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THE NORTHERN AND CALIFORNIA SPOTTED OWLS:  
IMPLICATIONS FOR CONSERVATION**

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## COMMENTARY

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### REDEFINING THE DISTRIBUTIONAL BOUNDARIES OF THE NORTHERN AND CALIFORNIA SPOTTED OWLS: IMPLICATIONS FOR CONSERVATION.

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**Abstract.** The Northern Spotted Owl (*Strix occidentalis caurina*) is listed as a threatened species. However, the range description given at the time of listing is inconsistent with the range delineation given by the American Ornithologists' Union checklist of North American birds. Despite the quandary that this inconsistency represents regarding the area of protection afforded the Northern Spotted Owl, the range used in listing is consistent with the actual range suggested by mtDNA haplotypes diagnostic for the subspecies. The range description used in the listing decision of the Northern Spotted Owl and in many conservation plans have been repeated through time without a formal revision or basis for support. Based on current knowledge of Spotted Owl locations we revise the range limits for both Northern and California (*S. o. occidentalis*) Spotted Owls.

**Key words:** *California Spotted Owl, distribution, Northern Spotted Owl, Strix occidentalis caurina, Strix occidentalis occidentalis.*

#### Redefinición de los Límites de las Distribuciones de *Strix occidentalis caurina* y *S. o. occidentalis*: Implicaciones para Conservación

**Resumen.** La lechuza *Strix occidentalis caurina* se considera amenazada. Sin embargo, la descripción de su rango de distribución hecha al momento en que fue incluida en la lista de especies amenazadas es inconsistente con la delimitación de su rango hecha por la lista de chequeo de aves de Norte América de la American Ornithologists' Union. A pesar de la incertidumbre que esta inconsistencia representa con respecto al área de protección con que cuenta *S. o. caurina*, el rango empleado al incluirla en la lista es consistente con el rango real sugerido por haplotipos de ADN mitocondrial diagnósticos para esta subespecie. La descripción del rango de distribución empleada para tomar

la decisión de incluir a *S. o. caurina* en la lista de aves amenazadas y para muchos planes de conservación ha sido repetida a través del tiempo sin una revisión formal fundamentada. Con base en el conocimiento actual, en este estudio revisamos los límites de los rangos de *S. o. caurina* y de la subespecie de California, *S. o. occidentalis*.

The Northern Spotted Owl (*Strix occidentalis caurina*) is one of the most studied birds in the world because conservation of its habitat has enormous economic ramifications (Simberloff 1987, Gutiérrez et al. 1995). Indeed, virtually every conservation decision or major scientific finding that affects the owl's conservation has been controversial (Meslow 1993, Gutiérrez et al. 1996). The potential economic effect of habitat conservation for this subspecies even delayed its listing as a threatened species (Thomas and Verner 1992). This controversy has motivated research into many aspects of its ecology (Barrowclough et al. 1999, Franklin and Gutiérrez 2002, Forsman et al. 2002). This proliferation of research, in return, has supported many comprehensive literature reviews, life history summaries, and conservation plans, most of which include a range description (Gutiérrez 1985, Dawson et al. 1987, Thomas et al. 1990, USDI 1990, 2003, Gutiérrez et al. 1995). In the course of our research on genetic relationships of Spotted Owls, we discovered an apparent discrepancy between the Northern Spotted Owl's recognized range description (AOU 1957) and the range description given for the subspecies when it was listed as threatened (USDI 1990). This apparent discrepancy has not been noted in any modern conservation plan or review, and illustrates both a specific issue regarding the extent of protection that should be provided to the Northern Spotted Owl, and a general issue regarding the value of using intraspecific designators (i.e., subspecies) for conservation purposes (Zink 2004).

Because of the extensive research and conservation planning for Spotted Owls, we now have a much better knowledge of the distribution and taxonomic affinities of Spotted Owls in California than we did at the time of the last AOU delineations of subspecies ranges (AOU 1957 [hereafter AOU]). Therefore, our objectives here are to assist the conservation of both the Northern Spotted Owl and California Spotted Owl (*S. o. occidentalis*) by clarifying their respective ranges in California, and to describe their general continental ranges. This is timely because the status of the Northern Spotted Owl is under review, and the status of the California Spotted Owl is currently in litigation.

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## HISTORICAL TAXONOMY AND THE NORTHERN SPOTTED OWL LISTING DECISION

*Recognized taxonomy and distribution of Spotted Owls in California.* The AOU (1957) currently recognizes three Spotted Owl subspecies, Northern, California, and Mexican (*S. o. lucida*) that were described by Xantus (1859), Merriam (1898), and Nelson (1903), respectively. Two of these, Northern and California Spotted Owls, occur in California. Subspecies descriptions are based on plumage (Gutiérrez et al. 1995). However, because there is much overlap in plumage characteristics between Northern and California Spotted Owls, Oberholser (1915) recommended merging those two taxa. The AOU nomenclature committee did not accept that recommendation (AOU 1931, 1957). Two additional Spotted Owl subspecies have been named, *Strix occidentalis huachucae* (Swarth 1910, 1915) and *S. o. juanaphillipsae* (Dickerman 1997), but affect only the distribution of the Mexican Spotted Owl. Mexican subspecies of the Spotted Owl will not be discussed further.

Grinnell and Miller's (1944) description of the distribution of Spotted Owls in California was the most recent, comprehensive treatment prior to the AOU checklist. They gave the eastern extent of the Northern Spotted Owl's range as western Siskiyou County west of the Sacramento River (inferred from range map and written description in Grinnell and Miller 1944). They gave the range of the California Spotted Owl as Tehama County south to Tulare County in the Sierra Nevada and Santa Barbara County south to San Diego County elsewhere in California. The abbreviated range description in the AOU checklist mirrors Grinnell and Miller's (1944) more extensive description. Since Alden Miller was on the AOU (1957) checklist committee, we surmise that the intent of the AOU range descriptions for the Spotted Owl in California was to follow closely Grinnell and Miller's (1944) range delineations. We are aware of no subsequent formal revision of this account. Hence, the generally accepted subspecies range for both these taxa follows the AOU (1957) description. It is also evident that the geographic area now perceived as the contact zone between the Northern and California Spotted Owl subspecies was not covered in these descriptions because Spotted Owls were not known to occur between Mt. Shasta and Mt. Lassen at the time of Grinnell and Miller (1944) and AOU (1957). Spotted Owls are now known to occur throughout this zone, as well as north of Santa Barbara County, California (Gould 1977, Gutiérrez 1994, California Fish and Game Spotted Owl database, 29 June 2004 version). Gould (1977) did not specifically allocate owls found at new localities to subspecies. Thus, the taxonomic status of birds in these areas was unknown. Further, since the Northern Spotted Owl was listed as an entire taxon (USDI 1990:26114), the conservation status of this subspecies outside the AOU range is ambiguous.

*Taxonomy and subspecies range limits associated with the listing decision.* The Northern Spotted Owl was both petitioned for listing and listed as threatened as an entire taxon under the provisions of the Endangered Species Act (USDI 1990). The range designation provided within this decision was "southwestern British

Columbia, through western Washington, western Oregon, and northern California south to San Francisco Bay. The southeastern boundary of its range, separating this subspecies from the California Spotted Owl, is the Pit River area of Shasta County, California" (USDI 1990:26115). Further, it was stated that "presumably the geographic separation between these two subspecies occurs within a 12- to 15-mile gap of forested habitat between southeastern Shasta and northwestern Lassen National Forests, where the Sierra Nevada contacts the Klamath physiographic province; the Pit River is generally accepted as the boundary between the two subspecies in California (USDA 1988; G. Gould, California Dept. of Fish and Game, Sacramento, CA, pers. comm.)" (USDI 1990:26114). However, references cited directly or proximally to these statements do not provide the explicit criteria for a revised delineation of the accepted range (USDA 1988, USDI 1989; G. Gould, pers. comm.). Rather, it appears as if the range boundaries cited above were logical constructs derived by wildlife biologists which were based on the density of owls and their presumed geographic continuity.

## REVISION OF SPOTTED OWL RANGES IN CALIFORNIA

*Preliminary assessment of current range limits for Spotted Owls in California.* Following Gould (1977) there have been hundreds of thousands of point surveys to locate individual Spotted Owls in California and elsewhere (USDI 1995, Gutiérrez 1994, Forsman et al. 1996, Franklin et al. 2004). In addition to location surveys, limited surveys of mtDNA and other genetic markers have been completed (Barrowclough and Gutiérrez 1990, Barrowclough et al. 1999, Haig et al. 2001). These surveys have recovered diagnosable mtDNA haplotypes for all three recognized subspecies (Barrowclough et al. 1999). Thus, it is possible to determine the historical maternal lineage of individuals within populations. Evidence of this evolutionary history allows delineation of the relative boundaries of the Northern and California Spotted Owls in California and, more importantly, a reconciliation of the 1990 listing decision with its attendant range description (i.e., the geographic area influenced by conservation of the listed subspecies).

Barrowclough et al. (1999) reported California Spotted Owl haplotypes within the recognized range of the Northern Spotted Owl. However, Barrowclough et al. (1999) did not find Northern Spotted Owl haplotypes in the few owls they sampled from the Mount Lassen region (the presumptive range of the California Spotted Owl, but north of the AOU range boundary for the California Spotted Owl subspecies).

Barrowclough et al. (1999, 2005) identified haplotypes of California Spotted Owls in 1 of 13 (8%) birds north, 1 of 30 (3%) west, and 0 of 3 birds east of Mount Shasta. In the course of sequencing additional Spotted Owl samples from areas outside the recognized AOU range of the Spotted Owl in California near Mount Lassen, we (Barrowclough et al. 2005) discovered that 2 of 11 (18%) birds in the same area sampled by Barrowclough et al. (1999) had Northern Spotted Owl haplotypes, but the remainder were Cal-

ifornia Spotted Owls. This sample included birds north of the AOU boundary for California Spotted Owls (Lassen and Shasta Counties). In addition to these observations, we detected a haplotype diagnostic for California Spotted Owls in Monterey County north of Santa Barbara County (Barrowclough et al. 2005).

These haplotypes, in conjunction with the increased owl survey data, allow modification of the Grinnell and Miller (1944) map and AOU (1957) description. Figure 1 provides a general comparison of the Grinnell and Miller (1944) range map and the current known distribution of these owls in California.

**Range of the Northern Spotted Owl in California.** Based on genetic surveys, most of the birds sampled on all sides of Mount Shasta (i.e., east of the AOU range) are Northern Spotted Owls (see above). Location records are also present in the California Fish and Game database for western Tehama and western Glenn Counties, as well as Lake and Napa Counties, which represent eastern extensions to the original range description (see also Gould 1977). Because of the contiguous but low density nature of the owl distribution through central Shasta County, we presume those owls distributed from Siskiyou County south and east to the Pit River are Northern Spotted Owls because there are no apparent barriers separating these birds from owls to the west in Siskiyou County. In addition, the Sacramento River east of the Grinnell and Miller (1944) range boundary does not appear to act as a barrier to Northern Spotted Owls. However, we do not know precisely if the Pit River is a “true” boundary between the subspecies or whether there is a cline of haplotypes between Mount Shasta and Mount Lassen that spans the Pit River. The Pit River Valley is the primary major geographic feature separating Mount Shasta and Mount Lassen, and as noted above, there is a narrow band of suitable habitat that crosses this river. Resolution of the shape and length of a potential cline in haplotypes across this region requires further study.

We note for clarity that the 1990 listing decision described the owl’s range as extending through the “Klamath Physiographic Province” (USDI 1990: 26114). The Klamath Physiographic Province roughly follows the eastern extent of the Grinnell and Miller distribution (1944). Since the range of the Northern Spotted Owl obviously includes part of the California Cascades Province (e.g., Mount Shasta), we speculate that the U. S. Fish and Wildlife Service used a different delineation for this “province” than has been used in most planning documents for the Northern Spotted Owl.

Spotted Owls occur at three sites in Modoc County (California Fish and Game Spotted Owl database, 29 June 2004 version). These birds are currently managed as Northern Spotted Owls because this small area is part of the Northwest Forest Plan (USDA and USDI 1994, Barry Mulder U. S. Fish and Wildlife Service, pers. comm.). We have no basis for determining their taxonomic relationship, other than that they are at the eastern extent of a presumptive continuous distribution of Northern Spotted Owls. However, two of these sites are south of the Pit River (the arbitrary Federal boundary for the subspecies) and Highway 299 (the arbitrary State of California boundary for the subspecies). We

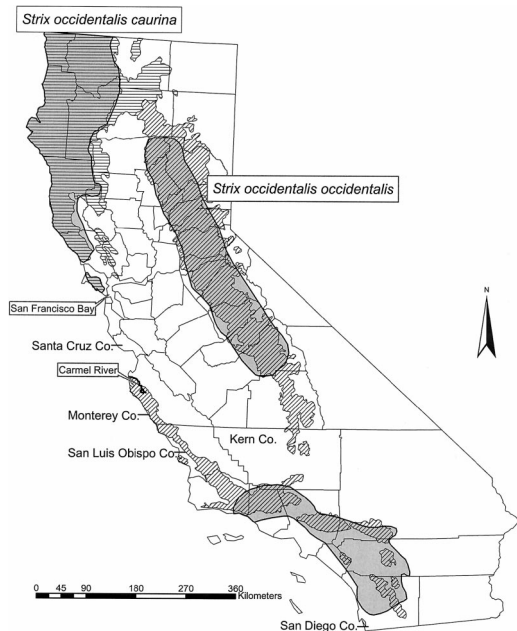


FIGURE 1. The historic and revised distributions of Spotted Owls in California. The shaded areas indicate the ranges depicted by Grinnell and Miller (1944). The horizontal and diagonal striped areas indicate the currently known ranges of the Northern and California Spotted Owl, respectively, based on the California Department of Fish and Game’s California Wildlife Habitat Relationship System species distribution coverages.

include these birds within the Northern Spotted Owl’s range until genetic surveys indicate otherwise.

**Range of the California Spotted Owl in California.** Based on genetic sampling and location data, the California Spotted Owl’s range should start at approximately the Pit River, Shasta County and extend southward to Kern County (Fig. 1 and 2). We chose the Pit River because there is an area of very low owl density south of the Pit River for 10–25 km to Mount Lassen, and 82% of the birds in the Mt. Lassen region we sampled were California Spotted Owls (Barrowclough et al. 2005). This new boundary extends the California Spotted Owl’s range north into the California Cascades Physiographic Province, and extends its range further south in Sierra Nevada Physiographic Province. In addition, Gould (1977) noted that Spotted Owls have been detected from as far north as Monterey County in the Central Coastal Province of California (Fig. 1). We also have captured birds as far north as the south edge of the Carmel River Valley in Monterey County (unpubl. data). These latter birds have a haplotype diagnostic for California Spotted Owls (Barrowclough et al. 2005). Spotted Owls also occur in San Luis Obispo County (considered likely to occur by Grinnell and Miller 1944, Gould 1977). There are no known records of Spotted Owls in Santa Cruz County (Gould 1977,

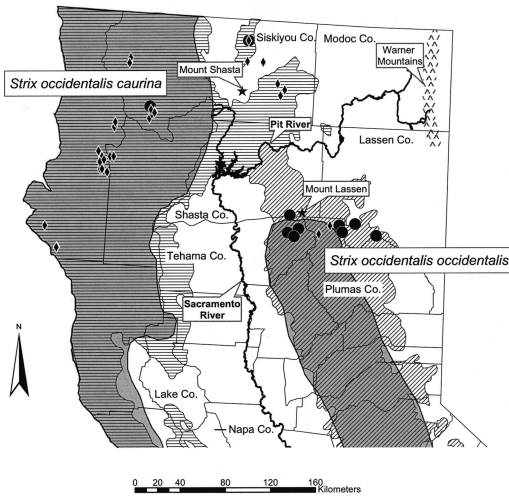


FIGURE 2. The distribution of Northern (diamonds) and California Spotted Owl (circles) mtDNA haplotypes in northern California. Northern and California Spotted Owl historic and revised ranges (see Fig. 1 caption) are depicted within counties identified in text. Some locations that contain multiple samples are indicated by one symbol.

Gutiérrez et al. 1995, California Fish and Game Spotted Owl database, June 29, 2004 version). We speculate that Spotted Owls probably inhabited the Santa Cruz Mountains prior to widespread loss of ancient redwood (*Sequoia sempervirens*) forests due to logging. Given the regeneration capacity of redwoods, we believe that suitable habitat may be available now or in the near future, and these forests are within dispersal or colonization range of the birds in Monterey County. Thus, because of geographic proximity to Monterey County and the presence of a substantial physical barrier (San Francisco Bay) between the Santa Cruz Mountains and the nearest Northern Spotted Owl population, we predict newly colonizing birds in this area will likely be California Spotted Owls.

*Revision of the range of Northern and California Spotted Owls.*

*Strix occidentalis caurina* (Merriam).

*Syrnium occidentale caurinum* Merriam, Auk 15, no. 1, Jan. 1898, pp. 39, 40. (Mt. Vernon, Skagit Valley, Washington)

From extreme southwestern British Columbia through western Washington (Olympic Peninsula and Western Washington Lowlands), Cascade Ranges of Washington (east and west slopes), western Oregon from Pacific Coast Ranges east to Cascade Ranges (except Willamette Valley), Cascade Ranges of Oregon (east and west slopes), coast ranges of California to San Francisco Bay (Marin County and Napa County), eastward from California coast ranges to western Lake, Glenn, Tehama Counties, Klamath Mountains, east from Klamath Mountains through Siskiyou County to eastern Modoc County, southeast to Pit River, Shasta County.

*Strix occidentalis occidentalis* (Xántus).

*Syrnium occidentale* Xántus, Proceedings of the Academy of Natural Sciences of Philadelphia, 11, sigs. 15–19, Aug–Sept., 1859 (10 Jan. 1860), p. 193. (Fort Tejon, California).

West slope (locally on east slope) of Sierra Nevada in California from Shasta (Pit River) and Lassen Counties south to Kern County, and mountains of central coastal, southern, and transverse ranges of California from Monterey (south side of Carmel Valley) and Kern Counties south through San Diego County to Cuyamaca Mountains in California, and Sierra San Pedro Martir in Baja California Norte, Mexico.

## DISCUSSION

It is clear from this abbreviated history that descriptions of the range boundaries of Northern and California Spotted Owls in California did not keep pace with the phenomenal effort by wildlife biologists and foresters to locate Spotted Owls. The decision to list the entire Northern Spotted Owl taxon as threatened, while including areas that were outside the original range description provided by the AOU (1957) seemingly renders ambiguous the frame of geographic reference for owl conservation planning. However, it is also evident that the Endangered Species Act allows for the listing of any species, subspecies, or “distinct population segment of any species” when determinations of a species status are made by the U. S. Secretary of Interior (Endangered Species Act 1988). We feel the issue is not trivial in the case of the Spotted Owl because had the listing decision adhered to the original AOU boundaries a very large area inhabited by Northern Spotted Owls may have been precluded from receiving conservation protection. On the other hand, if the population from eastern Siskiyou County southeast to the Pit River were actually California Spotted Owls, the decision could have resulted in “unnecessary” protection for the owl with subsequent economic consequences resulting from reduced logging opportunity. We recognize that the Pacific Northwest Forest Plan (USDA and USDI 1994) provides management protection for owls in this area regardless of their taxonomic affinity. Nevertheless, the matter is further complicated by the fact that the California Spotted Owl (as a subspecies) has been denied listing under the Endangered Species Act (USDI 2003), but its range boundaries were not reconciled by taxonomic revisions. Indeed, the subspecific identity of birds in Modoc County and the Warner Mountains of California is still in question (see above). We consider the one site in the Warner Mountains to be an extra limital observation until a population has been identified through additional sampling. Finally, range descriptions for these subspecies have been repeated throughout the past 2 decades without a basis of support.

Despite the disparity between the listing decision and old AOU range boundaries, the geographic scope of the listing was correct. Limited genetic surveys of genetic markers provide a mechanism to assign these heretofore “limbo” populations to an extant taxon, which conforms to boundaries in conservation documents. However, at this time we cannot determine if there is a graded zone of contact between Northern and

California Spotted Owls from Mount Shasta to the Pit River or if the separation is more truncated from the Pit River south to Mount Lassen and vicinity. We do know that 82% of a Spotted Owl sample from the vicinity of Mount Lassen are California Spotted Owls based on mtDNA sequencing, which is within the guidelines of the “75% rule” for subspecies (Amadon 1949, Patten and Unitt 2002). Further sampling will be needed to elucidate the taxonomic situation to the west of the Pit River. Nevertheless, it appears that the relatively low density of birds from Mount Shasta east to the Pit River merits continued conservation protection. The delineation of the Northern and California Spotted Owls’ ranges by wildlife biologists was based on logical conclusions about the observed distribution of owls and their habitat. We make this inference because we can find no formal description or discussion of the criteria for setting the new boundaries for Northern or California Spotted Owls’ ranges in conservation decisions (see all citations above). It appears that once a decision on the range boundaries was made during conservation planning exercises, the decision continued for nearly 2 decades without taxonomic nomenclature review (see Dawson et al. 1987 for an early reporting of this new range).

The general issue of using named intraspecific taxa, particularly subspecific taxa, is relevant to the Spotted Owl as well. Zink (2004) criticized the use of subspecies as units for conservation because they did not necessarily reflect inherent genetic diversity or independent evolutionary history of a species. Interestingly, Zink (2004) used the Spotted Owl as an example where the subspecies was valid for conservation purposes because the current owl subspecies reflect unique evolutionary histories (Barrowclough et al. 1999). While we agree with Zink’s assessment of appropriateness of using Spotted Owl subspecies for conservation planning, it is clear that a potential problem with conservation planning exists even here because the distributions of these taxa were not fully delineated. Thus, we suggest that greater consideration be given to listing populations or segments of populations, rather than subspecies. That is, listing decisions should be consistent with the threats affecting populations or population segments, especially when those populations also exhibit significant historical evolutionary history (sensu Zink 2004). Of course, this does not apply to the listing of an entire species-level taxon. In the case of the Spotted Owl, biological assessment of threats in combination with knowledge of owl biology and distribution, led to a correct decision in spite of a lack of genetic or other taxonomic information.

We thank Gordon Gould for making the California Fish and Game Spotted Owl database (Department of Fish and Game, June 29, 2004 version) available for our use, and for discussing the issue with us. Barry Mulder and the U.S. Fish and Wildlife Service provided very helpful information on the listing and management of the Northern Spotted Owl. David Grandmaison provided assistance in several ways. David Grandmaison and Guthrie Zimmerman read drafts of this paper. We thank Barry Noon and an anonymous reviewer for helpful comments on this paper. William

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## LITERATURE CITED

- AMADON, D. 1949. The seventy-five percent rule for subspecies. *Condor* 51:250–258.
- AMERICAN ORNITHOLOGISTS’ UNION. 1931. Check-list of North American Birds. 4th ed. American Ornithologists’ Union. Lancaster, PA.
- AMERICAN ORNITHOLOGISTS’ UNION. 1957. The Check-list of North American Birds. 5th ed. Lord Baltimore Press, Baltimore, MD.
- BARROWCLOUGH, G. F., AND R. J. GUTIÉRREZ. 1990. Genetic variation and differentiation in the Spotted Owl (*Strix occidentalis*). *Auk* 107:737–744.
- BARROWCLOUGH, G. F., R. J. GUTIÉRREZ, AND J. G. GROTH. 1999. Phylogeography of Spotted Owl (*Strix occidentalis*) populations based on mitochondrial DNA sequences: gene flow, genetic structure, and a novel biogeographic pattern. *Evolution* 53:919–931.
- BARROWCLOUGH, G. F., J. G. GROTH, L. A. MERTZ, AND R. J. GUTIÉRREZ. 2005. Genetic structure, introgression, and a narrow hybrid zone between Northern and California Spotted Owls (*Strix occidentalis*). *Molecular Ecology*, in press.
- DAWSON, W. R., J. D. LIGON, J. R. MURPHY, J. P. MYERS, D. SIMBERLOFF, AND J. VERNER. 1987. Report of the scientific advisory panel on the Spotted Owl. *Condor* 89:205–229.
- DICKERMAN, R. W. 1997. Systematics of the southwestern and Mexican populations of the Spotted Owl, with description of a new subspecies. In R. W. Dickerman [compiler], *The Era of Allan R. Phillips, A Festschrift*. Horizon Communications, Albuquerque, NM.
- ENDANGERED SPECIES ACT. 1988. Endangered Species Act of 1973. As amended through the 100th Congress. United States Fish and Wildlife Service, United States Department of the Interior. Washington, DC.
- FORSMAN, E. D., R. G. ANTHONY, J. A. REID, P. J. LOSCHL, S. G. SOVERN, M. TAYLOR, B. L. BISWELL, A. ELLINGSON, G. S. MILLER, E. C. MESLOW, K. A. SWINDLE, J. A. THRAILKILL, F. F. WAGNER, AND D. E. SEAMAN. 2002. Natal and Breeding Dispersal of Northern Spotted Owls. *Wildlife Monographs* 149.
- FORSMAN, E. D., S. G. SOVERN, D. E. SEAMAN, K. J. MAURICE, M. TAYLOR, AND J. J. ZISA. 1996. Demography of the Northern Spotted Owl on the Olympic Peninsula and east slope of the Cascade Range, Washington. *Studies in Avian Biology* 17: 21–30.
- FRANKLIN, A. B., AND R. J. GUTIÉRREZ. 2002. Spotted Owls, forest fragmentation, and forest heterogeneity. *Studies in Avian Biology* 25:203–220.

- FRANKLIN, A. B., R. J. GUTIÉRREZ, J. D. NICHOLS, M. E. SEAMANS, G. C. WHITE, G. S. ZIMMERMAN, J. E. HINES, R. E. MUNTON, W. S. LAHAYE, J. A. BLAKESLEY, G. N. STEGER, B. R. NOON, D. W. H. SHAW, J. J. KEANE, T. L. McDONALD, AND S. BRITTING. 2004. Population dynamics of the California Spotted Owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithological Monographs* 54:1–54.
- GOULD, G. I. JR. 1977. Distribution of the Spotted Owl in California. *Western Birds* 8:131–146.
- GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Berkeley, CA: Pacific Coast Avifauna, No. 27.
- GUTIÉRREZ, R. J. 1985. An overview of recent research on Spotted Owls. In R. J. Gutiérrez and A. B. Carey [tech. coords.], *Ecology and management of the Spotted Owl in the Pacific Northwest*. USDA Forest Service General Technical Report PNW-185.
- GUTIÉRREZ, R. J. 1994. Changes in the distribution and abundance of Spotted Owls during the past century. *Studies in Avian Biology* 15:293–300.
- GUTIÉRREZ, R. J., A. B. FRANKLIN, AND W. S. LAHAYE. 1995. Spotted Owl. *The Birds of North America* 179:1–28.
- GUTIÉRREZ, R. J., E. D. FORSMAN, A. B. FRANKLIN, AND E. C. MESLOW. 1996. History and demographic studies in the management of the Northern Spotted Owl. *Studies in Avian Biology* 17:6–11.
- HAIG, S. M., R. S. WAGNER, E. D. FORSMAN, AND T. D. MULLINS. 2001. Geographic variation and genetic structure in Spotted Owls. *Conservation Genetics* 2:25–40.
- MESLOW, E. C. 1993. Spotted Owl protection: unintentional evolution toward ecosystem management. *Endangered Species Update* 3/4:34–38.
- MERRIAM, C. H. 1898. *Syrnium occidentale caurinum*, a new owl from the Puget Sound region. *Auk* 15: 39–40.
- NELSON, E. W. 1903. Descriptions of new birds from southern Mexico. *Proceedings of the Biological Society of Washington* 16:151–159.
- OBERHOLSER, H. C. 1915. Critical notes on the subspecies of the Spotted Owl, {*Strix occidentalis*} (Xantus). *Proceedings of the U.S. National Museum* 49:251–257.
- PATTEN, M. A., AND P. UNITT. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. *Auk* 119:26–35.
- SIMBERLOFF, D. 1987. The Spotted Owl fracas: mixing academic, applied, and political ecology. *Ecology* 68:766–772.
- SWARTH, H. S. 1910. Two new owls from Arizona. *University of California Publications in Zoology* 7:1–8.
- SWARTH, H. S. 1915. The status of the Arizona Spotted Owl. *Condor* 17:15–19.
- THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON, AND J. VERNER. 1990. A conservation strategy for the Northern Spotted Owl. Report of the Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl. Portland, OR.
- THOMAS, J. W., AND J. VERNER. 1992. Accommodation with socio-economic factors under the endangered species act—more than meets the eye. *Transactions North American Wildlife Natural Resources Conference* 57:627–641.
- U.S. DEPARTMENT OF AGRICULTURE (USDA). 1988. Final supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide. 2 Volumes. USDA Forest Service, Portland, OR.
- U.S. DEPARTMENT OF AGRICULTURE (USDA) AND U.S. DEPARTMENT OF INTERIOR (USDI). 1994. Final environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. Volumes 1–2 + Record of Decision. U. S. Forest Service and U. S. Bureau of Land Management, Portland, OR.
- U.S. DEPARTMENT OF INTERIOR (USDI). 1989. The Northern Spotted Owl: a status review supplement. Unpublished Report, U. S. Fish and Wildlife Service, Portland, OR.
- U.S. DEPARTMENT OF INTERIOR (USDI). 1990. Endangered and threatened wildlife and plants; determination of threatened status for the Northern Spotted Owl. *Federal Register* 55:26114–26194.
- U.S. DEPARTMENT OF INTERIOR (USDI). 1995. Recovery plan for the Mexican Spotted Owl. U.S. Fish and Wildlife Service, Albuquerque, NM.
- U.S. DEPARTMENT OF INTERIOR (USDI). 2003. Endangered and threatened wildlife and plants; 12-month finding for a petition to list the California Spotted Owl (*Strix occidentalis occidentalis*). *Federal Register* 68:7580–7608.
- XANTUS, J. 1859. Catalogue of birds collected in the vicinity of Fort Tejon, California with a description of a new species of {*Syrnium*}: *Proceedings of the Academy of Natural Sciences of Philadelphia*.
- ZINK, R. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society of London Series B* 271:561–564.