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SPOTTED OWLS, FOREST FRAGMENTATION, AND FOREST HETEROGENEITY

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Abstract. The Spotted Owl (*Strix occidentalis*) has been a focal species in the United States in terms of loss and fragmentation of old coniferous forests. Past research has shown a strong association between Spotted Owls and old coniferous forests. Thus, these vegetation types are considered synonymous with Spotted Owl habitat. Past fragmentation of old coniferous forests in the Pacific Northwest, the Sierra Nevada, southern California, and the Southwest has resulted from natural disturbance (e.g., fire), edaphic conditions, and timber harvesting. These processes have occurred at different rates and levels. We reviewed the existing literature on the effects of forest fragmentation and heterogeneity on Spotted Owls at three different scales: a range-wide scale where once-connected populations have been isolated from each other, a population scale where populations with different fragmentation regimes have different demographics, and a territory scale where individuals occupying territories with different fragmentation regimes have different fitness. Studies at the range-wide scale have concentrated on processes, such as juvenile dispersal. There are no published studies on the effects of fragmentation or heterogeneity at the population scale, although the potential exists for examining those effects with current studies. Lack of empirical data on the effects of fragmentation on Spotted Owls led to the development of spatially-explicit simulation models as an aid to reserve design for this species. In addition, some populations of Spotted Owls are naturally disjunct at the range-wide scale. Most empirical studies have concentrated on the territory scale, and most of those studies have examined the effects of fragmentation and heterogeneity on occupancy. We attempted a simple meta-analysis using effect sizes estimated from these studies. However, this analysis was hampered by lack of replicated studies among subspecies and among provinces within subspecies. In addition, studies did not use similar metrics to describe fragmentation and heterogeneity. Thus, empirical studies following simulation models are equivocal in their conclusions. Many questions remain unanswered concerning the effects of forest fragmentation and heterogeneity on Spotted Owls. We provide a set of key questions that need to be addressed to better understand the effects of fragmentation and heterogeneity on Spotted Owls. We also suggest that future research concentrate on understanding natural disturbance regimes and the extent to which timber harvesting is compensatory or additive to natural disturbance regimes. Research on the effects of fragmentation on Spotted Owls should also include alternative hypotheses that some levels of fragmentation and/or heterogeneity may benefit Spotted Owl populations.

Key Words: habitat; habitat fragmentation; meta-analysis; population dynamics; Spotted Owl.

The Spotted Owl (*Strix occidentalis*) occurs in the western United States, Canada, and Mexico, and is comprised of three subspecies: the Northern Spotted Owl (*S. o. caurina*), the California Spotted Owl (*S. o. occidentalis*), and the Mexican Spotted Owl (*S. o. lucida*) (Gutiérrez et al. 1995; Fig. 1). All three subspecies have similar life-history characteristics, with high adult survival, low juvenile survival, and low reproduction (LaHaye et al. 1992, Noon et al. 1992, White et al. 1995, Forsman et al. 1996, Seamans et al. 1999).

Habitat associations of Spotted Owls are variable across and within subspecies. However, all three subspecies have a strong association with older forests for nesting, roosting, and foraging (Forsman et al. 1984, Carey et al. 1990, Solis and Gutiérrez 1990, Call et al. 1992, Gutiérrez et al. 1992; Buchanan et al. 1993, 1995; Ganey and Balda 1994, Seamans and Gutiérrez 1995, Forsman and Giese 1997, LaHaye et al. 1997, Steger et al. 1997, Hershey 1998, Young et al. 1998, LaHaye and Gutiérrez 1999). In general, these forests are characterized by an overstory of large (≥52 cm dbh) conifers, with a multilayered understory of conifers and/or hardwood trees and shrubs, and decadence in the form of snags and coarse woody debris. These association have been documented at several scales (see reviews in Gutiérrez et al. 1992, 1995; Ganey and Dick 1995). However, there are exceptions to the association of Spotted Owls with old coniferous forests. Mexican Spotted Owls are found in both old forests and in steep, incised canyon systems with little or no forest cover (Rinkevich and Gutiérrez 1996, Ganey and Dick 1995). Nevertheless, the majority of Mexican Spotted Owl populations are found in areas containing older coniferous forests where they strongly associate with these forests (Ward et al. 1995, Ganey and Dick 1995). In addition, owls frequently inhabit previously logged conifer forests or oak (*Quercus* spp.) forests (Gutiérrez et al. 1992, Folliard 1993). In these latter two situations, residual old trees are often present, the current forest has structural characters similar to

FIGURE 1. Geographic distribution of three subspecies of Spotted Owl (*Strix occidentalis*). Regions shown for Northern Spotted Owl are from Agee and Edmonds (1992).

old forests, and/or microclimates are modified by marine climates or streams.

In addition to differences between subspecies, there are subtle differences in forests used by Spotted Owls within subspecies. For example, Northern Spotted Owls are found in forests composed almost purely of conifers in their northern range. However, in the southern extent of their range many hardwood species dominate the mid- and understories while conifers still dominate the overstory. Despite these and other exceptions, it is generally believed that Spotted Owls associate with older coniferous forests and that these forests provide some key elements for their survival and reproduction.

Both the Northern and Mexican subspecies were listed as threatened under the Endangered Species Act of the United States (U.S. Fish and Wildlife Service 1990, 1993). One criterion that led to listing was habitat loss and fragmentation due to logging and forest management. Existing scientific information at the time of the listing of these two subspecies suggested that these owls were dependant on interior older forest for foraging, roosting, and nesting. Another criterion was the failure of existing regulatory mechanisms to control loss and fragmentation of older coniferous forest (U.S. Fish and Wildlife Service 1990, 1993). For similar reasons, the California subspecies was recently petitioned for listing (Center for Biological Diversity 2000).

In this paper, we first review the concepts of fragmentation and heterogeneity as they apply to Spotted Owls. Then, we review simulation models developed to facilitate conservation strategies. Next, we review the existing evidence on the effects of habitat fragmentation on population processes in the three subspecies of Spotted Owls. In particular, we examine habitat fragmentation at three scales: range-wide, population, and territory. The range-wide scale encompasses the geographic range of each subspecies. Habitat fragmentation at this scale may affect meta-population dynamics and gene flow between sub-populations (Gutiérrez and Harrison 1996). The population scale is nested within the range-wide scale. Habitat connectivity is determined by the dispersal ability of young Spotted Owls and local movements of individuals between territories. Potential source-sink population dynamics will be affected by habitat fragmentation and these effects are measurable by variation in rates of population change within populations. The final scale we consider is at the territory level. At this scale, the ability of individual territory holders to move across their territories may be affected by connectivity between blocks of habitat within individual territories. Effects of fragmentation will be expressed in terms of reproductive output and survival of individuals, and by inter-specific interactions such as competition, predation, and hybridization. Clearly, these scales overlap across the three categories (range-wide, population, and territory) that we examined. However, most studies on Spotted Owls encompass one or more of these three scales.

FRAGMENTATION, HETEROGENEITY, AND SPOTTED OWL HABITAT

Mature and old-growth forests are considered synonymous with Spotted Owl habitat. Thus, fragmentation of these forests is considered habitat fragmentation for Spotted Owls. Using the definition of Franklin et al. (*this volume*), habitat fragmentation occurs when habitat becomes discontinuous such that changes occur in population processes. For example, it is unlikely that road cuts (small-scale fragmentation) affects Spotted Owls to the same degree as large catastrophic fires or clearcuts. As Franklin et al. (*this volume*) point out, habitat fragmentation is essentially a binary outcome (habitat versus non-habitat) whereas heterogeneity is a multi-state outcome. In the context of the scales discussed

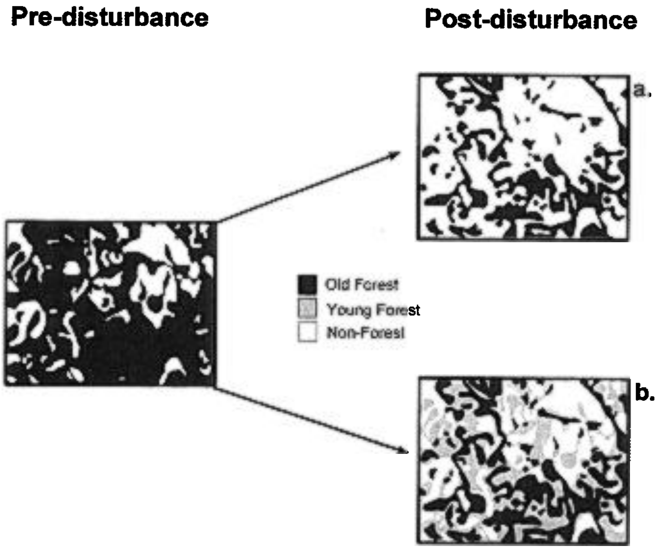

FIGURE 2. Two hypothetical scenarios in patterns of habitat fragmentation in Spotted Owls: (a) older forest alone is considered Spotted Owl habitat, and (b) older forest in some combination with younger forest is considered Spotted Owl habitat.

in this paper, forest heterogeneity is the diversity of vegetation types and seral stages within a given area.

For older forests to be synonymous with Spotted Owl habitat, these forests must provide the requisite resources and conditions that promote occupancy and allow individuals to survive and reproduce (see definitions in Franklin et al. *this volume*). However, there is evidence that other vegetation types may also contribute to Spotted Owl habitat. This evidence is mostly indirect and relates to abundances of Spotted Owl prey in different vegetation types (Rosenberg and Anthony 1992, Williams et al. 1992, Carey and Peeler 1995, Ward and Block 1995, Zabel et al. 1995, Sureda and Morrison 1998, Ward et al. 1998). Thus, ecotones between older forest and other seral stages may contribute to Spotted Owl habitat, an idea that we will explore further (see HABITAT FRAGMENTATION AT THE TERRITORY SCALE below).

If other seral stages contribute to Spotted Owl habitat as suggested above, then some conversion of older forest to younger seral stages does not necessarily represent habitat fragmentation for Spotted Owls. For example, assume a distribution of old forest shown in Figure 2 prior to disturbance. After disturbance fragments the older forest, a new distribution of young and old forest results. If only old forest is Spotted Owl habitat, then fragmentation of older forest alone, as depicted by scenario A in Figure 2, results in habitat fragmentation for Spotted Owls. However, if young forests in some combination with older forest constitutes Spotted Owl habitat, as represented by the condition in scenario B in Figure 2, then no habitat fragmentation occurs for Spotted Owls. In the latter scenario, forest fragmentation is represented by heterogeneity of seral stages. Therefore, we acknowledge that other vegetation types may contribute to Spotted Owl habitat (e.g., forest heterogeneity) in our examination of the empirical studies.

MODELS SIMULATING THE EFFECTS OF HABITAT LOSS AND FRAGMENTATION ON SPOTTED OWLS

The Spotted Owl became a conservation issue because of losses of old coniferous forest from logging. Several management plans were developed but empirical data were generally lacking to test the efficacy of these plans. Therefore, simulation models were developed to examine a critical question for management planners—what is the likely persistence of the owl if its habitat continues to be removed? These simulation models ranged from deterministic to stochastic and were used primarily in developing management strategies for the Northern Spotted Owl (Lande 1988, Doak 1989, Lamberson et al. 1992, McKelvey et al. 1992).

The assumption of these models varied but all assumed that (1) habitat in the form of old coniferous forest was either suitable or unsuitable, with no definitions of habitat quality; and (2) juvenile Spotted Owls searched the landscape during dispersal with some specific behavior, e.g., randomly or with some finite number of searches. All of the models predicted that Spotted Owls would not persist with continued loss of old coniferous forest. An early deterministic model (Lande 1988) predicted a critical threshold for Northern Spotted Owls when the proportion of suitable habitat (old coniferous forest) on the landscape fell below 0.21. Other simulation models did not make such explicit predictions because assumptions on how dispersing juvenile owls searched the landscape was critical in determining model results. Nevertheless, all the models clearly predicted the demise of Northern Spotted Owl populations, given the model assumptions and continued loss of old coniferous forest.

All of the models also assumed that habitat fragmentation would be a consequence of loss of old coniferous forest through logging. This was a reasonable assumption given the knowledge at that time concerning Spotted Owl dispersal and harvest unit strategies in western coniferous forests. However, there were few explicit predictions from the models regarding the nature of fragmentation resulting from habitat loss.

CAUSES OF FRAGMENTATION AND HETEROGENEITY

Historically, fire was the major disturbance affecting forested landscapes across the range of all three subspecies (Weatherspoon et al. 1992, Agee 1993, Skinner and Chang 1996, Swetnam and Baisan 1996a, Taylor and Skinner 1998). Before organized fire suppression programs, fire occurred throughout the range of the Spotted Owls at fairly frequent intervals with differing degrees of intensity (Table 1, Fig. 3). California and Mexican Spotted Owls experienced frequent low to moderate intensity fires, whereas Northern Spotted Owls experienced greater variation in fire return intervals (Table 1; see also Skinner and Chang 1996). Owls occurring in the West Cascades, Coast Ranges, and Redwood provinces were probably less affected by fire than in other parts of their range. However, these mesic provinces experienced higher fire intensities less frequently than drier portions of the owl's range. Of the 3,753 owl pairs reported within the range of the Northern Spotted Owl (Gutiérrez 1994), 37% were in the Klamath and Eastern Cascades provinces, which experienced fire regimes characterized by frequent, less-severe fires than those in western Oregon and Washington (Taylor and Skinner 1998).

Fire suppression by humans disrupted natural fire cycles beginning in the 20th century (Fig. 3; Weatherspoon et al. 1992, Agee 1993, Swetnam and Baisan 1996a), but was not relatively effective until the late 1940s (Wills 1991). The effects of fire suppression on landscapes occupied by Spotted Owls have been poorly understood,

TABLE 1. HISTORICAL FIRE REGIMES WITHIN THE RANGE OF THREE SUBSPECIES OF SPOTTED OWLS

Region[a]	Mean interval (years)	Intensity	Source
		Northern Spotted Owl	
West Cascades Province:			
Oregon Coast and Washington Cascades	230–900	moderate–high	Agee and Edmonds 1992, Long et al. 1998
Central Oregon Cascades	95–145	moderate–high	Agee and Edmonds 1992
East Cascades Province	12–52	low–moderate	Agee and Edmonds 1992
Klamath Province	10–50	low–moderate	Taylor and Skinner 1998, Agee and Edmonds 1992
Redwood Province	50–333	low	Veirs 1982
		California Spotted Owl	
Sierra Nevada Mountains	5–30	low–moderate	Weatherspoon et al. 1992
		Mexican Spotted Owl	
Arizona and New Mexico	3–25	low–moderate	Swetnam and Baisan 1996a,b

[a] Locations of provinces for Northern Spotted Owls are shown in Fig. 1.

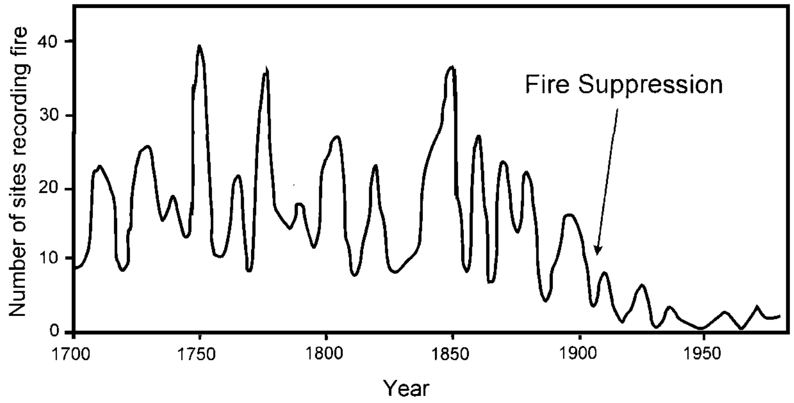

FIGURE 3. Fire occurrence within the range of the Mexican Spotted Owl before and after fire suppression at 63 fire history sites in Arizona and New Mexico (Swetnam and Baisan 1996a).

but several studies suggested that forests prior to fire suppression were less dense and had more openings. Comparing aerial photos from 1944 and 1985, Skinner (1995) found that openings (areas ≥0.1 ha occupied by vegetation less than a third the height of surrounding stands) decreased 39% within unlogged watersheds of the Klamath Province in northern California. In addition, openings became smaller and more dispersed across the landscape after 40 years of fire suppression. Sierran mixed-conifer forests occupied by California Spotted Owls shifted from frequent low- to moderate-severity fires, to long-interval, high-severity, stand-replacing fires after fire suppression (Weatherspoon et al. 1992). This situation probably also applied to forests occupied by Northern and Mexican Spotted Owls. Weatherspoon et al. (1992) also suggested that fire suppression on Sierran forests created more homogeneous landscapes in terms of forested stand configuration. Prior to fire suppression, forests probably were dominated by large, old trees intermixed with a complex array of small, even-aged stands representing a wide range of age- and size-classes (McKelvey and Johnston 1992, Weatherspoon et al. 1992), whereas post-fire suppression forests have become more homogeneous and even-aged. However, there has been considerable disagreement concerning forest conditions under natural fire regimes (Sierra Nevada Ecosystem Project 1996: 63). In either case, the composition and structure of post-fire suppression forests were complicated by logging activities, which have largely replaced fire as the most frequent disturbance to forests occupied by all three subspecies of Spotted Owl.

Coincident with fire suppression, logging began in forests across the range of the Spotted Owl at the turn of the 20th century. However, logging on publicly-owned forests, and subsequent fire suppression, did not begin until around 1940–1950 (Harris 1984, McKelvey and Johnston 1992). In most parts of the owl's range, logging practices shifted from uneven-aged management to even-aged management (Harris 1984, McKelvey and Johnston 1992, Moir et al. 1995) with clearcut logging as the predominate method. However, in the Sierra Nevada, logging prior to the 1980s rarely used clearcutting; selective logging of the largest trees was the predominant method (McKelvey and Johnston 1992). Habitat fragmentation may have occurred if selective logging degraded the quality of older forests for Spotted Owls. However, the matrix resulting from this type of logging may have different effects than one resulting from clearcut logging. On the other hand, clearcutting began earlier and increased over time within the range of the Northern and Mexican Spotted Owls than in the Sierra Nevada (Harris 1984, Moir et al. 1995). Clearcutting has dramatically altered at least part of the forested landscape used by Spotted Owls (Fig. 4). Ripple et al. (2000) found that prelogging landscapes in the Coast Range of Oregon had significantly greater amounts of old-growth forest (63% of landscape before logging versus 44% after logging). In addition to reducing the amounts of older forest, foresters attempted to disperse 10–20 ha clearcuts, which increased fragmentation of those forests; patch density and edge density increased while mean patch size, largest patch size, and amount of interior forest decreased. However, Ripple et al. (2000) also found that proportions of old-growth forest in pre-logging landscapes were highly variable, ranging from 16–100%, which may have been due to past stand-replacing fires.

Thus, both fire and past logging practices altered landscapes occupied by Spotted Owls.

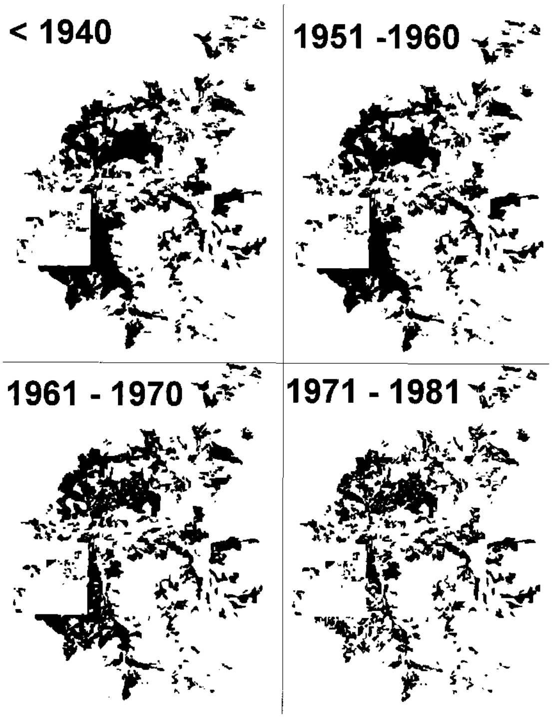

FIGURE 4. Distribution of old-growth forest on the Blue River and McKenzie Ranger Districts of the Willamette National Forest, Oregon (Harris 1984).

While clearcut logging may have been similar to severe stand-replacing fires in that all forest cover is removed, logging did not attempt to mimic natural disturbance regimes, such as fire, under which the owl evolved (McKelvey and Johnston 1992).

HABITAT FRAGMENTATION AT THE RANGE-WIDE SCALE

A number of authors argued that the population process of primary concern with respect to habitat fragmentation across the range of subspecies is juvenile dispersal (Gutiérrez and Harrison 1996, Turchin 1998). This was also recognized in the simulation models discussed previously (Lande 1988, Doak 1989, Lamberson et al. 1992).

Dispersal of juvenile Spotted Owls maintains gene flow and potential demographic connectivity between isolated populations. The importance of juvenile dispersal depends on the dynamics of Spotted Owl populations, e.g., whether population dynamics follow source-sink, meta-population, etc. Regardless of how population dynamics in Spotted Owls are structured, the movement of individual Spotted Owls across the landscape is primarily though juveniles. In general, once Spotted Owls establish a territory, they are relatively sedentary. Movements of territory holders to other territories is relatively rare and encompasses only short distances; Wagner et al. (1996) estimated that 1.5% of non-juvenile Northern Spotted Owls relocated to new territories each year while moving an average of 6.5 km. An exception was noted for the Mexican Spotted Owl, where an adult female was recovered 187 km from her original territory (Gutiérrez et al. 1996). In contrast to territory holders, juvenile Spotted Owls always disperse from their natal territories (Gutiérrez et al. 1985, Miller 1989, Ganey et al. 1998, Willey and van Riper 2000) and move considerably longer distances (Table 2). In addition, the distributional properties of dispersal distances for juvenile Spotted Owls are quite similar between the Northern and Mexican subspecies (Table 2); no data are available for the California subspecies.

If dispersal maintained demographic continuity, then the degree to which habitat fragmentation affects this connectivity will determine the influences of habitat fragmentation on population processes at the range-wide scale. A key question with respect to dispersal is, does habitat fragmentation affect connectivity between populations and subpopulations of Spotted Owls? Effects can be viewed as either complete disrup-

TABLE 2. FINAL DISPERSAL DISTANCES REPORTED FOR RADIO-TAGGED JUVENILE NORTHERN AND MEXICAN SPOTTED OWLS

Subspecies	Region	Final dispersal distance (km)[a] Mean	SD	Range	N	Source
Northern	California	30.5	23.5	1.0–100.0	23	Gutiérrez et al. 1985
	Oregon	28.1	17.3	3.2–75.8	25	Miller 1989
Mexican	Utah	29.2	22.5	1.7–92.3	26	Willey and van Riper 2000
	Arizona	26.2	22.3	0.6–72.1	17	Ganey et al. 1998

[a] Final dispersal distance is the straight-line distance from the nest to the location farthest from the nest (Ganey et al. 1998).

tion of the connection between populations or reduction in flow of individuals to some threshold point where the connection can be considered severed.

Much of the range of the Northern Spotted Owl and the Sierra Nevada portion occupied by California Spotted Owls has fairly continuous forests considered suitable for occupancy by owls. However, across the range of the Mexican Spotted Owl, the distribution of suitable forests is naturally disjunct (Fig. 5). For the geographic range of the Mexican Spotted Owl to be considered fragmented, connectivity must be affected to a greater degree than normally experienced in the naturally disjunct populations across the range of this subspecies. Although it is tempting to view Mexican Spotted Owl populations as a type of meta-population, there is little support for this (Keitt et al. 1995, Gutiérrez and Harrison 1998). Based on simulation modeling, Keitt et al. (1997) found that the degree to which the range of the Mexican Spotted Owl in the United States (Fig. 5) is connected could be described in terms of dispersal distance; with a dispersal distance of at least 40–50 km, forested patches went from being relatively disconnected to connected. Of 43 juveniles radio-marked by Ganey et al. (1998) and Willey and van Riper (2000), 25.6% dispersed distances at least 40–50 km (Table 3). For comparison, we examined the cumulative distribution of final dispersal distances for 48 radio-marked juvenile Northern Spotted Owls (Gutiérrez et al. 1985, Miller 1989; Table 3). If forested areas within the range of the Northern Spotted Owl were distributed in a manner similar to that of the Mexican Spotted Owl, 27.1% of the dispersing juveniles would be able to move between disjunct populations (Table 3). This suggested that a portion of a given year's juvenile cohort would be capable of connecting a landscape of disjunct habitat patches under the conditions of these studies. However, the question still remains, is this sufficient to maintain connectivity between populations and subpopulations within the geographic range to maintain both demographic processes and gene flow?

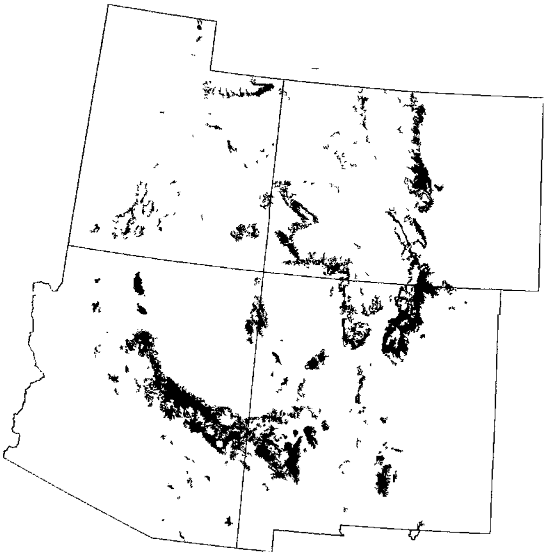

FIGURE 5. Distribution of forested areas within the range of the Mexican Spotted Owl.

We found few empirical data on the effects of fragmentation on Spotted Owl population processes at the scale of the geographic range. Only one study (Miller et al. 1997) on juvenile Northern Spotted Owl dispersal provided insights on the effect of forest fragmentation on connectivity between populations. First, Miller et al. (1997) found that juveniles used closed-canopy forests more often than expected during dispersal. Second, juveniles selected equally between less fragmented and more fragmented older forests. However, they did observe a negative relationship between net dispersal distance and the proportion of clearcuts on the landscape, suggesting that juveniles encountering more clearcuts during dispersal may be limited in their dispersal distance. Finally, mortality of juveniles appeared to increase with increased use of clearcuts when they temporarily colonized an area, but mortality decreased with increased use of open sapling stands. The openness of clearcuts

TABLE 3. CUMULATIVE DISTRIBUTION OF DISPERSAL DISTANCES OF RADIO-TAGGED JUVENILE MEXICAN AND NORTHERN SPOTTED OWLS

Final dispersal distance ≥ x km, where x =	% of juveniles dispersing at least x km		Simulated effect on range-wide forested landscape occupied by Mexican Spotted Owls (Keitt et al. 1997)
	Mexican	Northern	
10	74.4	81.3	
20	60.5	64.6	Highly disconnected
30	34.9	41.7	
40	25.6	27.1	Several independent subdivisions
50	14.0	12.5	Most patches joined
60	9.3	6.3	
70	7.0	4.2	
80	4.7	2.1	Highly interconnected

Note: Data on radio-tagged owls are from the sources listed in Table 2.

may make owls more vulnerable to predation or reduce the availability of prey because clearcuts are often dominated by dense, small shrubs. Use of other seral stages may be related to prey, such as the dusky-footed woodrat (*Neotoma fuscipes*), which achieve high abundances in early forest seral stages (Sakai and Noon 1993, Ward et al. 1998). Thus, some degree of fragmentation may not be detrimental to dispersing juvenile Northern Spotted Owls, but the effect of fragmentation of older forest may depend on the intervening matrix (i.e., clearcut versus sapling stands) between forest fragments.

Simulation models examined the potential effects of fragmentation on juvenile dispersal across the range, or portions of the range, of the three subspecies (Doak 1989, McKelvey et al. 1992, Noon and McKelvey 1992, Keitt et al. 1997). However, these models incorporated assumptions about juvenile dispersal behavior because little empirical data existed to parameterize the models. Consequently, these studies provided little real information on how habitat fragmentation affects Spotted Owls. However, the model by Keitt et al. (1997) provided valuable insights into what dispersal capabilities Mexican Spotted Owls require to connect populations across their range, and the models by Lamberson et al. (1994), McKelvey et al. (1992), and Noon and McKelvey (1992) made quantitative predictions about occupancy of habitat blocks containing different numbers of Northern Spotted Owl territories (see also review in Noon and McKelvey 1996). The predictions from these latter models have never been empirically tested.

Habitat fragmentation could potentially affect gene flow as well as population dynamics, which is a major concern of conservation biologists (Frankel and Soulé 1981). Despite the lack of support for a demographic meta-population, there is evidence of past gene flow among Mexican Spotted Owl populations, among Northern Spotted Owl populations and between Northern and California Spotted Owls (Barrowclough et al. 1999). Further, relatively little gene flow needs to occur to maintain genetic variability (Lande and Barrowclough 1987). Thus, it appears that fragmentation would likely have less effect on gene flow than demography, given what we know of juvenile Spotted Owl dispersal.

HABITAT FRAGMENTATION AT THE POPULATION SCALE

Abundance and reproductive success of Northern Spotted Owls increase with the amount of older forest (Bart and Forsman 1992). However, there are no studies relating metrics measuring forest fragmentation or heterogeneity with population performance. Although there are a large number of populations studies on Spotted Owls (see Noon et al. 1992, White et al. 1995, Forsman et al. 1996, Franklin et al. 1999 for reviews), none relate life-history traits and/or rates of population change (λ) to forest fragmentation or heterogeneity. Such studies would have to employ the population or subpopulation as the unit of comparison rather than the individual or territory (see HABITAT FRAGMENTATION AT THE TERRITORY SCALE below). For example, estimates of λ for Northern Spotted Owls on 15 studies ranged from 0.83 ($\widehat{se}(\hat{\lambda})$ = 0.02) to 0.98 ($\widehat{se}(\hat{\lambda})$ = 0.02), indicating that variation in rates of population change exists among subpopulations (Franklin et al. 1999). Thus, comparisons need to be made with subpopulations of owls inhabiting landscapes having different degrees of habitat fragmentation (e.g., the 15 separate demographic studies in Franklin et al. 1999). In addition, the methods for identifying habitats and quantifying habitat fragmentation would have to be standardized across study areas.

TABLE 4. META-ANALYSIS ON AMOUNTS OF MATURE AND OLD-GROWTH FOREST IN CIRCLES OCCUPIED BY SPOTTED OWLS VERSUS RANDOM CIRCLES ON THE SURROUNDING LANDSCAPE

Subspecies	k[a]	$\hat{\bar{d}}$	$\widehat{\text{var}}(\hat{\bar{d}})$	95% CI for $\hat{\bar{d}}$	$\hat{\sigma}^2_{process}$ (95% CI)	$\text{CV}_{process}$
Northern	7	0.680	0.011	0.474, 0.886	0.029 (0.000, 0.313)	0.251
California	1	0.352	0.085	0.218, 0.923	—[b]	—[b]
Mexican	1	0.466	0.053	0.016, 0.915	—[b]	—[b]
All subspecies	9	0.624	0.008	0.449, 0.799	0.022 (0.000, 0.230)	0.236

[a] Number of studies.

[b] Not estimable because of insufficient number of studies.

HABITAT FRAGMENTATION AT THE TERRITORY SCALE

Most research on effects of fragmentation and heterogeneity on Spotted Owls has been at the territory scale, and the majority of this work related occupancy to landscape characteristics within territories. In general, researchers examining the effects of habitat fragmentation and heterogeneity compared occupied sites (defined by circles of varying radii around an owl nest or location) with sites of equal size that were randomly placed on the surrounding landscape. Because of the large number of studies, we used some simple meta-analytical techniques to summarize the general findings (see Appendix 1 for methods). In summary, we first estimated effect sizes (d), and their sampling variance ($\text{var}(d)$) for each study. Here, the study was the sampling unit, with each study including 20–100 territories (see Appendix 1). Thus, we were able to estimate sampling variances and 95% confidence intervals of metrics for each study. Effect sizes were measures, in standard deviations, of the difference in metrics (e.g., amount of older forest) between occupied and random sites (Wolf 1986:27, VanderWerf 1992). Ideally, effect sizes should be compared with a distribution of effect sizes derived from published studies (Wolf 1986:27). Because such a distribution was unavailable, we used the rough guidelines of $\hat{d} = 0.2$ for small effects, $\hat{d} = 0.5$ for medium effects, and $\hat{d} = 0.8$ for large effects proposed by Cohen (1987). We used 95% confidence intervals to assess the degree to which effect sizes overlapped zero (no effect) for each study. Where we had ≥2 studies with the same metric (e.g., amount of old-growth), we estimated a weighted mean ($\hat{\bar{d}}$), its sampling variance ($\widehat{\text{var}}(\hat{\bar{d}})$), and an estimate of the process variation ($\hat{\sigma}^2_{process}$) of $\hat{\bar{d}}$. This process variation was an estimate of the variation in the metrics across studies and was derived by removing the sampling variation associated with each estimate of d (see Appendix 1). In most cases, there were only 2–3 studies with similar metrics. In these cases, we still estimated the effects size parameters and process variation. We recognized these estimates had limited validity for inference but we used them to pose alternative hypotheses and as an example of how a meta-analysis of these parameters would be useful if sufficient studies were available with similar metrics.

We first examined the effects of amounts of mature and old-growth coniferous forest on occupancy. We examined seven studies on the Northern Spotted Owl, ranging from Washington to northern California, one study on the California Spotted Owl, and one study on the Mexican Spotted Owl (Appendix 1). Effect sizes across all subspecies were positive, generally large, and, except for the California Spotted Owl, different from zero, indicating that sites occupied by Spotted Owls had greater amounts of older forest than sites randomly located on the forested landscape (Table 4). In addition, Northern Spotted Owls appeared to have greater effect sizes, suggesting a larger difference between occupied and random sites, than the other two subspecies (Appendix 1). However, the other two subspecies were each represented by only one study and, hence, we did not capture as much geographic variation as for the Northern Spotted Owl. In addition, sites occupied by Northern Spotted Owls on private timber lands in the Redwood Province (Fig. 1) had higher proportions of younger forests (41–60 years) than the other studies (Thome et al. 1999). On these private lands, there were few stands of older forest, but the younger stands often approached the structural characteristics of older conifer forest in the other studies because of higher growth rates in redwood (*Sequoia sempervirens*) forests (Folliard 1993).

Researchers comparing occupied and random sites used 16 different metrics of fragmentation and 6 different measures of heterogeneity (Appendix 1). Unfortunately, none of these metrics were represented by more than three studies, with most used in only a single study. In addition, the majority of the studies were on Northern Spotted Owls. We estimated effect sizes and process variance for six of the metrics examin-

TABLE 5. META-ANALYSIS OF INDICATORS OF FRAGMENTATION AND HETEROGENEITY IN CIRCLES OCCUPIED BY NORTHERN SPOTTED OWLS VERSUS RANDOM CIRCLES ON THE SURROUNDING LANDSCAPE

Metric[a]	k[b]	$\hat{d}$	$\widehat{\text{var}}(\hat{d})$	95% CI for $\hat{d}$	$\hat{\sigma}^2_{process}$ (95% CI)	$\text{CV}_{process}$
Indicators of Fragmentation						
Mean Patch Area	3	0.865	0.002	0.777, 0.953	0.000 (0.000, 0.341)	0.000
CV Patch Area	2	0.359	0.119	−0.317, 1.035	0.177 (0.000, 250.1)	0.953
Patch Density	2	0.563	0.163	−0.230, 1.354	0.260 (0.000, 338.1)	0.906
Patch Interior	2	0.440	0.045	0.024, 0.856	0.040 (0.000, 110.5)	0.455
Perimeter Density	3	0.289	0.124	−0.401, 0.979	0.342 (0.052, 15.69)	2.024
GISfrag Index	3	−0.638	0.061	−1.122, −0.154	0.141 (0.000, 8.175)	0.589
Indicators of Heterogeneity						
Shannon-Wiener Index	2	0.272	0.136	−0.451, 0.950	0.220 (0.002, 277.2)	1.676
Dominance	2	−0.307	0.169	−1.113, 0.499	0.285 (0.014, 343.9)	1.442
Contagion	2	0.642	1.147	−1.457, 2.741	0.401 (0.393, 340.3)	2.671

[a] See Appendix 1 for definitions of metrics.
[b] Number of studies.

ing fragmentation (represented by 2–3 studies) and three of the metrics examining heterogeneity (each represented by two studies; Table 5). Effects that appeared to be consistent across studies (i.e., exhibited relatively low CV in spatial process variation) were mean patch area, the amount of patch interior, and the GISfrag index of Ripple et al. (1991a; Table 5). Based on the GISfrag index, Northern Spotted Owls occupied areas having larger patches of older forest (which supported more interior forest) that were more numerous and closer together than the random sites. The effect sizes for these three metrics were different from zero based on 95% confidence intervals (Table 5). The remaining metrics for fragmentation and all the metrics for heterogeneity in Table 5 had large coefficients of spatial process variation, and had effect sizes with confidence intervals including zero. However, in almost all cases the estimates of spatial process variation had extremely large confidence intervals, indicating poor estimation due to inadequate numbers of studies. More importantly, our analysis demonstrates the lack of comparability among studies of Spotted Owl habitat fragmentation because few studies used the same metrics. Thus, there were insufficient samples for most metrics to allow meaningful conclusions.

We also partitioned the data by gross ecological provinces (West Cascades versus Klamath Provinces; Fig. 1) within the range of the Northern Spotted Owl to examine whether large differences between the provinces were responsible for the high coefficients of spatial process variation (Table 6). With the three metrics (mean patch area, interior, and GISfrag) that we considered consistent, effect sizes were similar between the two provinces and were different from zero for each individual study. With the other three metrics of fragmentation (CV patch area, patch density, and perimeter density), there appeared to be provincial differences that could have accounted for the high degree of spatial process variation observed when provinces were pooled in Table 5. Sites occupied by Northern Spotted Owls in the West Cascades province had less variable patch areas, lower patch density, and inconclusive perimeter densities in relation to random sites. The Klamath province, on the other hand, had more variable patch areas, higher patch densities, and higher perimeter densities than random sites. Only patch density was not different from zero.

Thus, it appears that Northern Spotted Owls occupy sites with greater amounts of older forest that retain higher amounts of interior forest than forested landscapes chosen at random across their range. This appeared to be consistent across provinces. However, the degree of fragmentation in occupied versus random sites in the Klamath province was greater than in the West Cascade province. This was suggested by more variable patch sizes and greater perimeter edge. However, this would only be considered habitat fragmentation if habitat for Northern Spotted Owls in the Klamath province was limited to older forest. If ecotones (represented by the perimeter of other vegetation types with older forest) are also Spotted Owl habitat, then this would not represent habitat fragmentation, but merely an additional component of Spotted Owl habitat (see Franklin et al. *this volume*).

In general, heterogeneity of vegetation types and forest seral stages appears to be higher in occupied than random sites of the Northern and Mexican Spotted Owl, but not the California subspecies (Table 7). For the Northern Spotted Owl in the West Cascades and Klamath provinces, Shannon-Wiener indices of vegetation type or seral stage diversity were higher on occupied sites, Simpson's index was lower, domi-

TABLE 6. PROVINCE DIFFERENCES IN EFFECT SIZES FOR SIX METRICS ASSOCIATED WITH FRAGMENTATION FOR NORTHERN SPOTTED OWLS

	West Cascade Province		Klamath Province	
Metric	Source	$\hat{d}$ (95% CI)	Source	$\hat{d}$ (95% CI)
Mean Patch Area	Lehmkuhl and Raphael 1993	0.914 (0.586, 1.243)	Ripple et al. 1997	0.716 (0.059, 1.372)
CV Patch Area	Lehmkuhl and Raphael 1993	0.071 (−0.242, 0.384)	Ripple et al. 1997	0.772 (0.113, 1.432)
Patch Density	Lehmkuhl and Raphael 1993	−0.405 (−0.721, −0.089)	Ripple et al. 1997	0.520 (−0.127, 1.167)
Interior	Johnson 1992	0.302 (0.001, 0.604)	Ripple et al. 1997	0.768 (0.109, 1.428)
Perimeter Density	Lehmkuhl and Raphael 1993	0.213 (−0.101, 0.527)	Ripple et al. 1997	1.028 (0.351, 1.705)
	Johnson 1992	−0.215 (−0.644, 0.085)	—	—
GISfrag Index	Lehmkuhl and Raphael 1993	−0.329 (−0.644, −0.014)	Ripple et al. 1997	−1.218 (−1.910, −0.525)
	—	—	Hunter et al. 1995	−0.591 (−1.036, −0.146)

nance was lower, and contagion was lower. The results from the East Cascades province were opposite in terms of the Shannon-Wiener index, dominance, and contagion. (Morganti 1993; Table 7). However, only contagion was different from zero. In addition, Morganti (1993) only used 3 vegetation types whereas the other researchers used 5–7; increasing vegetation types can affect the direction and the relative magnitude of all the heterogeneity metrics explored here (Morganti 1993, Meyer et al. 1998). Thus, while Spotted Owls may occupy sites with some degree of forest fragmentation in some areas, sites occupied by Northern Spotted Owls appeared to be more consistent in having higher heterogeneity throughout their range. The one study on Mexican Spotted Owls (Peery et al. 1999) had a similar effect size for Simpson's index as for the Northern Spotted Owl in California, indicating that seral stage and vegetation type diversity was higher in occupied than random sites. California Spotted Owls had the opposite trend, with occupied sites having less heterogeneity than random sites.

A few researchers examined the effects of landscape metrics on life-history traits, such as survival and reproduction. Bart (1995) found that survival increased with the amount of older forest within sites occupied by Northern Spotted Owls. However, survival in this study was measured from turnover events of unmarked birds (U. S. Dept. Interior 1992) and may not have been an unbiased measure of survival. Similarly, Ripple et al. (1997) found that a reproductive index was correlated ($r = 0.64$, $P = 0.03$) with amounts of older forest in occupied sites. However, metrics other than the amount of older forest were not included in the analyses in these two studies. In the Redwood province of northern California, Thome et al. (1999) found highest reproductive success in Northern Spotted Owls at sites that had high proportions of 21–40 year old forest stands and lower proportions of older forest. In the Klamath Province of Oregon, average annual reproductive output increased at sites with greater fractal dimension (indicating greater landscape complexity with increased edge), more older forest patches, and greater proportions of hardwood forest (Meyer et al. 1998). Their multiple regression model accounted for 56% of the variation in reproductive output. In the West Cascades province, average annual reproductive output was not explained by any of the habitat and landscape variables measured, but rather by decreased density of owls in the surrounding area, which explained 85% of the variation in reproductive output (Meyer et al. 1998). Finally, Franklin et al. (2000) examined reproductive output, survival, and the

TABLE 7. EFFECT SIZES FOR METRICS OF HETEROGENEITY MEASURED ON SITES OCCUPIED BY SPOTTED OWLS VERSUS RANDOM SITES

Metric[a]	Subspecies	Region[b]	$\hat{d}$	95% CI	Source
Shannon-Wiener Index	Northern	WCAS & KLA (OR)	0.629	0.224, 1.033	Meyer et al. 1998
Shannon-Wiener Index	Northern	ECAS (OR)	−0.109	−0.593, 0.374	Morganti 1993
Simpson's Index	Northern	KLA (CA)	−0.690	−1.147, −0.233	Hunter et al. 1995
Dominance	Northern	WCAS & KLA (OR)	−0.706	−1.114, −0.298	Meyer et al. 1998
Dominance	Northern	ECAS (OR)	0.116	−0.374, 0.607	Morganti 1993
Contagion	Northern	WCAS & KLA (OR)	−0.378	−0.778, 0.022	Meyer et al. 1998
Contagion	Northern	ECAS (OR)	1.766	1.189, 2.344	Morganti 1993
Baxter and Wolf Index	California	SIERRA	−0.775[c]	−1.366, −0.184	two studies
Simpson's Index	Mexican	NM	−0.791	−1.251, −0.330	Peery et al. 1999

[a] See Appendix 1 for definitions of metrics.

[b] WCAS = West Cascades province, KLA = Klamath province, ECAS = East Cascades province, SIERRA = Sierra Nevada Mountains; state acronyms are in parentheses.

[c] Weighted mean for two studies (Bias and Gutièrrez 1992, Moen & Gutièrrez 1997) in the same area; $\widehat{\mathrm{var}}(\hat{\bar{d}}) = 0.091$.

combination of the two in a measure of habitat-based fitness in relation to landscape habitat variables of sites occupied by Northern Spotted Owls in the Klamath province. They found that reproductive output increased at sites with more edge between older forest and other vegetation types and decreased with the amount of interior forest. Survival, however, increased with more interior older forest and increased edge. Thus, sites with high fitness represented a tradeoff, balancing the amount of interior forest with edge to achieve optimal survival and reproduction (Fig. 6).

DISCUSSION

The effects of habitat fragmentation on species richness and animal population dynamics have long been of interest to ecologists. Consequently, negative impacts of forest fragmentation on Spotted Owls were assumed without critical examination because this bird's habitat has been highly disrupted by logging over the past century (Gutiérrez 1994). Further, the Spotted Owl is thought to be declining across its range, presumably in response to loss of habitat (and by corollary to increased habitat fragmentation). The loss of habitat, owl population declines, and the federal listing of two subspecies have prompted a plethora of studies on the bird which potentially lends itself to a meta-analysis of fragmentation patterns.

Most of the initial simulation models on Spotted Owls emphasized loss of habitat rather than the explicit effects of habitat fragmentation. As

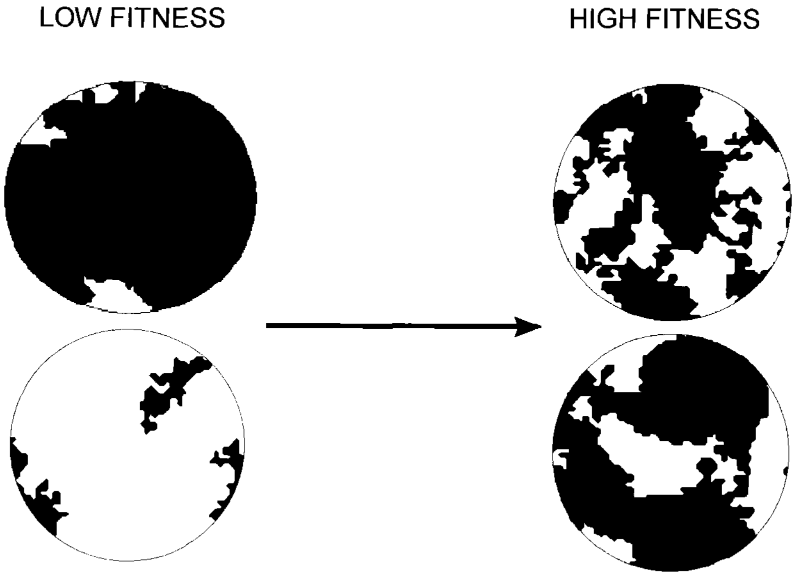

FIGURE 6. Example of occupied Northern Spotted Owl sites exhibiting low and high fitness based on habitat characteristics of those sites (Franklin et al. 2000).

Franklin et al. (*this volume*) point out, habitat loss and habitat fragmentation can have different effects when they are considered separately and at different scales. For example, the model developed by Lande (1988) predicted a threshold amount of suitable Spotted Owl habitat (older forest) below which populations should decline to extinction. This was partially corroborated by empirical studies that found no or few owls in large areas where older forests had been mostly eliminated (Bart and Forsman 1992, Johnson 1992, U. S. Dept. Interior 1992, Gutiérrez 1994). However, these results do not address the issue of critical thresholds for habitat fragmentation in Spotted Owls. Later models became more sophisticated but still only examined loss of suitable habitat (e.g., Doak 1989, Lamberson et al. 1992). The models developed by Lamberson et al. (1994), McKelvey et al. (1992) and Noon and McKelvey (1992) did make quantitative predictions about occupancy by Northern and California Spotted Owls at the range-wide scale in relation to forest patch sizes with different shapes, sizes, and inter-patch distances. However, these predictions have yet to be tested with empirical data. There has been an unfortunate disconnect between theoretical predictions made by simulation models concerning the effects of fragmentation on Spotted Owls and the testing of those predictions with empirical studies. However, this is not unique to Spotted Owls; Doak et al. (1992) argue for better merging of theory and experimentation in understanding habitat fragmentation in general.

At the three scales in the empirical studies that we examined, all three subspecies of Spotted Owl exhibit some degree of association with the structural characteristics of old conifer forest. Even when older forest is not present (e.g., the Redwood Province in the range of the Northern Spotted Owl), Spotted Owls still occupy sites that have forests structurally similar to older forest in other parts of the owl's range. However, at the territory scale there is evidence that early forest seral stages and ecotones (i.e., the interface between conifer forests and other vegetation types) may contribute to Northern Spotted Owl habitat in some areas (Franklin et al. 2000). In particular, early seral stages bordering older forest may provide both abundant and available prey for Northern Spotted Owls in the Klamath province where hardwood trees are important components of the forests occupied by Northern Spotted Owls. Thus, there is some evidence that Spotted Owls in some parts of their range may benefit from forest heterogeneity. Some of this heterogeneity may result from logging or other anthropocentric disturbance. These changes are not necessarily fragmentation (sensu Franklin et al. *this volume*), but the introduction of openings and peninsulas of different seral stages that provide edge while maintaining interior forest (see Fig. 6) and heterogeneity. The mechanisms that produce potential benefits are still poorly understood but may relate to prey abundance and availability (see Thome et al. 1999, Franklin et al. 2000). This situation may only apply to areas occupied by Northern Spotted Owls (and other subspecies) where forests are mixtures of conifers and hardwoods.

Despite the plethora of habitat-based studies on Spotted Owls, the effects of forest fragmentation and heterogeneity are still poorly understood. Even at the territory scale where most of the studies have been conducted, the many different measures and indices used in the various studies reduced our ability to draw inferences. There is no unified set of metrics for measuring fragmentation of Spotted Owl habitats; an abundance of ad hoc measures exist and often researchers develop their own. However, to understand the effects of habitat fragmentation on Spotted Owls, appropriate metrics need to be developed that can be applied across studies. In the absence of large-scale experiments, reliable knowledge (sensu Romesburg 1981) can only be achieved through replication of observational studies that use similar metrics. Such consistency does not preclude novel approaches by individual investigators. Our attempt to synthesize such studies for Spotted Owls failed in terms of inferences on the effects of fragmentation because researchers did not use similar metrics to quantify habitat fragmentation. That is, each metric of interest was represented by 3 studies at the most. Our sample of studies was also hampered because a number of researchers did not present the requisite information (means and/or standard deviations) to estimate effect sizes. However, the patterns we observed in our meta-analysis can be considered hypotheses that can be tested with more detailed meta-analyses or experimentation.

To understand forest fragmentation, habitat fragmentation, and forest heterogeneity in Spotted Owls, a number of key questions need to be addressed, such as:

1. *What is Spotted Owl habitat?* Older coniferous forest has always been considered synonymous with Spotted Owl habitat but recent studies suggest other vegetation types and landscape attributes may contribute to Spotted Owl habitat as well. Before habitat fragmentation can be assessed and understood, habitat must be properly defined (Franklin et al. *this volume*). In addition, definitions of Spotted Owl habitat can only be achieved

when the mechanisms behind the importance of various components are understood. This probably can only be achieved through analysis of empirical data (particularly of replicated studies) followed by carefully controlled experiments.

2. *Can Northern Spotted Owls and California Spotted Owls maintain viable populations under the same range-wide fragmentation as Mexican Spotted Owls?* While preliminary information on juvenile dispersal, a key process in the effects of fragmentation at the range-wide scale, is available for Northern and Mexican Spotted Owls, this information is still lacking for California Spotted Owls (Verner et al. 1992). In addition, there have been no long-term studies of juvenile dispersal specifically designed to examine the effects of heterogeneity and fragmentation.
3. *Do landscape configurations within subpopulations have the same effect as they do at the territory scale?* This question relates to habitat quality at a population scale, similar to the findings of Franklin et al. (2000) at the territory scale; that is, whether populations can be represented as meta-populations, source/sink populations, etc., with respect to fragmentation and heterogeneity. For example, populations of Spotted Owls may be able to maintain stationary populations in fragmented landscape, but are they bolstered by outside recruitment?
4. *Is timber harvesting compensatory or additive with natural disturbance regimes, such as fire?* Since fire suppression, timber harvesting has become the dominant disturbance causing fragmentation and heterogeneity on landscapes occupied by Spotted Owls. To be completely compensatory, timber harvesting activities would have to impact forests in the same manner as fire, and to be completely additive, timber harvest would have to impact the landscape in a manner very different from fire. Aside from any geochemical differences, the effects of timber harvesting on the landscape probably lie somewhere between these two extremes. Here, we use the terms compensatory and additive similarly to those used in waterfowl harvest (Nichols et al. 1984). The degree to which timber harvest and fire disturbance affect landscapes occupied by Spotted Owls is crucial to understanding land management options and potential strategies. For example, Weatherspoon et al. (1992) argue that a management policy of allowing forest succession to proceed uninterrupted by periodic natural disturbance would likely lead to habitat degradation for California Spotted Owls rather than toward biologically healthy and diverse systems. Rather, they argue management should use natural processes as a guide to management.

RECOMMENDATIONS FOR FUTURE ANALYSES OF FRAGMENTATION EFFECTS ON SPOTTED OWLS

Given the limitations with extant data on studies of fragmentation/landscape characteristics of Spotted Owls we encountered, we recommend the following:

1. Development of stronger theoretical/analytical basis for studies of fragmentation using simulation to understand how fragmentation indices relate to actual landscape configurations (Li and Reynolds 1994).
2. Testing of predictions from simulation models with empirical studies and exposition of explicit predictions from simulation models to allow for such empirical testing.
3. Linkage of useful landscape metrics with life history traits, particularly survival, reproduction, and juvenile dispersal.
4. Inclusion of alternative hypotheses that include a range of effects from positive to negative in terms of fragmentation and heterogeneity.
5. Reporting of mean and standard deviations of landscape metrics used to characterize Spotted Owl habitats.
6. Consistent reporting of useful metrics even if other, better techniques are developed (i.e., researchers should continue to use a baseline of metrics even if they use novel or additional metrics). This has become standard practice with studies of Spotted Owl home range where the Minimum Convex Polygon is consistently used in addition to other estimators even though scientists recognize that it is often biased.
7. Peer referees and editors should recognize the utility and necessity of publishing studies replicating earlier research on the same topic. Clearly, higher standards can be incorporated into replicated studies by sample size requirements (subsequent studies should have a larger or "better" sample than earlier studies), and geographic representation of sampling (studies in areas where there have not been studies previously executed).

We believe that these few recommendations will lead to stronger inference regarding the effect of habitat fragmentation on Spotted Owls. Further, we think these recommendations may serve to advance the understanding of fragmentation on other bird species and the effects of fragmentation on species in general.

ACKNOWLEDGMENTS

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APPENDIX 1

META-ANALYSIS AND HABITAT METRICS

For each metric measured in each study, we estimated an effect size (d) as:

$$\hat{d} = \frac{\bar{x}_o - \bar{x}_r}{\hat{S}}$$

(Hunter and Schmidt 1990:271) where $\bar{x}_o$ and $\bar{x}_r$ are the estimated mean from occupied and random sites, respectively, and $\hat{S}$ is the estimated pooled standard deviation, calculated as:

$$\hat{S} = \sqrt{\frac{(n_o - 1)(\hat{S}_o)^2 + (n_r - 1)(\hat{S}_r)^2}{n_o + n_r - 2}}$$

(Hunter and Schmidt 1990:271) where n_o, n_r, $\hat{S}_o$, and $\hat{S}_r$ are the sample sizes and standard deviations, respectively, for occupied and random sites within each study. In one case (Lemkuhl and Raphael 1993), standard deviations were not available so we estimated effect size between metrics from reported F-statistics (Wolf 1986:35) as:

$$\hat{d} = \frac{2\sqrt{F}}{\sqrt{df_{error}}}.$$

The sampling variance for $\hat{d}$ was estimated (Hunter and Schmidt 1990) as:

$$\widehat{\text{var}}(\hat{d}) = \left(\frac{n_o + n_r - 1}{n_o + n_r - 3}\right)\left(\frac{4}{n_o + n_r}\right)\left(1 + \frac{\hat{d}^2}{8}\right)$$

We estimated a cumulative effect size ($\hat{\hat{d}}$; sensu Rosenberg et al. 2000) across studies as:

$$\hat{\hat{d}} = \frac{\sum_{i=1}^{k} w_i \hat{d}_i}{\sum_{i=1}^{k} w_i} \qquad (1)$$

where k is the number of studies, $\hat{d}_i$ is the effect size for the kth study, and $w_i = 1/[\hat{\sigma}^2_{process} + \widehat{\text{var}}(\hat{d})]$ and the sampling variance for $\hat{\hat{d}}$ as:

$$\widehat{\text{var}}(\hat{\hat{d}}) = \frac{1}{\sum_{i=1}^{k} w_i} \qquad (2)$$

after Burnham et al. (1987:260–266). In this analysis, we partitioned process variance ($\sigma^2_{process}$; the variation across studies) in each metric from the sampling variance associated with estimating the $\hat{d}$ for each study. We estimated process variation by iteratively solving:

$$\frac{1}{n-1}\sum_{i=1}^{n}\left(\frac{1}{\sigma^2_{process} + \widehat{\text{var}}(\hat{d}_i)}\right)(\hat{d}_i - \hat{\hat{d}})^2 = 1 \qquad (3)$$

after Burnham et al. (1987:260–266). Equations (1) and (2) were solved simultaneously with equation (3) to obtain $\hat{\hat{d}}$ and $\widehat{\text{var}}(\hat{\hat{d}})$. These procedures were similar to those proposed by Rosenberg et al. (2000) for random effects modeling of d. To assess the spatial variability in metrics across studies, we used a coefficient of process variation ($CV_{process}$) estimates as:

$$CV_{process} = \frac{\hat{\sigma}_{process}}{\hat{\hat{d}}}.$$

TABLE A1. DATA USED IN META-ANALYSIS

Source	Subspecies	Province^a	Radius^b (m)	Grain^c (ha)	Occupied			Random			Effect size		
					$\bar{x}_o$	S_o	n_o	$\bar{x}_r$	S_r	n_r	$\hat{d}$	$\widehat{\text{var}}(\hat{d})$	95% CI
AMOUNT OF MATURE AND OLD-GROWTH FOREST (area [ha] of mature and old growth forest within the circular samples)													
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	1100.0	—	59	1714.0	—	100	0.405	0.026	0.089, 0.721
Ripple et al. 1991b	Northern	OR-CAS	910	0.56	203.4	30.7	30	164.4	52.6	30	0.907	0.076	0.366, 1.447
Johnson 1992	Northern	OR-CAS	1261	0.56	301.9	94.3	103	266.3	103.7	70	0.362	0.024	0.060, 0.664
Meyer et al. 1998	Northern	OR-W	800	0.25	96.3	58.8	50	49.7	47.3	50	0.874	0.045	0.460, 1.289
Ripple et al. 1997	Northern	OR-SW	1200	0.02	150.8	99.9	20	54.3	71.1	20	1.112	0.122	0.429, 1.796
Hunter et al. 1995	Northern	CA	800	0.09	94.1	26.2	33	71.8	28.1	50	0.815	0.053	0.362, 1.268
Morganti 1993	Northern	OR-S	1951	0.81	609.6	117.2	34	463.8	216.2	32	0.845	0.068	0.334, 1.357
Moen and Gutiérrez 1997	California	Sierras	1207	0.09	68.8	63.6	25	50.4	38.1	25	0.352	0.085	−0.218, 0.923
Peery et al. 1999	Mexican	NM	1000	0.09	64.7	59.5	40	34.1	71.5	40	0.466	0.053	0.016, 0.915
MEAN PATCH AREA (mean area of patches of mature and old-growth forest)													
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	544.0	559.4	59	188.0	238.6	100	0.914	0.028	0.586, 1.243
Meyer et al. 1998	Northern	OR-W	800	0.25	35.1	41.7	50	8.5	14.9	50	0.849	0.045	0.436, 1.263
Ripple et al. 1997	Northern	OR-SW	2400	0.02	167.4	225.8	20	50.1	52.4	20	0.716	0.112	0.059, 1.372
CV PATCH AREA (coefficient of variation for mean area of old-conifer forest patches)													
Ripple et al. 1997	Northern	OR-SW	2400	0.02	1.19	0.54	20	0.72	0.67	20	0.772	0.113	0.113, 1.432
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	1.94	—	59	2.02	—	100	0.071	0.025	−0.242, 0.384
PATCH DENSITY (number of patches of old-conifer forest per km^2)													
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	0.23	—	59	0.32	—	100	−0.405	0.026	−0.721, −0.089
Ripple et al. 1997	Northern	OR-SW	2400	0.02	0.31	0.31	20	0.18	0.17	20	0.520	0.109	−0.127, 1.167
INTERIOR (area [ha] of old-conifer forest remaining after subtracting a 105-m [Ripple 1997] or 100-m [Johnson 1992] wide band from the edge of each patch; Ripple et al. 1997)													
Johnson 1992	Northern	OR-CAS	1261	0.56	178.5	105.5	103	146.7	104.6	70	0.302	0.024	0.001, 0.604
Ripple et al. 1997	Northern	OR-SW	2400	0.02	214.6	216.8	20	82.1	111.6	20	0.768	0.113	0.109, 1.428
INTERIOR RATIO (proportion of all patches that are interior old-conifer forest; see Interior definition)													
Ripple et al. 1997	Northern	OR-SW	2400	0.02	0.33	0.13	20	0.17	0.16	20	1.098	0.121	0.415, 1.780
PERIMETER (perimeter [km] of mature/old-growth stands)													
Johnson 1992	Northern	OR-CAS	1261	0.56	10.38	3.65	103	10.34	4.10	70	0.010	0.023	−0.289, 0.310
PERIMETER DENSITY (km of perimeter of old-conifer forest patches divided by the amount of old-conifer forest [km^2] within sample circles; referred to as Edge/Area index in Johnson 1992)													
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	2.25	—	59	1.98	—	100	0.213	0.026	−0.101, 0.527
Ripple et al. 1997	Northern	OR-SW	2400	0.02	2.76	1.08	20	1.41	1.51	20	1.028	0.119	0.351, 1.705
Johnson 1992	Northern	OR-CAS	1261	0.56	0.04	0.03	103	0.05	0.02	70	−0.215	0.024	−0.516, 0.085
EDGE (ha of old forest within 100 m of the perimeter interior to a mature/old growth stand)													
Johnson 1992	Northern	OR-CAS	1261	0.56	123.4	41.6	103	119.6	41.0	70	0.092	0.023	−0.208, 0.392
EDGE % (percentage of total edge cells that were between Spotted Owl habitat and other habitats)													
Morganti 1993	Northern	OR-S	1951	0.81	21.6	5.6	34	18.7	6.7	32	0.471	0.064	−0.026, 0.968

TABLE A1. CONTINUED

Source	Subspecies	Province[a]	Radius[b] (m)	Grain[c] (ha)	Occupied			Random			Effect size		
					$\bar{x}_o$	S_o	n_o	$\bar{x}_r$	S_r	n_r	$\hat{d}$	$\widehat{\mathrm{var}}(\hat{d})$	95% CI
EDGE INDEX (Patton [1975] edge index that relates the linear extent of edge for stands of a given type to the perimeter of a circle derived from the area of stands [circles have least perimeter for a given area]; values range from 1, indicating no increase in edge, to >1 indicating proportional increase in edge over that of a circle).													
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	5.22	—	59	5.68	—	100	0.174	0.026	−0.140, 0.487
EDGE/AREA RATIO (index of the proportional deviation of the amount of edge around old-growth patches from the amount of edge expected for old-growth patches containing that much area; values ranged from <0, indicating more edge than expected to >0, indicating less edge than expected for the area of old growth present)													
Meyer et al. 1998	Northern	OR-W	800	0.25	1.03	0.21	50	1.02	0.16	50	0.022	0.041	−0.374, 0.418
PERIMETER/AREA FRACTAL (fractal index based on O'Neill et al. 1988)													
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	1.28	—	59	1.25	—	100	0.160	0.026	−0.154, 0.473
FRACTAL DIMENSION (fractal dimension of all successional stages; values ranged from 1, indicating square patches, to 2, indicating highly convoluted patch perimeters).													
Meyer et al 1998	Northern	OR-W	800	0.25	1.29	0.07	50	1.31	0.07	50	−0.325	0.041	−0.724, 0.073
NEIGHBORHOOD INDEX (index of owl habitat availability within the daily foraging range of an owl; values ranged from 0 to 1)													
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	0.50	0.27	59	0.32	0.22	100	0.751	0.027	0.427, 1.075
DISPERSION SCORE (relative index of how clumped [minimum fragmentation] or dispersed [maximum fragmentation] old-forest stands were distributed; values ranged from −1500, indicating maximally dispersed forest stands, to 1500, indicating maximum clumping of old forest)													
Johnson 1992	Northern	OR-CAS	1261	0.56	−168.0	162.4	103	−153.0	133.9	70	−0.099	0.023	−0.399, 0.201
GISFRAG INDEX (the mean distance to the nearest old-conifer forest patch from each grid cell in the sample area based on Ripple et al. [1991a]; values ranged from near 0, indicating more old-conifer forest patches and shorter distances between patches, to high values, indicating fewer old-conifer forest patches, less connectivity, and longer distances between patches; Hunter et al. [1995] and Lemkuhl and Raphael [1993] used modified version of this index)													
Ripple et al. 1997	Northern	OR-SW	2400	0.02	373.00	272.00	20	1331.0	1079.0	20	−1.218	0.125	−1.91, 0.525
Hunter et al. 1995	Northern	CA	800	0.09	26.30	12.60	33	39.70	27.30	50	−0.591	0.052	−1.036, 0.146
Lehmkuhl and Raphael 1993	Northern	WA-OLY	3218	1.00	0.032	—	59	0.084	—	100	−0.329	0.026	−0.644, −0.014
TAYLOR INDEX (Taylor [1977] index of patchiness that is the probability of encountering a different successional stage when traveling from 1 raster cell to the next along the vertical and horizontal center of the raster map; values ranged from 0, indicating only 1 successional stage encountered, to 1, indicating no 2 adjacent grid points along the axes had the same successional stage)													
Meyer et al. 1998	Northern	OR-W	800	0.25	0.11	0.04	50	0.01	0.05	50	0.304	0.041	−0.095, 0.702
SIMPSON'S INDEX (Simpson [1949] diversity index that provides a measure of vegetation stand and seral stage heterogeneity; values range from 0, indicating highest diversity to 1, indicating no diversity)													
Hunter et al. 1995	Northern	CA	800	0.09	0.64	0.09	33	0.69	0.06	50	−0.690	0.054	−1.147, −0.233
Peery et al. 1999	Mexican	NM	1000	0.09	0.48	0.13	40	0.58	0.13	40	−0.791	0.055	−1.251, −0.331
SHANNON-WIENER DIVERSITY INDEX (combines information on the number of successional stages [s] with evenness of their percent representation; values range from near 0, indicating dominance by one successional stage, to $\log_e[s]$, indicating all successional stages were equally represented; maximum value was $\log_e[7] = 1.95$ and $\log_e[3] = 1.10$ for Meyer et al. [1998] and Morganti [1993], respectively)													
Meyer et al. 1998	Northern	OR-W	800	0.25	1.25	0.25	50	1.05	0.37	50	0.629	0.043	0.224, 1.003
Morganti 1993	Northern	OR-S	1951	0.81	0.96	0.10	34	0.97	0.10	32	−0.109	0.061	−0.593, 0.374

TABLE A1. CONTINUED

Source	Subspecies	Province[a]	Radius[b] (m)	Grain[c] (ha)	Occupied			Random			Effect size		
					$\bar{x}_o$	S_o	n_o	$\bar{x}_r$	S_r	n_r	$\hat{d}$	$\widehat{\mathrm{var}}(\hat{d})$	95% CI
DOMINANCE (scaled index of dominance of forest successional stages; values range from 0, indicating equal representation of all successional stages or vegetation types, to 1, indicating complete dominance by a single seral stage or vegetation type)													
Meyer et al. 1998	Northern	OR-W	800	0.25	0.19	0.11	50	0.30	0.19	50	−0.706	0.043	−1.114, −0.298
Morganti 1993	Northern	OR-S	1951	0.81	0.51	0.05	34	0.50	0.05	32	0.116	0.063	−0.374, 0.607
BAXTER AND WOLF INDEX (count of changes in vegetation along 2 perpendicular transects; Baxter and Wolf 1972)													
Moen and Gutiérrez 1997	California	Sierra	1207	0.09	18.24	4.25	25	23.60	5.08	25	−1.145	0.097	−1.757, −0.533
Bias and Gutiérrez 1992	California	Sierra	1000	0.09	3.85	1.23	52	4.99	2.21	760	−0.529	0.021	−0.812, −0.245
CONTAGION (scaled index of the patchiness of successional stages and vegetation types; values range from 0, indicating numerous small patches, to 1, indicating few, large patches)													
Meyer et al. 1998	Northern	OR-W	800	0.25	0.76	0.07	50	0.79	0.09	50	−0.378	0.042	−0.778, 0.022
Morganti 1993	Northern	OR-S	1951	0.81	0.95	0.01	34	0.93	0.01	32	1.766	0.087	1.189, 2.344

[a] WA = Washington, OR = Oregon, CA = California, NM = New Mexico, OLY = Olympia, CAS = Cascades, W = western, SW = southwestern, S = southern.

[b] Radius of the circle used to define occupied and random sites.

[c] Resolution of smallest patch.