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Dependence of northern spotted owls *Strix occidentalis caurina* on old-growth forests in the western USA

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Habitat requirements of northern spotted owls *Strix occidentalis caurina* have become the focus of a major controversy over how much old-growth forest in the western United States should be preserved. Analysis of three large data sets showed that the subspecies was rare or absent in areas with little older (i.e. >80-year-old) forest but with extensive stands nearing harvest age. The owls were also rare in areas with the small amounts of old-growth typically left after harvest operations. Old-growth stands in Wilderness Areas supported sparse populations of northern spotted owls, and their reproductive success was only about half that of owls outside Wilderness Areas. The results indicate that timber harvest operations, as currently practiced, lead to declines in numbers of northern spotted owls, and that currently protected old-growth stands are unlikely to provide enough high-quality habitat to maintain self-supporting populations of northern spotted owls.

INTRODUCTION

The northern spotted owl *Strix occidentalis caurina* has recently become the focus of an intense debate over how the remaining old-growth and mature forests on public lands in the western United States should be managed. Although the controversy raises pervasive questions about how the American public wishes to allocate resources between timber production and forest preservation, the specific issue being examined most closely is how dependent spotted owls are on old-growth forests.

Old-growth forests within the range of the northern spotted owl now occur mainly on public land (Thomas *et al.*, 1990). If harvest rates during the past few decades continue, most of the currently unprotected old-growth in the range of the northern spotted owl will disappear within a few decades (Fig. 1). Decisions about the dependence of this subspecies on old-growth forests thus need to be made during the next few years or the options for protecting the remaining old-growth forests will be sharply curtailed.

The US Fish and Wildlife Service has recently listed the northern spotted owl as Threatened under the Threatened and Endangered Species Act. This new designation for the subspecies, which formerly had no special protection under federal law, is likely to have profound effects on how much old-growth is harvested on public land within its range (much of western Washington, Oregon, and California). Still to be decided, however, is the difficult question of just how much older forest is needed by the owls.

The dependence of northern spotted owls on old-growth forest has been hotly debated during

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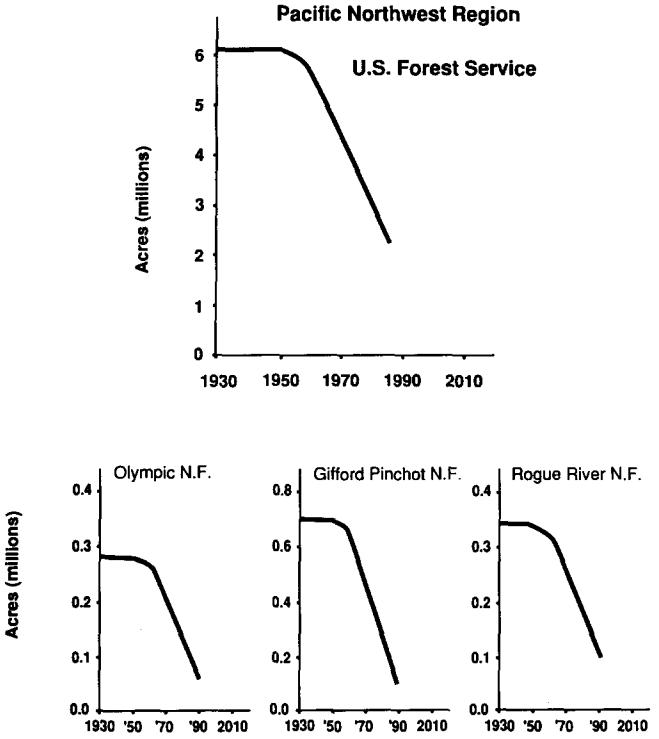

Fig. 1. Decline of northern spotted owl habitat on US Forest Service land in Washington and Oregon outside of Wilderness Areas (from Anderson *et al.*, 1990).

the past several years. Many biologists contend that the subspecies is largely dependent on forests more than 80 years old (referred to in this paper as 'older forest') (Thomas *et al.*, 1990). They point out that few owls have been found in extensive areas lacking older forests (Forsman *et al.*, 1977), and telemetry studies show that birds concentrate their activities in older forest and avoid very young forests (Forsman *et al.*, 1984). Critics, however, have argued that few thorough searches have been reported from areas where regenerating forests are near harvesting age (expected to be about 80 years—Brown, 1985), and that the telemetry studies do not prove that spotted owls require older forest, but only show that they select older forest when it is available (Irwin, 1989). Critics also note that recent surveys in California revealed spotted owls in forests 50–80 years old, and the birds there appeared to be reproducing successfully (Irwin *et al.*, 1989). Thus, the debate over how dependent spotted owls are on older forests has been difficult to resolve conclusively because too few studies, surveying both older and younger forests with similar methods, have been published.

During the past two to three years, this situation has changed dramatically as the US Forest Service, Bureau of Land Management, and State Wildlife Departments have begun extensive surveys for spotted owls on the lands they manage. Here, we use the results from these surveys to address three questions, all of which bear on the larger issue of how timber harvest activities are likely to affect spotted owls: (1) Do landscapes consisting almost exclusively of young (i.e. <80-year-old), regenerating forests support northern spotted owls? (2) Do landscapes with the small amounts of older forest left after timber harvest operations (usually <20%, Anderson *et al.*, 1990) support northern spotted owls? (3) Do protected forests in National Parks and Wilderness Areas provide high-quality habitat for northern spotted owls? These protected areas are widely distributed and could, if they contain high-quality habitat, provide an extensive system of refuges for the owls. Wilderness Areas and National Parks, however, are often placed on high-elevation land, whereas northern spotted owls are thought to reach higher abundance at lower elevations (Thomas *et al.*, 1990). There is thus some question about the suitability of the habitat in these protected sites.

METHODS

We used results of surveys for northern spotted owls on areas scheduled for timber harvest, on intensively studied research areas, and on randomly selected, 400-ha circles on US Forest Service lands. For the first two data sets, we obtained habitat maps of each surveyed area and delineated compartments within which the distribution of older forest was fairly uniform. We then determined the fraction of each compartment covered by older forest. We restricted the analysis to compartments of at least 20 km^2 to minimize edge effects. Most timber sale areas were surveyed three times in 1989, though a few were surveyed more times or also in 1988. Intensively surveyed areas were visited up to 12 times per year, most for at least two consecutive years. Results from these two data sets were very similar (Anderson *et al.*, 1990) and are therefore combined here.

Two sets of 400-ha circles were available. The first was randomly selected from US Forest Service land throughout the range of the northern spotted owl. The second was randomly selected from 'spotted owl habitat areas' (SOHAs) on US Forest Service land in Washington and Oregon. Most circles were surveyed in 1988 and 1989, and all were surveyed following a detailed protocol

requiring up to six visits (O'Halloran, 1989; Simon-Jackson, 1989). Surveyors recorded number of owls, number of pairs, and, in many cases, number of young fledged per pair.

We investigated the first issue—owl abundance in young, regenerating forests—by selecting compartments with extensive stands 50–80 years old, and little older forest. Each was paired with a nearby compartment having extensive older forest. We compared the density of owls, and pairs of owls, in these two habitats.

Owl abundance and productivity on areas with <20% older forest was investigated by calculating rangewide estimates of the average number of owls/km^2, pairs/km^2, fledglings/km^2, and fledglings/pair in compartments with different amounts of older forest. Our main purpose was to compare compartments with <20% and >60% older forest, but we also report the measures above for compartments with intermediate levels.

The third issue—whether currently protected older forest provides high quality habitat for northern spotted owls—was studied by two analyses of survey results from the randomly selected, 400-ha circles. The first used the circles selected from throughout the range of northern spotted owls on US Forest Service land. We compared number of owls/km^2, pairs/km^2, fledglings/km^2, and fledglings/pair inside and outside Wilderness Areas in good habitat (defined as circles with >40% older forest). The second analysis, carried out using circles in SOHAs, was similar except that we only compared young fledged per pair. Measures of abundance were not compared because SOHAs were usually placed in locations known to contain spotted owls.

RESULTS

Information was obtained from 185 compartments, including five intensive sites, in 45 study areas (Fig. 2). The compartments varied in size from 20 to 690 km^2, and covered a total area of 11 057 km^2. Seven compartments, covering a total area of 1029 km^2, had extensive 50–80-year-old forest but little forest >80 years old. Data were available from 254 of the 400-ha circles. The only physiographic province not covered by our data was the redwood zone in coastal California, which covers less than 7% of the range of the northern spotted owl (Anderson *et al.*, 1990).

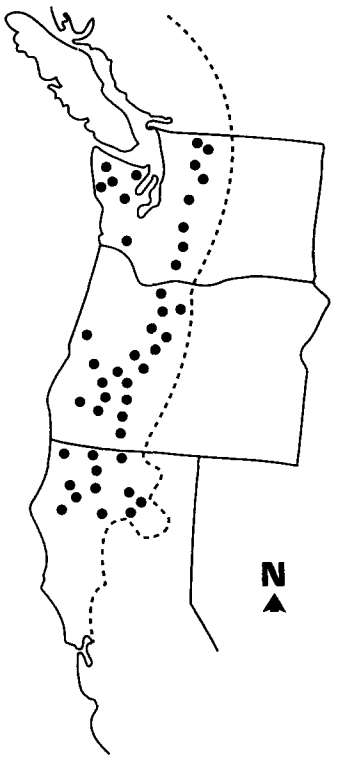

Fig. 2. Location of study areas in Washington, Oregon and California. All areas on public land, of at least 164 km^2, that had been surveyed at least three times in at least one year were included in the analysis.

Virtually no owls were found in compartments dominated by 50–80-year-old forest but lacking older forest (Table 1). In contrast, detections of single and paired owls were common in the nearby compartments with extensive older forest. Owls were approximately 40 times more common on the areas with older forest than on the areas lacking older forest. This analysis indicates that

Table 1. Density of northern spotted owls in regenerating stands 50–80 years old and in nearby areas with extensive older forest

State	No. of sites	Total area (km^2)	Percentage of area covered by 50–80-year-old stands	Owls per km^2	Pairs per km^2	Owls/km^2 in adjacent sites with extensive older forest
Washington	4	207	50–92	0·00	0·00	0·05
Oregon	2	417	57–68	0·02	0·01	0·32
California	1	474	59	0·00	0·00	0·27

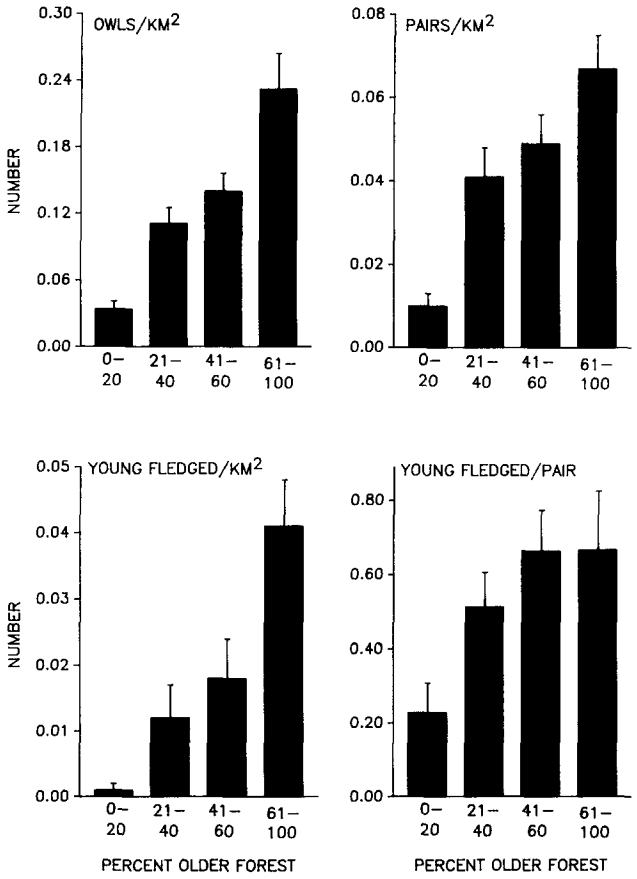

Fig. 3. Density and reproductive success of northern spotted owls in relation to amount of older forest on the surveyed area. Vertical lines indicate 1 SE.

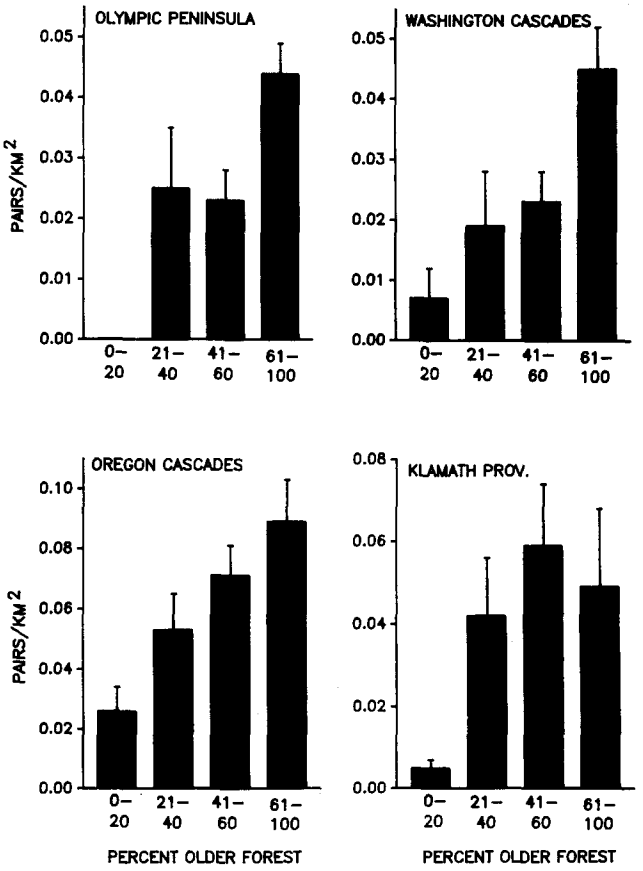

Fig. 4. Abundance of spotted owls, in four portions of their range, in relation to the amount of older forest on the surveyed areas. Vertical lines indicate 1 SE.

50–80-year-old forests do not provide suitable habitat for northern spotted owls.

Surveys on timber sale areas and intensively studied areas (Fig. 3) showed that abundance and productivity increased steadily with increasing amounts of older forest. All measures of abundance or productivity were significantly lower ($p < 0{\cdot}05$, t test) on areas with <20% older forest than on areas with >60% older forest. Approximately 50 times more young owls fledged/km² in areas with >60% older forest than in areas with ≤20% older forest. Similar results were obtained from the 400-ha circles (Table 2). Trends were similar in different parts of the range (Fig. 4) and in each of the five intensively studied areas (see Anderson *et al.*, 1990 for additional details). This analysis shows that landscapes with less than 20% coverage by older forest rarely provide suitable habitat for northern spotted owls.

Table 2. Density and reproductive success of northern spotted owls in relation to amount of older forest as indicated by US Forest Service monitoring data

Variable	Percentage suitable habitat			
	0–20	21–40	41–60	> 60
Owls/site	0·31[a]	0·64[b]	0·85[b]	0·95[b]
Pairs/site	0·04[a]	0·19[b]	0·29[b]	0·28[b]
Fledglings/site	0·01[a]	0·13[b]	0·21[b]	0·22[b]
Fledglings/pair	0·33	0·77	0·67	0·93
Number of sites	101	56	58	39

Different superscripts within rows indicate significantly different values (t test, $p < 0{\cdot}05$).

Table 3. Density and reproductive success of northern spotted owls in randomly selected sites within Wilderness Areas and in good habitat (older forests covering >40% of the site) outside of Wilderness Areas

Variable	Location of site	
	Wilderness	Good habitat
Owls/site	0·61[a]	0·97[b]
Pairs/site	0·18[a]	0·29[b]
Fledglings/site	0·14[a]	0·43[b]
Fledglings/pair	0·54[a]	0·96[b]
Number of sites	104	51

Different superscripts within rows indicate significantly different values (t test, $p < 0{\cdot}05$).

All measures of abundance and productivity in the 400-ha circles were lower inside than outside Wilderness Areas (Table 3). Productivity inside Wilderness Areas was only 30–50% as high as productivity outside. Similar results were obtained from circles in SOHAs. Pairs inside Wilderness Areas fledged an average of 0·42 young per attempt whereas pairs outside Wilderness Areas produced 0·89 fledglings/year ($p < 0{\cdot}05$, t test). This analysis shows that land within Wilderness Areas classified as spotted owl habitat does not, on average, provide high-quality habitat for the owls.

DISCUSSION

This study showed that northern spotted owls are rare, and have low productivity, in 50–80-year-old forests or areas with only the small amounts of older forest left after timber harvest activities. Owls were virtually absent in 50–80-year-old forests (Table 1). The study areas covered >1000 km^2 and were surveyed for two years, but only one pair (in one year) was found and it did not produce any fledglings. On areas with <20% older forest a few single owls were found but pairs were scarce, and productivity was far below the levels found on areas with extensive older forest. This pattern was found on timber sale areas and intensively studied areas (Fig. 2), on randomly selected, 400-ha circles (Table 2), and in four different portions of the range (Fig. 3). The general pattern appears to be that a few solitary owls use areas with <20% older forest but that these areas only rarely provide habitat of sufficient quality to support successful reproduction.

The study also showed that the older forest in Wilderness Areas does not generally provide high-quality habitat for northern spotted owls. Abundance and productivity were somewhat higher than in areas where the timber had been harvested, but were still significantly below the levels found in high-quality habitat outside Wilderness Areas. No comparable survey data were available from National Parks, but much of the older forest in these areas, like that in the Wilderness Areas, is at high elevation and seems unlikely to provide substantially better habitat than the older forest in Wilderness Areas. Thus, while surveying older forest in National Parks should be a high priority, it appears that currently protected older forest may be unable to support self-sustaining populations of northern spotted owls.

The issue of whether protected land will be adequate for protecting spotted owls has previously been addressed with demographic models (e.g. Lande, 1988; Doak, 1989). Some investigators have reached different conclusions, and obtaining a consensus has not been easy (Anderson *et al.*, 1990; Thomas *et al.*, 1990). Our comparison of abundance and productivity in protected and unprotected areas represents a different approach, perhaps most closely aligned with the 'source–sink' view of population dynamics (Pulliam, 1988). This paradigm applies well to northern spotted owls residing inside and outside of the protected areas. Owls in protected areas are less abundant than in good habitat outside protected areas, they are at the upper edge of their elevational range, and, most importantly, they exhibit sharply reduced productivity compared to populations in good habitat. These statements are true both of the protected areas in general and of the best sites (the SOHAs) within the protected areas. We suspect that the source–sink model may be useful for evaluating management strategies in many situations where only a small amount of the existing habitat is guaranteed protection.

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