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POPULATION DENSITY OF NORTHERN SPOTTED OWLS IN MANAGED YOUNG-GROWTH FORESTS IN COASTAL NORTHERN CALIFORNIA

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ABSTRACT.—We estimated population densities of Northern Spotted Owls (*Strix occidentalis caurina*) in managed young-growth forests in coastal northern California from 1991–97. The 1266 km^2 study area was divided into three subregions (Klamath—666 km^2, Korbel—392 km^2 and Mad River—208 km^2) and completely surveyed each of the seven years. A total of 446 individual owls was marked to generate both empirical and Jolly-Seber (J-S) estimates of density. Mean empirical and J-S estimates of abundance were similar but mean estimates of crude density (territorial owls/km^2) differed among the three subregions (Klamath—0.092 ± 0.006 [±SE], Korbel—0.351 ± 0.011, Mad River—0.313 ± 0.017 and overall mean—0.209 ± 0.009). Significant differences in forest age-class composition among the three subregions provided a plausible explanation for the low Klamath density but did not account for the similar densities observed in Korbel and Mad River. Ecological densities (number of individuals/area of habitat) were higher than crude densities but the interpretation of this was limited because only nesting habitat was used to estimate suitable habitat. Compared to limited published reports, densities were relatively high in two of the three subregions in our study but this was probably typical of Northern Spotted Owl densities for portions of coastal northern California. Recognizing the limitations of using density to indicate habitat quality, our study provided valuable baseline data for assessing long-term trends in Northern Spotted Owl population dynamics within the study area.

KEY WORDS: *Northern Spotted Owl*; Strix occidentalis caurina; *California*; *density*; *managed forests*; *mark-recapture.*

Densidad poblacional de *Strix Occidentalis caurina* en los bosques jóvenes y manejados de las costas del norte de California

RESUMEN.—Estimamos la densidad poblacional de *Strix occidentalis caurina* en bosques jóvenes y manejados de las costas del norte de California entre 1991–97. Los 1266 km^2 del área de estudio fueron divididos en tres subregiones (Klamath—666 km^2, Korbel—392 km^2 y Mad River—208 km^2) y los monitoreamos durante los siete años. Un total de 446 individuos de buhos fueron marcados con el fin de generar estimativos de densidad empíricos y de Jolly-Seber (J-S). La media empírica y los estimativos de J-S de abundancia fueron similares, pero la media de densidad cruda (buhos territoriales/km^2) difirió en las tres subregiones (Klamath—0.092 ± 0.006 [±SE], Korbel—0.351 ± 0.011, Mad River—0.313 ± 0.017 y la media promedio—0.209 ± 0.009). Las diferencias significativas en la edad y clase de la composición de los bosques entre las tres subregiones pueden ser la explicación de la baja densidad de Klamath pero no para las densidades similares observadas en Korbel y Mad River. Las densidades ecológicas (número de individuos/área de habitat) fueron mayores que las densidades crudas. La interpretación de esta fue limitada debido a que se utiliza el habitat de anidación para estimar habitats convenientes. Al comparar la limitada publicación de reportes, se encontró que las densidades fueron relativamente altas en dos de las tres subregiones de nuestro estudio. Quizas esto sea típico de las densidades de *Strix occidentalis caurina* en porciones costeras del norte de California. Al reconocer las limitaciones de usar densidades para indicar la calidad de habitat, nuestro estudio provee valiosos datos para evaluar tendencias en el largo plazo sobre la dinámica poblacional de *Strix occidentalis caurina* dentro del área de estudio.

[Traducción de César Márquez]

The Northern Spotted Owl (*Strix occidentalis caurina*) is associated with mature and old-growth forests throughout much of its range. This relationship has been studied primarily through radiotelemetry data that infers habitat selection through disproportionate use of mature- and old-growth forests relative to their occurrence within a landscape (Forsman et al. 1984, Carey et al. 1990, Solis and Gutiérrez 1990, Carey et al. 1992). In addition, studies of Northern Spotted Owl occurrence and abundance have shown a greater number of owl sites in mature- and old-growth forests relative to adjacent young forests (Forsman et al. 1977, Forsman et al. 1987, Forsman 1988, Bart and Forsman 1992, Blakesley et al. 1992). Given the economic value of mature- and old-growth forests, the association of Northern Spotted Owls with these forests places it at the center of a major controversy in the Pacific Northwest. The 1990 listing of the Northern Spotted Owl under the federal Endangered Species Act (USDI 1992) instituted management policies limiting timber harvest of Northern Spotted Owl habitat on public and private lands (Thomas et al. 1990, Gutiérrez et al. 1996, Marcot and Thomas 1997).

The population density of a species is important to resource managers for several reasons. In harvested game species, it is important to increase population density to generate a greater harvestable surplus, and it may also be important to understand the population density relative to carrying capacity (Krebs 1985, Caughley and Sinclair 1994). In species of conservation concern, population density has been used as one of the indicators of habitat quality (Forsman 1988, Thomas et al. 1990, Bart and Forsman 1992), and one of the criteria for establishing federally designated critical habitat areas (USDI 1992). In many populations, density has been used as a surrogate for knowing vital rates of populations that allow estimation of the population stability or viability.

Most attempts to compare abundance of Northern Spotted Owls in different habitats have relied on estimates of relative abundance (Forsman et al. 1977, Marcot and Gardetto 1980), because estimating population density has been difficult for a species that exists in low numbers and occupies large home ranges. As a result, reliable estimates were not possible unless large areas were surveyed (Franklin et al. 1990).

We surveyed 1266 km^2 of managed young-growth forests for seven years as part of a monitoring plan for the Northern Spotted Owl under Simpson Timber Company's (STC) Habitat Conservation Plan (Simpson Timber Company 1992). The primary objective of this study was to estimate population density of owls in three subregions with different forest age-class compositions to provide baseline data for assessing long-term trends in Northern Spotted Owl populations within a managed young-growth landscape. We compared crude (number of individuals/total area, Odum 1971) and ecological densities (number of individuals/area of habitat; Odum 1971), and assessed changes in owl density during the study period (1991–97). In addition, we compared estimates of abundance based on empirical (direct counts of individuals for which differences in detectability and sampling variation associated with the estimate are not known) and mark-recapture methods. Comparability of these two approaches, empirical versus mark-recapture, is important since most of the reported estimates of Spotted Owl population density are based on abundance estimates derived from empirical data.

STUDY AREA

The study area was primarily within 1558 km^2 of land owned by STC located in Del Norte, Humboldt and Trinity counties, northwestern California. Most of this property lies within 32 km of the coast, but can extend up to 85 km inland. The study area was located within the Northern California Coast Range physiographic province where fog is common (Mayer 1988). Near the coast, mean summer and winter temperatures are about 18°C and 5°C, respectively, whereas extremes of 38°C in summer and −1°C in winter are not uncommon beyond the longitudinal belt of coastal influence approximately 48 km from the coast. Precipitation ranges from 102–254 cm annually, with 90% of this falling from October–April (Elford 1974).

Predominate forest stands in the study area were coastal redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga *menziesii*), and oak woodlands (Zinke 1988). Species characterizing the oak woodlands included tanoak (*Lithocarpus densiflorus*), California black oak (*Quercus kelloggii*) and Oregon white oak (*Q. garryana*). Many of the redwood and Douglas-fir stands also contained a large component of the following hardwoods: tanoak, bigleaf maple (*Acer macrophyllum*), madrone (*Arbutus menziesii*), California bay (*Umbellularia californica*), and red alder (*Alnus rubra*).

Since the late 1960s, the primary silvicultural practice has been even-aged management involving relatively small clearcuts (12–24 ha in size) followed by prompt replanting. About 97% of the study area consisted of young forests ranging from 0–80 yr old. Residual trees (left from past logging operations) were a component of some forest stands and commonly the largest, oldest trees present.

METHODS

Within STC lands, Northern Spotted Owl survey boundaries were established *a-priori* based on ownership patterns, topographic features, vehicular access and other logistic considerations. The resulting study area was further subdivided due to geographic and vegetative patterns. In a nearby study area, Franklin et al. (1990) determined that areas exceeding 90–130 km^2 were sufficient to accurately estimate Northern Spotted Owl density. Three subregions in our study area met this criterion and hereafter are referred to as Klamath (666 km^2), Korbel (392 km^2) and Mad River (208 km^2; Fig. 1). Other isolated tracts of STC property were too small to be included as separate subregions. Following Thome et al. (1999), we created six categories of stand age to classify habitat: 0–5, 6–20, 21–40, 41–60, 61–80, and >80 yr (Table 1). The 61–80 and >80 yr age classes were combined for this analysis, because there was very little area of one or both of these age classes in the three subregions.

We surveyed the entire STC study area for Northern Spotted Owls at least twice each season using a complete and systematic search protocol from 1 March–30 August, 1991–97. Prior to initiation of surveys, we inspected the entire study area using 1:24 000 aerial photographs. We plotted call points at strategic locations that maximized observer ability to solicit and detect responses from owls. Call points were usually positioned at relatively high elevations with unobstructed forest openings to ensure a clear and far-ranging broadcast of the call. Solicitations consisted of playing recorded Northern Spotted Owl calls or vocalizing imitations of calls for a minimum duration of 10 min. We used a jet boat to access and survey STC property bordering the Klamath River. All surveys using this protocol were conducted nocturnally, beginning no earlier than dusk. If an owl responded to a nocturnal call, its location was plotted, and a daytime follow up effort was initiated, where an observer attempted to locate the roosting owl by pursuing responses made to imitated or recorded calls (Forsman 1983). We captured owls using noose or snare poles (Forsman 1983) and banded them with a USGS band on one leg and a plastic, color-coded band on the other (serving as a unique identifying mark; Forsman et al. 1996). Sex and age were determined following Forsman (1981, 1983) and Moen et al. (1991).

We calculated forest stand ages using STC's timber inventory database in Intergraph's CAD system, integrated with the Modular Graphics Environment 5.0 (Intergraph Corporation 1994) geographic information system (GIS). Forest stands were distinguished based on date of harvest and polygons were drawn around unique forest stands. Only GIS data from 1997 were available for analysis Landscape data from 1997 were considered adequate because the mean annual percent change in the landscape (from timber harvest) during this study was 0.7 ± 0.08 [±SE], 1.0 ± 0.18 and 0.5 ± 0.16% for the Klamath, Korbel and Mad River study areas, respectively.

Not all of the land surveyed was owned by STC, because other private lands (in-holdings) were common within our study area, and survey boundaries were set by topographic features and access points rather than ownership boundaries. Since GIS coverage was limited to STC lands, we were able to assess age-class conditions for 90% (599 km^2) of Klamath, 75% (294 km^2) of Korbel and 70% (145 km^2) of Mad River. Despite this, we believe the GIS coverage was representative of the entire study area, since most of the landscape was subjected to the same historic timber harvesting practices that created entire watersheds with similar aged stands. In addition, the in-holdings and adjacent lands associated with the Korbel and Mad River subregions (areas with the least GIS coverage) were virtually all private lands zoned for timber production. We compared the amount of forest in the five age classes among the three subregions (Table 2) using Chi-square analysis (Hintze 1997).

We used the Jolly-Seber (J-S) capture-recapture model (Jolly 1965, Seber 1965, 1982) that allowed for death and immigration in open populations. We used program JOLLY (Pollock et al. 1990) to calculate J-S estimates of annual abundance (N_t). Because population and density estimates on STC lands had never been documented, we were primarily interested in these parameters from the modeling. We subjectively chose the reduced parameter J-S model (model D in program JOLLY) to analyze the data, because reduced parameter models compute abundance estimates with greater precision than models saturated with parameters (Jolly 1982). Ninety-five percent confidence intervals were calculated as 1.96 (SE [N_t]). Goodness-of-fit tests (Pollock et al. 1985) in program JOLLY were used to determine if the models fit the data. When goodness-of-fit tests suggested lack of fit, we used a variance inflation factor, $\hat{c}$, based on quasi-likelihood theory (Burnham et al. 1987:243–246, McCullagh and Nelder 1989) to adjust variances in models with overdispersed data (Lebreton et al. 1992, Anderson et al. 1994). The variance inflation factor is calculated as χ^2/v where χ^2 was the goodness-of-fit statistic with v degrees of freedom. Expected values for $\hat{c}$ are not, on average, different from 1.0 with models that fit the data, and do not exceed ≈4 in models that attain structural adequacy, but may need variance inflation measures (values of 6–10 indicate complete model inadequacy requiring an entirely new model). If $\hat{c}$ indicated that variance inflation measures were necessary, the standard error of each population parameter was calculated as $\sqrt{\hat{c}\{SE\}}$ (Anderson et al. 1994).

Empirical estimates of annual abundance (N_t) followed criteria established in Franklin et al. (1990), which

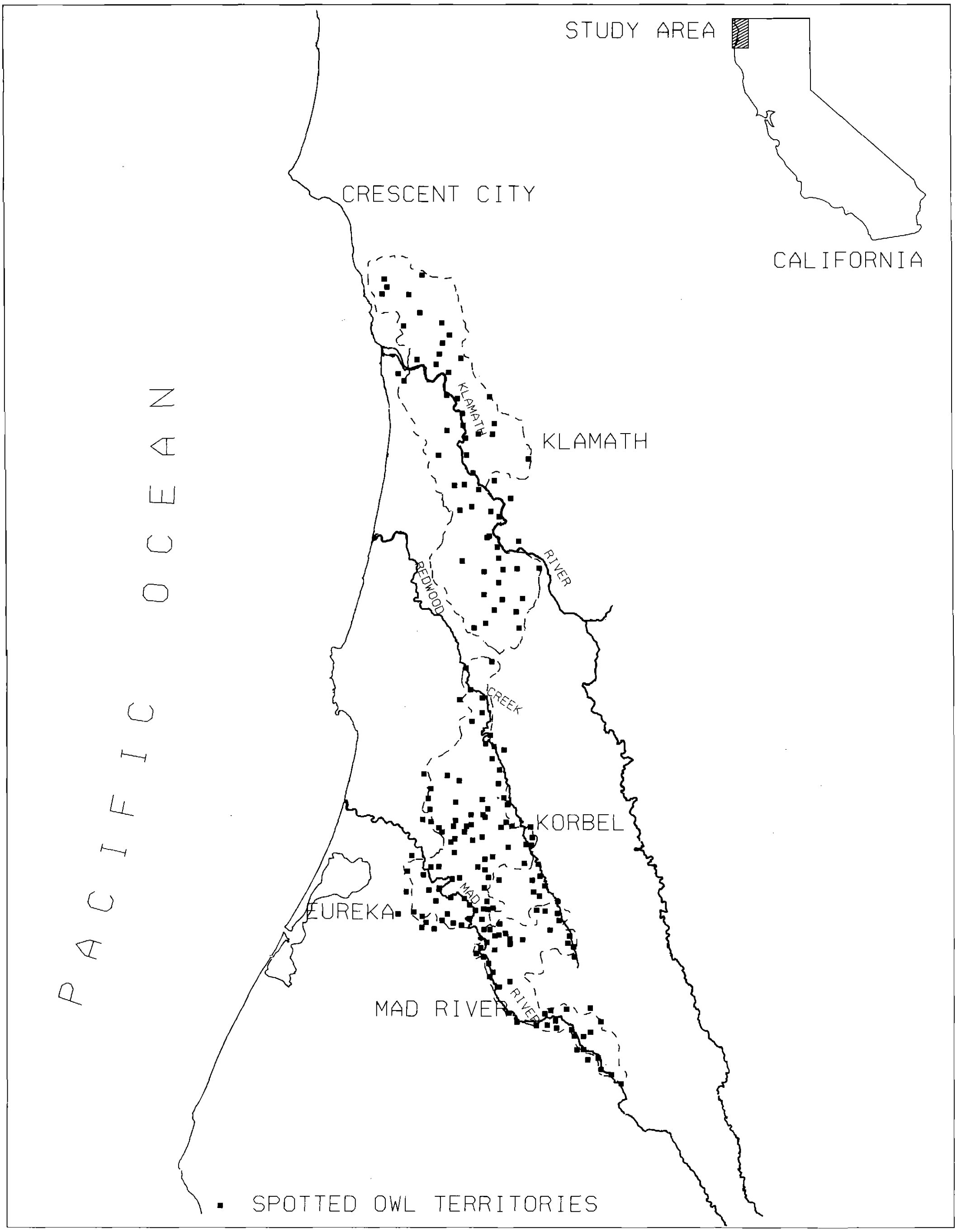

Figure 1. Map of the Simpson Timber Company study area, northwest California. Dots represent Northern Spotted Owl locations within and adjacent to Klamath, Korbel and Mad River subregion boundaries.

Table 1. Description of six forest age categories used in analysis of Northern Spotted Owl ecological density for the Simpson Timber Company study area in northern California, 1991–97.

AGE CATEGORY	TREES/ha $\bar{x}$	TREES/ha SD	BASAL AREA[a] $\bar{x}$	BASAL AREA[a] SD	VOLUME[b] $\bar{x}$	VOLUME[b] SD
0–5	0.9	5.9	0.2	1.0	0.1	0.7
6–20	42.2	160.8	2.3	8.4	0.8	4.3
21–40	558.6	292.6	29.7	15.8	6.7	7.4
41–60	708.2	320.9	46.9	18.5	14.6	11.2
61–80	591.4	384.9	59.1	18.3	29.8	19.8
>80	811.6	598.9	58.4	30.7	28.7	27.8

[a] m^2/ha.

[b] Million board m/ha.

assumed an annual census of territorial owls in which all individuals known to be alive in the study area were counted. The total annual count was based on surveys over the 7-yr period and included the: number of identified (banded) individuals; number of unidentified individuals mated to identified owls; and number of unidentified individuals assumed different from identified individuals in nearby territories.

Population density was estimated as crude density (N_t /total area; Odum 1971) and ecological density (N_t /area of habitat; Odum 1971). We used J-S estimates of adult and subadult Northern Spotted Owls within the three subregions for N_t. Following the rationale of Franklin et al. (1990), we used the estimated total quantity of Northern Spotted Owl habitat as the divisor to calculate ecological densities. In their study, the proportion of telemetry locations of owls in different habitats was used as one method to estimate total owl habitat. Old-growth, which had the highest proportion of telemetry locations, was assigned a weight of 1.0 with other habitats weighted based on the proportion of telemetry locations in those habitats relative to those in old-growth (Franklin et al. 1990). Since we had no telemetry data to assess foraging habitat in our study area, we calculated the total owl habitat in each subregion based on the relative amount of nesting habitat.

To calculate ecological densities, we assigned a weight of 1.0 for the >60 yr age class, because it had the highest proportion of nest sites relative to the total forested area in the age class (0.27 nests/km^2). Other age classes were then weighted (normalized) by dividing the proportion of nest sites in those age classes by the proportion of nests in the >60 yr old age class (Table 3). For example, there were 0.18 nests/km^2 in the 41–60 yr age class, which was 68.5% of the density found in the >60 yr old age class. Crude densities were calculated as N_t (J-S) divided by the size of the associated subregion. Ninety-five percent confidence intervals for the density estimates were calculated by dividing the population confidence intervals by the subregion size (Seber 1982).

Abundance estimates cannot be computed for the initial year of study using program JOLLY. Therefore, we used preliminary capture data from 1990 as the first year of analyses, even though a complete census protocol was not established until 1991 (Franklin et al. 1990). In 1990, we banded and subsequently entered in the analysis, 14, 76 and 17 owls from Klamath, Korbel, and Mad River, respectively. We used program CONTRAST (Hines and Sauer 1989) to examine differences in abundance estimates among years for the three subregions. Program CONTRAST uses a general Chi-square statistic to test differences among abundance estimates using contrasts (Sauer and Williams 1989). We first tested for overall homogeneity in abundance estimates for each subregion. If a test yielded significant results, we then tested *a-posteriori* to determine which years were causing heterogeneity. Alpha levels for *a-posteriori* tests were adjusted to maintain the overall experiment-wise error rate (Neter and Wasserman 1974). We used the Bonferroni approach of using α/m as the significance level for unplanned compar-

Table 2. Percent of forest habitat in five age classes and percent of nonforest on three subregions of the Simpson Timber Company (STC) study area in northern California.

	FOREST AGE CLASS IN YEARS						
SUBREGION	0–5	6–20	21–40	41–60	>61	NONFOREST	NONSTC[a]
Klamath	4.3	27.9	49.4	5.2	10.6	2.6	10.0
Korbel	6.0	24.8	31.2	24.3	10.1	3.5	25.0
Mad River	3.6	3.8	16.0	23.8	34.2	18.6	30.0

[a] Percent of total study area within each subregion that was not within STC ownership or for which there was no forest age class information.

Table 3. Habitat weight and amount of weighted habitat in each age class for three subregions of the Simpson Timber Company study area in northern California. Habitat weights were calculated from 86 nest sites of Northern Spotted Owls, 1991–97.

	FOREST AGE CLASS IN YEARS					
	0–5	6–20	21–40	41–60	>61	TOTAL[a]
Habitat weight[b]	0	0.02	0.20	0.68	1.00	
Amount of weighted habitat[c] by subregion (km^2)						
Klamath	0	2.8	66.4	23.8	70.8	163.7
Korbel	0	1.4	24.7	65.3	39.6	131.1
Mad River	0	0.1	6.7	33.9	71.1	111.9

[a] Excludes nonforested areas.

[b] See methods for description of approach used.

[c] Amount of forest multiplied by habitat weight.

isons, where *m* was the number of unplanned tests. All tests were performed with a significance level of 0.05.

RESULTS

A Chi-square analysis indicated that there was a significant difference in forest age-class composition among subregions ($\chi^2 = 201.30$, df = 8, $P < 0.001$; Table 2). Klamath had the highest proportion of stands in younger age classes (83.7% <40 yr old) followed by Korbel (64.3% <40 yr old) and Mad River (28.7% <40 yr old).

A total of 103, 228 and 115 adult and subadult Northern Spotted Owls were banded at 55, 80 and 47 territories in the Klamath, Korbel and Mad River study areas, respectively, from 1990–97 (Fig. 1). Estimates of capture and survival probabilities were generally high and were similar among all three study areas (Table 4). The J-S model fit the data well for Klamath ($\chi^2 = 19.51$, df = 18, $P = 0.361$), but not for Korbel ($\chi^2 = 89.37$, df = 24, $P < 0.001$) and Mad River ($\chi^2 = 54.91$, df = 18, $P < 0.001$). We used variance inflation factors for Korbel ($\hat{c} = 3.72$) and Mad River ($\hat{c} = 3.05$) to adjust the sampling variance of the abundance estimates.

Abundance estimates appeared to increase over the first two years of the study (Fig. 2). The overall test of homogeneity for abundance estimates over the seven years yielded significant differences for Klamath ($\chi^2 = 22.80$, df = 6, $P < 0.001$), Korbel ($\chi^2 = 27.49$, df = 6, $P < 0.001$) and Mad River ($\chi^2 = 14.14$, df = 6, $P = 0.028$). The 1991 abundance estimates for Klamath (48.91 ± 3.65 [±SE]) and Korbel (117.24 ± 6.62) were significantly lower than their mean estimates for the other years, 1992–97 (Klamath: $\bar{x} = 63.09 \pm 1.23$; $\chi^2 = 13.56$, df = 1, $P < 0.001$; and Korbel: $\bar{x} = 140.81 \pm 2.69$; $\chi^2 = 10.88$, df = 1, $P = 0.001$). The Mad River abundance estimate for 1994 (78.50 ± 4.67) was significantly different from the mean estimate for the other years ($\bar{x} = 62.82 \pm 2.00$; $\chi^2 = 9.52$, df = 1, $P = 0.002$). Bonferroni adjustments of the alpha level prevented identifying additional significant differences.

Table 4. Jolly-Seber estimates of capture probabilities (*P*), apparent survival probabilities (ϕ) and percent coefficient of variation (CV) for mean abundance estimates of Northern Spotted Owls for three subregions of the Simpson Timber Company study area in northern California, 1991–97.

SUBREGION	*P*	SE (*P*)	ϕ	SE (ϕ)	CV (%)
Klamath	0.78	0.03	0.87	0.02	6.7
Korbel	0.84	0.01	0.88	0.01	3.1
Mad River	0.82	0.02	0.85	0.02	5.6

Empirical and J-S estimates of abundance showed similar general trends for all subregions, but there were some differences in individual estimates among some years. The confidence intervals for J-S estimates did not overlap empirical estimates of the abundance during 1992–94, 1993–96 and 1995 for Klamath, Korbel and Mad River, respectively (Fig. 2). The mean empirical and J-S estimates of abundance (Table 5) differed for Korbel ($\chi^2 = 6.805$, df = 1, $P = 0.009$), but were not significantly different for Klamath ($\chi^2 = 0.623$, df = 1, $P = 0.430$) or Mad River ($\chi^2 = 0.792$, df = 1, $P = 0.373$).

Mean J-S crude densities were highest for Korbel followed by Mad River and Klamath (Table 5) with an overall mean of 0.209 owls/km^2 (95% C.I. = 0.190–0.228). Ecological densities followed the same trend as crude densities (Fig. 2) but calculated values were higher (Table 5). Comparisons of mean crude and ecological densities indicated that the three subregions were significantly different for both variables ($\chi^2 = 2038.098$, df = 2, $P < 0.001$ and $\chi^2 = 1249.670$, df = 2, $P < 0.001$ for the crude and ecological comparisons, respectively). *Post hoc* comparisons showed crude and ecological density estimates for all subregions to be different from each other (Table 5, ecological densities: Korbel vs. Klamath; $\chi^2 = 4871.43$, df = 1, $P < 0.001$; Korbel vs. Mad River; $\chi^2 = 38.35$, df = 1, $P < 0.001$; Klamath vs. Mad River; $\chi^2 = 1679.44$, df = 1, $P <$

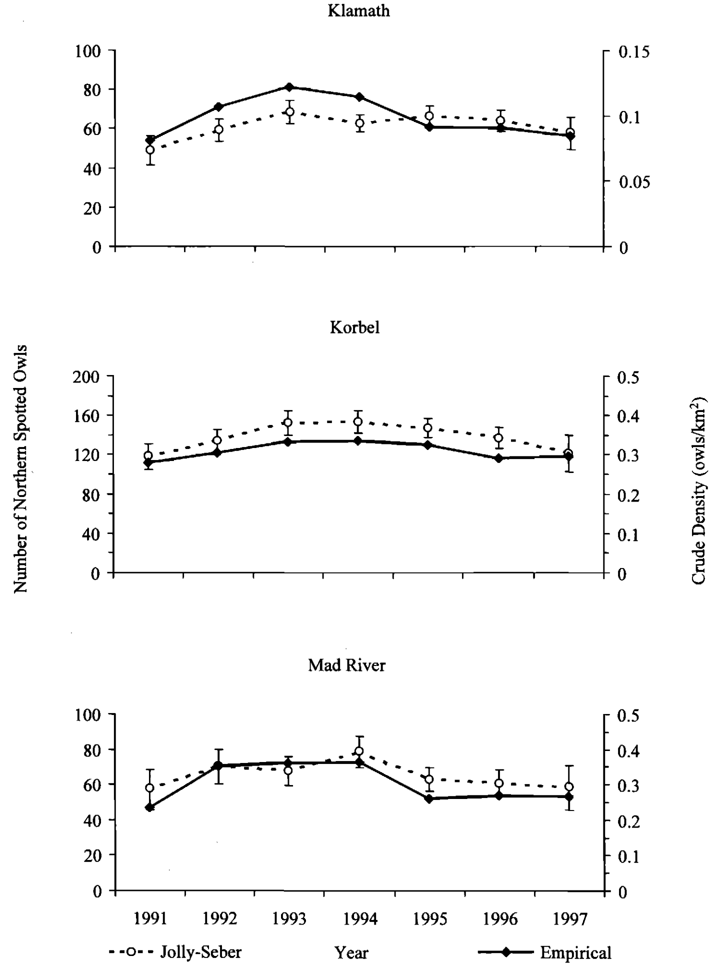

Figure 2. Number and crude density of Northern Spotted Owls on Simpson Timber Company study area subregions, northwest California. Spotted Owls were counted using mark-recapture (Jolly-Seber) and empirical methods. Bars represent 95% confidence intervals for Jolly-Seber estimates.

0.001; crude densities: Korbel vs. Klamath; χ^2 = 3084.67, df = 1, $P < 0.001$; Korbel vs. Mad River; χ^2 = 1176, df = 1, $P < 0.001$; Klamath vs. Mad River; χ^2 = 309.18, df = 1, $P < 0.001$).

DISCUSSION

Others have reported that Northern Spotted Owl roost and nest sites (territory centers) tend to be located in the lower portions of drainages (Blakesley et al. 1992, Folliard 1993, Hershey et al. 1998, Lahaye and Gutiérrez 1999). In our study, many owl territories were associated with major river systems and large blocks of land without any owl territories were typically associated with major ridgelines or extensive areas of nonhabitat. In the Klamath and Korbel subregions, nonhabitat usually consisted of large forested areas which were too young (generally <40 yr) to support roosting or nesting, while in Mad River, extensive areas of coastal oak woodlands (Holland 1988) were considered nonhabitat.

Our smallest subregion (Mad River at 208 km²) far exceeded the minimum area of 90–130 km² estimated by Franklin et al. (1990) as necessary to provide an unbiased estimate of Northern Spotted Owl densities. However, the convoluted nature of the boundaries for this subregion may have created an edge effect that positively biased density es-

Table 5. Mean empirical and Jolly-Seber (J-S) estimates of Northern Spotted Owl abundance along with estimated crude and ecological densities for three study area subregions of the Simpson Timber Company study area in northern California, 1991–97.

	ABUNDANCE ESTIMATES				DENSITY ESTIMATES (OWLS/km^2)			
	EMPIRICAL		J-S		CRUDE[a]		ECOLOGICAL[b]	
SUBREGION	$\bar{x}$	±SE	$\bar{x}$	±SE	$\bar{x}$	±SE	$\bar{x}$	±SE
Klamath	65.6A[c]	3.95	61.1A	4.12	0.092A[d]	0	0.373A	0.015
Korbel	123.3A	3.36	137.4B	4.26	0.351B	0.014	1.049B	0.041
Mad River	60.1A	4.17	65.1A	3.63	0.313C	0.014	0.581C	0.026

[a] J-S estimates used as the dividend to calculate number of owls/total area (Odum 1971).

[b] J-S estimates used as the dividend to calculate number of owls/area of habitat (Odum 1971).

[c] Means within rows and within abundance estimates followed by the same letter do not differ ($P > 0.05$).

[d] Means within columns and within density estimates followed by the same letter do not differ ($P > 0.05$).

timates. The other subregions (Klamath at 666 km^2 and Korbel at 392 km^2) were large enough that edge effects should not have been a factor.

This study was patterned after the Northern Spotted Owl density study by Franklin et al. (1990) in the Willow Creek study area (WCSA) immediately to the east of the Mad River subregion. They concluded that, because of the high capture and survival probabilities and the corroborative evidence provided by the empirical estimates, the J-S model provided both an accurate and precise estimate of Northern Spotted Owl density. We also found close agreement between the J-S and empirical estimates, indicating that our estimates were also accurate. The empirical estimate did significantly underestimate density relative to J-S for the Korbel subregion, but the magnitude of the difference was only 10.3%. The mean capture probability in our study area ($\bar{x} = 0.81 \pm 0.02$) was lower than that observed in the WCSA (J-S model D, $\bar{x} = 0.91 \pm 0.30$; Franklin et al. 1990), but comparisons using program CONTRAST showed no statistical differences between the two study areas ($\chi^2 = 0.103$, df = 1, $P = 0.748$). Comparison of mean survival probabilities between the WCSA ($\bar{x} = 0.89 \pm 0.02$; Franklin et al. 1990) and our study area ($\bar{x} = 0.87 \pm 0.01$) also showed no difference ($\chi^2 = 1.197$, df = 1, $P = 0.274$).

The apparent increasing abundance trend over the first few years in all subregions was most likely related to increased cumulative sampling effort and not a real increase in abundance. Despite our attempt to survey the entire study area each year, some resident owls apparently were not located until the second or even third year of the study. This conclusion was based on the observation that many of these newly discovered owls were adult breeding pairs. If the newly discovered sites had resulted from new birds that colonized sites subsequent to the start of the study, they would most likely have been nonbreeding subadult owls. Other owls were missed in areas not surveyed in the early years of the study because they were assumed to be nonhabitat but were subsequently found to contain owls.

Similar to findings reported by Franklin et al. (1990), we noted a close agreement between J-S and empirical estimates. Mean absolute differences between J-S and empirical abundance estimates were only 10.3, 7.6 and 7.4% for Korbel, Mad River and Klamath, respectively. The results of both studies could be interpreted to indicate that reliable estimates of abundance (density) can be obtained through empirical estimates without the effort and cost associated with marking and recapturing birds to obtain J-S estimates. However, we believe that if a large portion of the population is unmarked, empirical estimates would likely vary substantially due to the high potential for "double counting" individuals in some situations and discounting new birds in other circumstances. In addition, meaningful comparisons among years or study areas would be problematic because empirical estimates do not account for differences in detectability or sampling variation.

Our crude density estimates for the three subregions (Klamath—0.092 owls/km^2; Korbel—0.351 owls/km^2; and Mad River—0.313 owls/km^2) span the reported ranges of population density for both the Northern Spotted Owl and the California Spotted Owl (*S. o. occidentalis*). Marcot and Gardetto (1980) reported the equivalent of approximately

0.325 owls/km^2 in the Six Rivers National Forest which is similar to our estimates for Korbel and Mad River. However, as noted by Franklin et al. (1990), their estimate was based on empirical counts from night surveys without marking birds, and their largest study area was only 58.2 km^2. Both of these factors would likely positively bias their estimates making comparisons to this study problematic. The lower population density in Klamath is similar to many of the reported densities of California Spotted Owls in the Sierra and San Bernadino Mountains (Roberts 1993, Moen and Gutiérrez 1993, Lahaye and Gutiérrez 1994). Franklin et al. (1990) provided the most rigorous estimate reported for the population density of Northern Spotted Owls. They estimated a density of 0.235 owls/km^2 for the 292 km^2 WCSA, which was intermediate in study area size between the Korbel and Mad River subregions of our study. Their estimate was similar to our combined estimate (0.209 owls/km^2), but less than either Korbel or Mad River, which were located in closest proximity to the WCSA. Tanner and Gutiérrez (1995) estimated 0.219 owls/km^2 for a 137.7 km^2 study area in Redwood National Park, which was the only previous estimate of density for Northern Spotted Owls in the coastal redwood region. This was an empirical estimate based on two years of surveys, but most owls were marked, thus the estimate was likely accurate.

Without other density studies in the coastal redwood region of Northern California, it is difficult to know the extent to which this study is representative of the region. However, we believe the pattern of density we observed was reflective of the region in general. This was based on a qualitative assessment we conducted using the 1996 California Natural Diversity Database (G. Gould, California Department of Fish and Game, unpubl. data) of reported Northern Spotted Owl locations across the entire range of the subspecies in California and on unpublished data from an adjacent large industrial land owner (S. Chinnici, Pacific Lumber Company, pers. comm.).

There was a significant difference in the amount of forested habitat in specific age classes among the three subregions. We could only speculate on how this might have influenced owl density since the study was not designed to assess this. Although some young stands (20–40 yr) in the STC study area were associated with high Northern Spotted Owl fecundity and low turnover rates, forests <40 yr old were not selected in proportion to their availability by owls for nesting (Thome et al. 1999). Thus, high proportions of stands <40 yr old might limit owl density. Klamath had significantly lower densities of owls than the other subregions along with the highest proportion of the landscape in younger stands (83.7% <40 yr old). Klamath also tended to have extensive areas of homogeneous younger age classes, although we have not quantified this difference. In comparison, Korbel had high densities of owls, with 64.3% of forest stands <40 yr old. Based on extensive harvesting in the last 10–15 yr with relatively small clearcuts (10–24 ha), Korbel tended to have a much more heterogeneous mixture of stand ages relative to Klamath. In the same study area, Folliard (1993) noted that landscapes supporting Northern Spotted Owls had more edge and greater stand diversity than randomly selected landscapes. Finally, like Korbel, Mad River had high densities of owls, but only 28.7% of stands were <40 yr old. We had no data to establish a direct cause and effect relationship between habitat variables and the density of owls in the different subregions and comparing density to habitat variables was not the primary objective of this study. However, as noted by Thome et al. (1999), a combination of different age classes (older stands for nesting and younger stands for foraging) may provide the best habitat for Northern Spotted Owls in our region.

By definition, ecological densities are equal to or greater than crude densities, and one can predict that the magnitude of the difference will increase as the proportion of habitat for a given species decreases on the landscape. Ecological densities were 4.05, 2.99 and 1.86 times higher than crude densities for Klamath, Korbel and Mad River, respectively, which supported the predicted differences based on the relative amounts of habitat in each region. In comparison, Franklin et al. (1990) reported ecological densities that were 2.81 and 2.31 times higher than crude densities depending upon the approach used for defining owl habitat.

It is difficult to make meaningful comparisons of ecological densities among studies in different areas unless the same criteria are used to calculate ecological densities. Using mature/old-growth forests to represent owl habitat, Franklin et al. (1990) reported an ecological density of 0.660 owls/km^2 in the WCSA. Their estimate of ecological density was greater than our estimate for the Klamath region (0.373 owls/km^2), less than Korbel (1.049

owls/km^2) but quite similar to Mad River (0.581 owls/km^2). In addition to being closest in proximity to the WCSA, Mad River also had the highest proportion of mature stands (36.9% >80 yr in age, although it lacked old growth habitat) compared to 35.6% mature/old growth in the WCSA.

There is some question as to the extent comparisons of Northern Spotted Owl densities, either within or between study areas, can be used for developing management prescriptions. As noted by Van Horne (1983), population density of a species can be a misleading indicator of habitat quality. Although some of the attributes of Northern Spotted Owl populations do not meet the criteria for habitat quality-density decoupling, a prediction consistent with decoupling habitat quality and density is that high owl densities on selected managed lands result from displacement of owls from adjacent harvested areas. However, we believe this was unlikely because the densities in our study area appeared to be relatively stable throughout a time period when, due to its federally-listed status (USDI 1992), significant habitat alteration of Northern Spotted Owl habitat was not permitted on adjacent private lands. In addition, there was a 90–95% reduction in annual timber harvest on adjacent public land (Six Rivers National Forest) just prior to and after the listing of the Northern Spotted Owl (USDA 1995). Finally, we have observed that the highest reproduction tends to be associated with areas of highest densities (L. Diller, unpubl. data), but it was beyond the scope of this study to quantify the relationship between reproduction and density.

Although it was unlikely that the densities of owls in our study area were influenced by displacement from adjacent areas, we could not assess habitat quality in our study area based on density of owls. First and foremost, we could not establish causal relationships between the observed differences in density and corresponding differences in habitat attributes without undertaking an experimental approach over large areas. Correlative studies to elucidate patterns between habitat attributes and density were not possible when only a few subregions were available for comparison. In addition, we could only estimate the density of the territorial population of owls, and true density, which would include nonterritorial floaters, was unknown. Given the difficulty of undertaking experiments with a protected species over large areas, we believe that more immediate insight can be gained concerning habitat quality by relating demographic parameters to habitat attributes in a manner described in Thome et al. (1999). Ultimately, knowing population density is of limited immediate benefit for developing conservation strategies for Northern Spotted Owls without knowing the habitat attributes that result in demographic parameters that will sustain populations over time. However, establishing reliable estimates of population densities for Northern Spotted Owls should provide valuable baseline data for assessing long-term trends in their populations. Similar studies should be conducted in selected areas throughout the range of the Northern Spotted Owl to allow future assessment of the long-term response of this species to current management strategies now being implemented.

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