy-owl density might increase with the diameter of dominant trees. However, there are ecological reasons why forest dominated by large trees might be high quality habitat for pygmy-owls. Woodpeckers prefer large-diameter trees and snags for excavation, so forest with large trees (which later become snags) may have more potential nest sites for pygmy-owls. Other forest components or characteristics often associated with large trees might also contribute to habitat quality, such as forest canopy volume, open understories, structural complexity, high woodpecker abundance due to the presence of downed woody debris for foraging, or the abundances of other animal species. According to Cramp (1984:506), the Eurasian pygmy-owl is most abundant in tall forest interiors because it "...is concerned as much with structure of forest as with its composition of tree species." Cramp speculated that Eurasian pygmy-owls select such forests because the owls are able to use them more efficiently for foraging, and because they provide escape cover. This may also explain habitat use by the northern pygmy-owl, which has similar hunting behaviors (Bent 1938), and has been recorded in the diet of other owls, such as the spotted owl (*Strix occidentalis*) (Forsman et al. 1984).

There are also reasons why carrying capacity for northern pygmy-owls might be highest in forest dominated by large-diameter trees. Compared to forests with small trees, such forests are generally taller and have deeper canopies. This may allow pygmy-owls to maintain territories that are larger in the vertical but smaller in the horizontal dimension, resulting in higher numbers of owls per km². Alternatively, other resources required by pygmy-owls, such as prey, could be more abundant or higher quality in forest

dominated by large trees, resulting in higher owl density but not necessarily higher owl fitness (Van Horne 1983).

Pygmy-owls did not appear to be associated with large trees in all forest types and ecoregions, perhaps because characteristics and conditions in some habitats make forest dominated by large trees less important to pygmy-owls. Alternatively, different pressures may make the owls less able to select such forests as habitat, or homogenous forest conditions may make effects of selection less obvious. In any case, this possible inconsistency in northern pygmy-owl habitat selection in different areas suggests that whatever benefits the owls might be gaining from association with forest dominated by large trees may not be of utmost importance to the persistence of the species. Though separate analyses within forest types and ecoregions were limited to categories with ≥ 30 transects, sample sizes in some forest types or ecoregions may still have been too small to allow associations to be detected. Even where associations existed, they could have been obscured because pygmy-owls did not occupy all available habitat. Low owl counts were obtained in many areas with large trees, and many locations within transects had large trees but were not associated with owls. In my analyses, this tended to decrease the strength of the association between owls and large trees, or the magnitude of the difference in diameter rankings between locations within a transect that were or were not associated with owls.

Counts of owls varied greatly among transects that had similar average diameter rankings and were also in the same forest type and ecoregion. This variation could have been due to chance fluctuations in local pygmy-owl abundance or responsiveness.

Alternatively, a factor uncorrelated with any of my explanatory variables, such as local prey abundance, could have been affecting pygmy-owl distributions. Population densities of Eurasian pygmy-owls fluctuate substantially in some areas, depending on vole population cycles (Cramp 1985).

It is not surprising that the number of owls detected decreased over the course of the survey season or with increasing time after sunrise. Northern pygmy-owls in the Pacific Northwest establish territories in March and April, when spontaneous calling appears to reach a peak (Bent 1938). With the onset of incubation in April or May (Holt and Norton 1986), breeding males apparently are less likely to call, and may become even more quiet when young hatch about 1 month later. By July, when the most dramatic decrease in numbers of detections per transect occurred, pygmy-owls in Oregon are either caring for fledged young, or finished breeding. However, high levels of calling and responsiveness are noted in this species in autumn (Bent 1938:406), which apparently indicates a resurgence of calling activity in conjunction with dispersal after the end of the breeding season. Northern pygmy-owls are mostly crepuscular (Voous 1988, Giese pers. comm.), explaining why responsiveness appeared highest around sunrise and decreased gradually after sunrise. Some surveys in this study were conducted in July or continued until 5-6 hrs after sunrise, but this did not seem to change the results of my analyses as long as survey day and average hours after sunrise were included as variables in regression models.

I did not have the time or resources to test the abilities of surveyors to detect or identify pygmy-owls. Differences in hearing ability likely increased variation in detection

rates, but it seems unlikely that it should have biased the results in any particular direction because there were so many different surveyors involved in my study. With the exception of myself (45 surveys), each surveyor conducted an average of 2 surveys. All surveyors were experienced with bird identification and should have been able to reliably identify the unique call of the pygmy-owl. Misidentification of pygmy-owls in my data also seems unlikely, because surveyors reported no errors in 65 cases (about 25 of which were mine) where they identified pygmy-owls based on calls alone, and then confirmed the identifications visually.

It would have been preferable to train and test surveyors and to require greater standardization in transect start and end times, survey dates and years, broadcast devices and broadcast volumes. Had I done so, my sample size and study area would have been much smaller. I feel that the scale of my study was crucial to my objective, namely, to increase understanding of northern pygmy-owl habitat associations in a relatively coarse-grained manner, such that results would be applicable throughout Oregon. Although I cannot prove that the validity of my results was not compromised by the number of surveyors and variation in survey conditions involved in my study, I believe that inclusion of survey variables in inferential regression models accounted for much of the variation in survey conditions.

Acoustic lure surveys seemed to be an effective method for locating northern pygmy-owls, and the survey protocol used in this study could be easily repeated to evaluate pygmy-owl population trends. If acoustic lure surveys are used to estimate trends in pygmy-owl populations, I suggest limiting the survey season to 1 April - 30 June, starting

surveys at sunrise and completing them by 5 hours after sunrise, and standardizing decibel levels of call broadcast. However, more information is required before results from such surveys should be used to do anything but suggest general trends in large samples. Counts of pygmy-owls on acoustic lure surveys may not provide comparable indices of local population densities if detectability of the owls differs depending on such things as forest type or ecoregion. Topography, vegetation, and ambient noise from rivers and wind varied among forest types and ecoregions, and these factors could have affected the distance that calls were audible to owls, or that owls were audible to humans (Dawson 1981, Schieck 1997). However, it did not seem that the results in this study were overly biased by such variation. Many transects with low numbers of pygmy-owl detections, such as those in western juniper woodlands, were in relatively flat, open and quiet areas, while many transects with high numbers of detections were in mountainous, densely vegetated areas with numerous high gradient streams, such as the Western Cascades.

High owl densities could cause a positive bias in owl counts on acoustic lure surveys if proximal owls are more likely to respond to each other than to a tape broadcast. Again, this did not appear to be an important issue in my study, because regression results were unchanged even when pygmy-owls detected less than 2.4 km from a previously detected owl were omitted from the sample. Finally, owl response locations during acoustic lure surveys may not accurately represent habitat associations if owls move toward the observer and do not respond from locations representative of typical habitat. However, I believe that owls generally responded in or near their territories, and that calling locations

represented potential breeding sites (Hayward and Garton 1988). Owls tended to respond from prominent perches for several minutes or more, individuals were usually spaced at least 0.4 km apart, and, once detected, generally did not move more than about 0.3 km to approach survey points.

CONCLUSIONS

I sampled all major forest types in the state, using a stratified sample with random starting points for transects, so inferences can reasonably be extended to northern pygmy-owls throughout Oregon, though possibly only to territorial owls occurring within approximately 0.8 km of roads during the breeding season. Much more research is needed before we can understand habitat use by northern pygmy-owls in Oregon. Until more information is available, it might be possible to monitor changes in northern pygmy-owl populations with acoustic lure surveys that use a methodology consistent with that used in this study, so detection numbers can be compared to those I obtained. Although my surveys provide 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, dispersal, genetics, and population trends would help to understand these factors, and would enable managers to make better-documented predictions of the effects of management practices on northern pygmy-owls.

Our surveys suggest that it is prudent for land managers to continue to regard the northern pygmy-owl as a probable associate of late-successional forests in Oregon, though the owl is not limited to such forest. It is also reasonable to regard the owl as a well-distributed habitat generalist with respect to forest vegetation associations. Where the goal of management is to avoid declines in northern pygmy-owl populations, decreases in the amount of structurally complex, late-successional forest should probably be minimized. Although my modeling of the relationship between pygmy-owls and large trees is crude, more complicated or sensitive modeling may not be required for prediction of the effects of gross, large-scale habitat changes on wildlife (Morrison et al. 1992: 104).

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