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CHANGES IN THE DISTRIBUTION AND ABUNDANCE OF SPOTTED OWLS DURING THE PAST CENTURY

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Abstract. The Spotted Owl (*Strix occidentalis*) occurs from southwestern British Columbia, Canada south to Michoacán, México. Approximately 12,127 Spotted Owls are known to exist in the United States. Throughout its entire range one can infer that the species has declined over the past century due to a rapid decline in its habitat, mature and old growth conifer forests. Most habitat loss is due to logging of original forests, but other factors (e.g., urbanization) also have contributed. The inference of decline is supported by observed gaps in the owl's original geographic distribution, trends in habitat loss, declining demographic trends, and differences in owl densities among and between populations. Where owls are found in previously logged forests, those forests almost always contain residual elements of the original forests.

Key Words: *Strix occidentalis*; Spotted Owl; distribution; abundance.

The Spotted Owl (*Strix occidentalis*) is distributed from southern British Columbia, Canada south through the Pacific coast states and the southwestern United States to the highlands of central México (Dunbar et al. 1991; USDI 1992a, 1993; Verner et al. 1992) Because of past decline and expected future decline in habitat, primary (mature and older) forests, both Northern and Mexican Spotted Owls (*S. occidentalis caurina* and *S. occidentalis lucida,* respectively) have been declared threatened subspecies in the United States (USDI 1990, 1993).

In this paper I examine changes in Spotted Owl populations and their habitat north of Mexico during the past century. Since historic surveys are not available, I will use information on current owl distribution, changes in habitat or habitat characteristics, and population trends based on intensive demographic studies to infer how populations have been affected.

METHODS

DISTRIBUTION AND ABUNDANCE

Distribution and abundance of Northern Spotted Owls were estimated using a Geographic Information System (GIS) established by the Northern Spotted Owl recovery team (USDI 1992a). The data supporting the GIS were derived from extensive owl surveys conducted by the U.S. Forest Service, Bureau of Land Management, National Park Service, California Department of Fish and Game (CDFG), university researchers, and private timber companies. Although these surveys were not exhaustive they can be used to infer relative differences in distribution and abundance of Northern Spotted Owls within geographic provinces of the Pacific Northwest.

Distribution and abundance of California (*S. o. occidentalis*) and Mexican Spotted Owls were taken from databases maintained by the CDFG (G. Gould, Jr., pers. comm.) and Region 3 (i.e., southwestern United States) of the U.S. Forest Service (K. Fletcher, pers. comm.). The proportion of pairs and of single owls at sites (a location where an owl was detected at least once) in the Sierra Nevada and southwestern United States (Arizona and New Mexico) were estimated from average territory occupancy by pairs and individuals measured at thoroughly surveyed sites.

CHANGES IN HABITAT

Three sources of information were used to assess changes in habitat: 1) U.S. government forest inventory data (loss of habitat characteristics associated with areas of owl use was used to infer changes in owl distribution and abundance); 2) egg records (Western Foundation of Vertebrate Zoology); and 3) distribution of owls within hous-

TABLE 1. DISTRIBUTION AND ABUNDANCE OF NORTHERN SPOTTED OWLS AND THEIR HABITAT IN THE UNITED STATES

Area	Acreage			Number of owls		Federal lands[2]	
	Federal	Nonfederal	Total	Pairs[1]	Singles[1]	Potential habitat	Suitable habitat
CA Cascades	1,042,800	1,449,100	2,491,900	40	23	696,100	73,500
CA Coast	467,700	5,214,400	5,682,100	482	112	279,800	14,200
CA Klamath	4,518,600	1,568,200	6,086,800	589	246	2,316,700	1,075,600
Eastern OR Cascades	1,512,500	710,500	2,223,000	181	39	964,600	410,400
Western OR Cascades	4,532,200	2,149,300	6,681,500	1,081	308	3,177,000	2,113,800
OR Coast	1,385,000	4,408,600	5,793,600	303	77	1,338,000	478,200
OR Klamath	2,120,000	1,893,600	4,013,600	402	74	1,591,400	839,900
Willamette Valley	13,900	2,628,300	2,642,200	4	0	13,900	3,600
Eastern WA Cascades	3,405,200	2,203,600	5,608,800	218	12	1,114,900	697,300
Western WA Cascades	3,762,100	2,445,700	6,207,800	290	45	1,435,500	1,403,400
Olympic Peninsula	1,530,300	1,500,200	3,030,500	157	40	449,400	507,700
Western WA Lowlands	86,000	6,394,900	6,480,900	6	4	65,900	0
Total	24,376,300	32,566,400	56,942,700	3,753	980	13,443,200	7,608,800

[1] Northern Spotted Owls verified between 1986–1991 (1992 data used for State of Oregon, California, Crater Lake National Park lands, and Western Washington Lowlands).
[2] Suitable habitat = current habitat potentially used by nesting, roosting, or foraging owls; potential habitat = land that would be capable of producing suitable habitat if trees were allowed to grow to old age (this habitat is currently unsuitable due to logging and other impacts).

ing developments. Sources two and three were used to infer the effects of urbanization on owls.

DEMOGRAPHY

Throughout the range of each subspecies current trends in population dynamics and density of owls have been estimated from data gathered during long-term studies (Gutiérrez and Pritchard 1990, Anderson and Burnham 1992, Noon et al. 1992, Gutiérrez et al. 1993, LaHaye et al. 1992). Age specific estimates of survival and fecundity as well as density estimates have been derived from thousands of observations of color-banded birds. These studies all followed the design outlined in Franklin et al. (1990). Herein, demographic information is used to exemplify recent changes in Spotted Owl populations across its range.

RESULTS

DISTRIBUTION AND ABUNDANCE

The exact numerical decline of Spotted Owls cannot be calculated because the relationship between habitat loss (and habitat fragmentation) and owl desertion or death is unknown. However, it is apparent that dramatic declines in owl populations have occurred throughout the Pacific Northwest due to habitat loss (Table 1). The majority (56%; 4772 individual birds) of the known Northern Spotted Owl population occurs within only 29% of its range (Table 1, Fig. 1). Spotted Owls also have declined during the past century in British Columbia, Canada primarily as a result of extensive logging and perhaps because of the invasion of Barred Owls (*Strix varia*; Dunbar et al. 1991).

Variation in observed number of owls among geographic provinces can be attributed to differences in completeness of surveys, demographic trends, natural variation in habitat distribution and quality, human caused habitat loss (e.g., logging, water development, urbanization), and natural environmental changes (e.g., fire, volcanic eruptions). However, logging has caused the greatest decline in habitat for all three subspecies (USDI 1992a, 1993; Verner et al. 1992). Declines in primary forest range from 51–100% on federal lands in the Pacific Northwest (Table 1). On private land, primary forest has declined by 95–100% (Table 1, USDI 1992a). The most striking examples have occurred in the Western Washington Lowlands and Oregon Coast Range

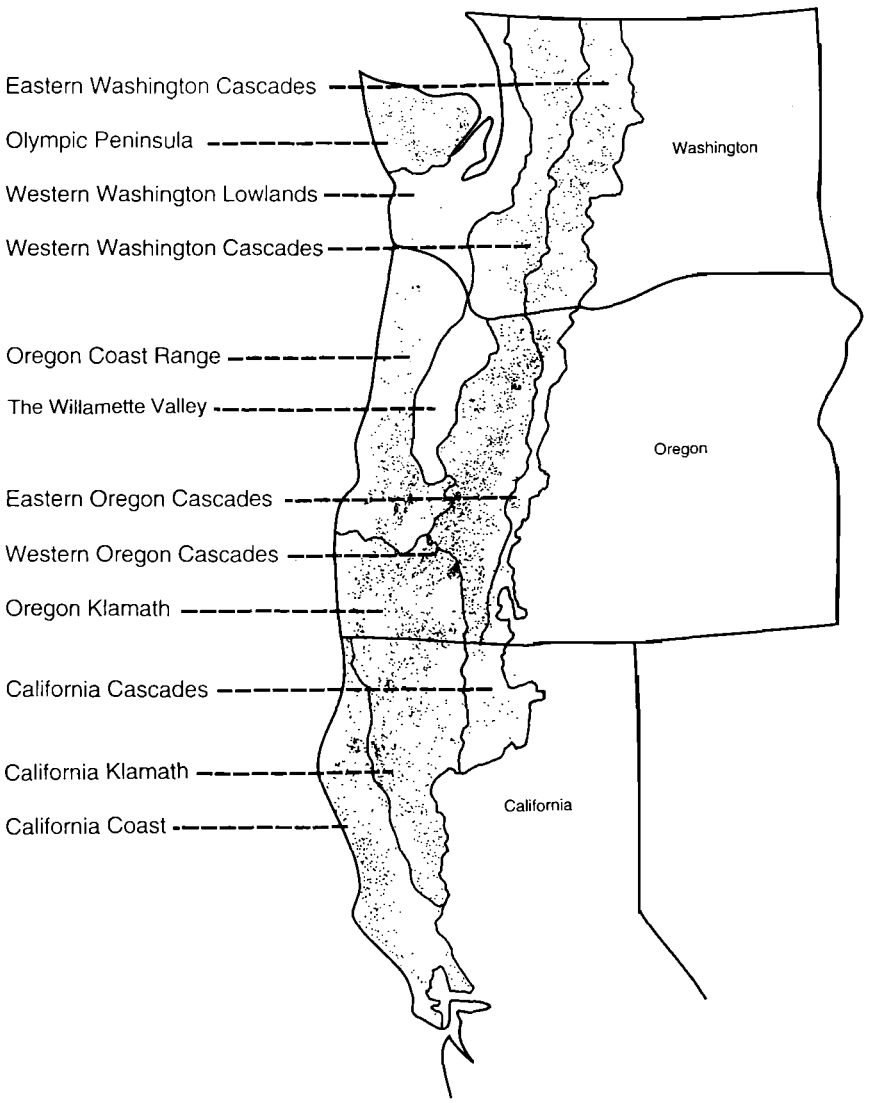

FIGURE 1. Distribution of Northern Spotted Owls by geographic province in the United States. Each dot represents the location of pairs or single owls reported in Table 1.

provinces (Table 1, Fig. 1, USDI 1992a). Only six pairs and four single owls could be found in 1992 on what was once approximately 2,400,000 ha of primary forest in the Western Washington Lowlands Province.

In the Sierra Nevada of California, Spotted Owls are widely distributed on public land, but apparently are not as numerous on private land. There are a minimum of 2452 (1008 pairs and 436 single) owls known to occur in the Sierra Nevada as of 1992 with approximately 5% occurring on private land (CDFG data base).

In southern California, Spotted Owls are distributed as an archipelago of isolated populations (LaHaye et al. 1994). Approximately 598 individuals are known in 15 populations ranging from 3–270 individuals (CDFG data base; see also LaHaye et al. 1994). Loss of habitat and early resource exploitation in southern California is sim-

ilar to that of the Sierra Nevada, although not as intensive (McKelvey and Johnston 1992).

Of particular interest is the apparent absence of Spotted Owls from the Santa Cruz Mountains and forests north of Monterey Bay, California. Spotted Owls currently occur in both conifer and hardwood forests within the Santa Lucia Range, south of Monterey Bay. Their absence to the north could be a historic anomaly, a natural extinction event, or a result of the almost complete logging of primary conifer forests in the Santa Cruz Mountains. If logging is responsible owls may recolonize the Santa Cruz Mountains as forests mature.

The Mexican Spotted Owl, the least known of the subspecies, is found throughout forested canyons and conifer regions of the southwest and is known from 725 sites (Fletcher, pers. comm.). I estimated that 579 of these sites would be occupied by pairs and 117 by single owls, based on data from New Mexico and Arizona (Gutiérrez et al. 1993). Most locations are from mixed conifer and pine-oak zones of Arizona and New Mexico with <20% of locations from canyons and riparian forests (Fletcher, pers. comm.).

Trends in Habitat Loss

Impacts of logging

Rapid loss of primary forests has occurred since 1960 on public land in the Pacific Northwest (USDI 1990, Table 1). By 1992, suitable habitat remaining on public lands ranged from 0–46% (Table 1). Clearcutting has led not only to habitat loss but also to a high degree of forest fragmentation (Harris 1984). Fragmentation has been shown to be detrimental to Spotted Owls (Bart and Forsman 1992, Carey et al. 1992, Johnson 1992).

McKelvey and Johnston (1992) traced historic trends in forest conditions in the Sierra Nevada which were different than the Pacific Northwest. Sierran forests, although strongly influenced by fire, were a mosaic of stands with different structure (i.e., open to dense). Areas with diverse forest structure probably formed the core of Spotted Owl habitat in presettlement days.

In the Sierra Nevada it is possible that Spotted Owls could have undergone as many as three periods of decline resulting from the activities of Europeans. First, extensive and intensive livestock grazing in conjunction with human-set fires during the 1800s (McKelvey and Johnston 1992) may have removed much of the habitat for some major owl prey species (e.g., *Neotoma fuscipes*). Next, in the 1870s logging removed many of the basic elements of owl habitat over large areas, potentially rendering them temporarily unsuitable. However, with wildfire control and prevention, ingrowth of conifers and hardwood trees was prevalent both in relict old stands and residual stands (McKelvey and Johnston 1992). This process resulted in the present forest structure that is used by owls (i.e., stands dominated by large, old trees with an uneven diameter distribution of smaller trees forming secondary canopy layers, Verner et al. 1992). Thus, regrowth of the secondary forest beneath the original or remnant stands probably resulted in a recolonization of disturbed areas of the Sierra Nevada. The current trend in removal of key habitat elements (see below) during logging may precipitate another decline in the Sierran owl population (Bias and Gutiérrez 1992, McKelvey and Weatherspoon 1992, Verner et al. 1992).

Many key elements (e.g., nest trees, coarse woody debris) associated with Spotted Owl habitat in the Sierra Nevada were remnants of original forests (Verner et al. 1992). Because of lower intensity logging in the Sierra, these key habitat elements were still widely distributed in 1992 (Verner et al. 1992). However, their removal had dramatic effects on nesting owls in some areas. For example, "sanitation" logging, which removes old trees that often are used as nest sites apparently caused abandonment of an area (e.g., Bias and Gutiérrez 1992). This area was a patchwork of alternating public

(60%) and private (40%) land. Since 1986 20 nests representing 20 different pairs have been found on public land (Gutiérrez et al., unpubl. data) and none on private land where "sanitation" logging was practiced. The probability that none of the nests would be found on private land was extremely low ($P = 0.6^{20} = 0.00004$).

Mexican Spotted Owls primarily use three kinds of habitat: montane conifer (over 80% of the owls are found in this habitat, USDI 1993), riparian, and steep, rocky canyons. Between 6–36% of the owl's conifer habitat has been lost on national forests in Arizona and New Mexico because of logging and other events such as wildfire (Fletcher, pers. comm.). Riparian habitat also has decreased substantially since Bendire (1882) first collected a nesting owl in this habitat type. Canyon habitats probably have not changed as extensively as conifer and riparian habitats.

Two additional sources of information gathered from field studies indicated owl populations have declined in the southwest. First the difference in density between study populations in Arizona and New Mexico (0.106 and 0.172 owls/km^2, respectively; Gutiérrez et al. 1993) may have been the result of more intensive tree cutting in Arizona. Second, within the New Mexico study area, two adjacent canyons of similar size were censused repeatedly and equally during 1991 and 1992; one contained six pairs and one single owl while the other contained three pairs of owls. Approximately half of the canyon with the lower density had been logged in the recent past.

Declines due to urbanization and other factors

Although rarely considered a major impact, urbanization and agriculture have had a significant effect on the distribution and abundance of Spotted Owls. Urban expansion and agricultural development have claimed at least 224,000 and 392,000 ha, respectively, of formerly suitable habitat from south Tacoma to Everett, Washington since the turn of the century (D. Hays, pers. comm.). No resident owls have been reported in this area in the past decade (D. Hays, pers. comm.). In the San Bernardino Mountains of southern California 6700 ha of dispersed housing (houses and developments scattered throughout otherwise suitable owl habitat) have been surveyed for owls since 1987 (LaHaye and Gutiérrez, unpubl. data). Although the area surrounding the developed forest contained dense and productive owl populations, residential areas did not contain owls. Further, egg and nest records from southern California between 1900 and 1930 indicated Spotted Owls were nesting in relatively low elevation evergreen/riparian forests within canyons. Most of these habitats have been eliminated by urban expansion.

Dispersed housing and suburban development is increasing rapidly in the Sierra Nevada, southern California, and in some areas of the southwest (McKelvey and Weatherspoon 1992). The mid-elevation counties in the Sierra Nevada are among the fastest growing in California (McKelvey and Weatherspoon 1992). Although current impacts are unknown, this development probably is affecting the distribution and abundance of Spotted Owls.

Owls in previously logged forests

Spotted Owls may occur in forests that have been previously logged (Forsman et al. 1977, Forsman 1988), primarily on private lands within the California coast province (Table 1, USDI 1992a). The fact that Spotted Owls occur in forests other than in primary forests has been used as evidence that owls are either adaptable or compatible with timber harvesting (e.g., USDI 1992b). Since they have been observed in a variety of habitats throughout their range (e.g., Forsman et al. 1984, Carey et al. 1992, Verner et al. 1992, USDI 1993), occupation of some previously logged forests does not conflict with the general inference that Spotted Owls are declining where even-aged forest management occurs.

In almost all cases in which Spotted Owls occur in forests with prior logging, these sites contain remnants from the original forests. These forests are heterogeneous in structure and often contain elements similar to natural, unlogged forests (Bart and Earnst 1992). In addition, coastal redwood (*Sequoia sempervirens*) forests can achieve tree size typical of Spotted Owl habitat within 80 years following logging. When these forests also contain an understory of tanoak (*Lithocarpus densiflorus*), they are frequently used. Nevertheless, the ability of these forests to sustain owl populations is unknown.

In assessing possible changes over the past century in previously logged forests, I judge (from early photographs [see McKelvey and Johnston 1992 for examples of Sierra Nevada logging]) that partial logging probably resulted in temporary displacement of Spotted Owls. In order to predict future changes in Spotted Owl populations in recently recolonized areas scientists need to know if future harvest patterns and methods will perpetuate conditions that currently attract owls. If owls are found only in heterogeneous or uneven-aged forests, then clearcutting (a primary method of harvest on private and public land), which results in even-age forests, probably will lead to their extirpation.

Demographic trends

Spotted Owl densities vary from 0.105–0.273 owls/km^2 across the species range (USDI 1992a, Noon et al. 1992, Gutiérrez et al. 1993). The finite rate of annual population change (λ) derived from estimates of fecundity and survival from territorial populations throughout the Pacific Northwest show that all study populations are declining at annual rates of 6–12% (Anderson and Burnham 1992). Forsman et al. (1984) estimated an empirical rate of decline of approximately 1.1% per year based on observations of territorial birds. Forsman et al. (1987:54) also reported a decline in one population of 18–29% over a 10-year period, presumably due to logging. Differences between empirical and projected rates of decline could be accounted for by bias in the estimates of the vital rates used to calculate λ and/or to the stabilizing effect of floaters on the territorial population (Franklin 1992). Anderson and Burnham (1992) also reported that the rate of decline was accelerating over the period each population was studied. This was related to an increasing rate of adult female mortality, suggesting a changing source of bias if one existed or an accelerating response to continued disturbance. Noon and Biles (1990) demonstrated that adult female survival was the most important parameter affecting estimates of λ for Northern Spotted Owls.

Of the two Spotted Owl populations studied in the Sierra Nevada neither could be demonstrated to be declining (Noon et al. 1992). However, two other populations were declining in southern California. LaHaye et al. (1992) projected an annual decline of 14% in the San Bernardino Mountains, while I (unpubl.) estimated an empirical decline of 16% on Mount San Jacinto. Empirical changes in the San Bernardino population did not show the same rate of decline predicted by estimates of λ (e.g., LaHaye et al. 1992). However, changes in numbers of territorial birds may be buffered by the presence of floaters (nonterritorial birds; see Franklin 1992).

DISCUSSION

Spotted Owl Populations: The Next Century

Documenting the decline of a species is an odious task for an ecologist. However, in the case of the Spotted Owl, there is hope that its populations can be stabilized and will recover in the next century. Both the Northern and Mexican races are listed as threatened, not only because of their current and past population trends but also because of projected declining trends in their habitat (USDI 1990, 1992a, 1993). In fact, the habitat of all three subspecies is expected to decline substantially under projected U.S.

Forest Service (the primary steward of Spotted Owl habitat) harvest scenarios (USDI 1990, 1993; McKelvey and Weatherspoon 1992). However, conservation plans have been developed to arrest the decline of the Northern and Californian races and their habitat (Thomas et al. 1990, USDI 1992a, Verner et al. 1992), and one plan is being developed for the Mexican Spotted Owl. Their implementation is essential for the owl, species that share its habitat, and stable local economies. Because these are only plans formulated on the best available information, they should be considered "conservation hypotheses." Their test, through monitoring population trends, will be stabilization and recovery of Spotted Owl populations.

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