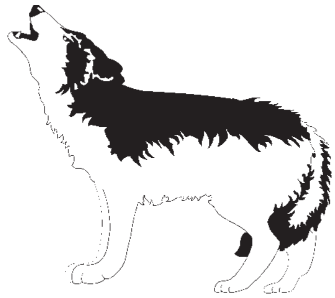
In My Opinion: Managing habitat for dispersing northern spotted owls—are the current management strategies adequate?



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When the northern spotted owl (*Strix occidentalis caurina*) was listed under the Endangered Species Act (ESA) as threatened in 1990, a number of challenges immediately became apparent. One of the first to surface was the need to develop definitions of suitable habitat that could be used in the regulatory environment. Consequently, in the early years following ESA listing, much attention was directed at defining habitats that spotted owls used for nesting, roosting, or foraging. The emphasis of research on various aspects of the structure, quality, quantity, or landscape configuration of nesting habitats throughout the owl's distribution was considerable (e.g., Carey et al. 1990, Lehmkuhl and Raphael 1993, Buchanan et al. 1995, Meyer et al. 1998, LaHaye and Gutiérrez 1999) and overshadowed efforts to investigate the habitat conditions used by owls during dispersal (Miller et al. 1997).

After the Northwest Forest Plan was adopted to manage spotted owl populations on federal lands (Forest Ecosystem Management Assessment Team [FEMAT] 1993), regulations were implemented for the management of nonfederal lands in the region. In Washington, for example, the Northwest Forest Plan and state forest practices rules (in 1996) identified key landscape areas where the emphasis of spotted owl conservation would be the management of nesting, roosting, foraging, and dispersal habitats. On federal lands, spotted owl nesting habitat would be managed in late-successional reserves (LSRs). Federal lands between the LSRs would be managed largely for timber production (within the "matrix") or a combination of wildlife and human needs in "adaptive management areas" (FEMAT 1993). Areas between the LSRs would need to facilitate movement by juvenile and adult spotted owls among the LSRs. Nonfederal landscapes designated as Spotted Owl Special Emphasis Areas (SOSEAs) would provide demographic support, dispersal support, or a combination of these 2 functions under the state's forest practices rules (Washington Administrative Code 222-16-086). The SOSEAs are all adjacent to federal lands, and several are expressly designated as, or contain sub-units designated as, landscapes where spotted owl dispersal is of primary management importance.

In 1992 the United States Fish and Wildlife Service (USFWS) approved the first Habitat Conservation Plan (HCP) for spotted owls in the region (Simpson Timber Company 1992). This was followed by implementation of additional HCPs, many of which provided dispersal habitat as mitigation for incidental take permits that allowed harvest of forest used by territorial spotted owls for nesting, roosting, or foraging. These dispersal-based plans have been implemented on hundreds of thousands of hectares in the Pacific Northwest.

Despite this shift from retention of mature and older forests to management of younger forests as dispersal habitat, an interest in investigating the effectiveness of dispersal management plans has not emerged. This is surprising because dispersal long has been recognized as an essential component of spotted owl management (e.g., see Appendix P in Thomas et al. 1990). Moreover, dispersal has been an important ecological and management consideration for other listed species. Researchers and managers in the southeastern United States learned, for example, that poor landscape connectivity required the translocation of red-cockaded woodpeckers (*Picoides borealis*) to establish or maintain population clusters (DeFazio et al. 1987). Consequently, the importance of developing credible landscape-level dispersal management plans is not a trivial concern. For this reason, I reviewed the available proposed and implemented dispersal management plans for northern spotted owls. The objectives of this paper are to 1) describe and explain the origins of the various definitions of dispersal habitat used in management, and 2) provide a preliminary evaluation of the suite of dispersal management strategies developed for spotted owls in the Pacific Northwest.

Dispersal and dispersal habitat

Dispersal is an important life-history stage for all wildlife species. It is a primary mechanism of gene flow among populations and by which individuals search out and acquire mates and colonize new territories. For this reason a considerable amount of effort has gone into studies of spotted owl dispersal behavior (Forsman et al. 1984, Miller et al. 1997, Ganey et al. 1998, LaHaye et al. 2001, Forsman et al. 2002). Much of this research has been used in ongoing spotted owl conservation efforts. Estimates of λ (lambda; the rate of population growth or decline), an analytical tool used to evaluate population performance, are sensitive to rates of emigration by juveniles (Forsman et al. 1996, Raphael et al. 1996). Dispersal was a key consideration in conservation strategies developed by the Interagency Spotted Owl Scientific Committee (Thomas et al. 1990; see Murphy and Noon 1992), the Spotted Owl Recovery Team (United States Department of the Interior [USDI] 1992), and for implementation of the Northwest Forest Plan (FEMAT 1993). The recovery strategy involved establishing a network of reserves across the landscape that would each support a cluster of breeding pairs. The amount of suitable habitat, size and spacing of reserves, and likelihood of successful dispersal were all important considerations in this reserve network design (Lamberson et al. 1992, 1994).

Dispersal can be defined in several ways. A variety of movements, such as might occur following a failed breeding attempt or efforts to prospect for new mates or territories, might be described as dispersal behavior because they involve an animal moving across a landscape, perhaps in unfamiliar terrain, searching for prey, habitat, or a mate (e.g., this would include "breeding dispersal" by spotted owls; see Forsman et al. 2002). For the purposes of this discussion, however, dispersal is defined as the collective movements of a juvenile during the period starting at departure from the natal area and ending at territory acquisition (Greenwood 1980, Miller et al. 1997). Miller et al. (1997) considered the dispersal process to consist of 2 distinct phases that they referred to as transience and colonization. The transient phase of dispersal included extensive or rapid movement through an area, whereas colonization indicated nonterritorial, short-term residence in an area. Juvenile spotted owls in the Pacific Northwest annually begin dispersing in September and October (Forsman et al. 1984, 2002) and typically move rapidly away from the natal area (transience), followed by varying periods of colonization and transience (Forsman et al. 2002).

Only one study has been conducted to examine the relationship between dispersing spotted owls and forest conditions across a landscape. This study, conducted in western Oregon, found a strong association between locations of dispersing spotted owls and old-growth forests (Miller et al. 1997). During the transience phase of dispersal, old-growth forest was used in proportion to its availability in the landscape (mean use = 35%; mean availability = 31%), whereas during colonization old-growth forest was used more than expected (mean use = 61%, mean availability = 33%; Miller et al. 1997). Closed sapling-pole-sawtimber stands (CSPS; stands of 2.5–53.3 cm dbh [diameter at breast height] trees with canopy closure of >60%) and "other" (reservoirs, rock outcrops, pastures, towns) landscape attributes were used in proportion to their availability during transience. Open sapling-pole stands (OSP; stands of 2.5–22.9 cm dbh trees and <60% canopy closure) and clearcuts (stands of <2.5 cm dbh trees and <40% canopy closure) were used proportionally less than would be expected based on availability during transience. During the colonization phase, the CSPS cover type was used slightly more than expected, and the OSP and "other" cover types were used proportionally less than expected (Miller et al. 1997).

The mortality rate of dispersing owls in western Oregon was associated with differing use of forest cover types (Miller et al. 1997). The mean mortality rate was lower for owls that used more OSP stands, compared to owls that did not use this cover type, and this may have been due to an abundance of an important food source, the dusky-footed woodrat (*Neotoma fuscipes*), in those stands (Miller et al. 1997). The primary sources of mortality among dispersing spotted owls were predation (68%) and starvation (26%) (Forsman et al. 2002). The degree to which starvation predisposed dispersing spotted owls to predation was unknown (Forsman et al. 2002). The study by Miller et al. (1997) did not evaluate the influences of landscape composition, in terms of stand age or successional stage, on mortality or the dispersal behavior of spotted owls. Their study landscapes contained stands of older forest and therefore likely differed from most of the landscapes where dispersal plans have been developed on nonfederal lands.

Management strategies for dispersal habitat

A number of different strategies have been developed for spotted owl dispersal management since 1990. These strategies included definitions of stand and landscape level features, some of which have become key elements of ongoing management efforts on federal and nonfederal lands. Many of the 18 proposed or implemented definitions (Table 1) were derived from a definition negotiated for the Murray Pacific Habitat Conservation Plan (Beak Consultants 1993). Some definitions were similar to or adopted the definition proposed by the Interagency Spotted Owl Scientific Committee (the "50-11-40" rule; Thomas et al. 1990).

Although the definitions differed in a number of ways, there were substantial similarities (Table 1). All of the definitions had a component for tree abundance, basal area, or canopy closure. Most definitions (72%) stated a proportion of the landscape that would be managed to a specific stand-level value. Two definitions included a description of the maximum allowable distance between patches of suitable dispersal habitat, and 4 definitions defined minimum patch size. Although several definitions called for snag retention, none of them *required* retention and many allowed snags to be removed and accounted for by "green recruitment trees." In most cases these trees could be small (e.g. 25–30 cm dbh). Nearly all stand-level definitions characterized dispersal habitat as very young forest lacking elements of structural diversity. Several elements of the Beak Consultants (1993) definition were based solely on aspects of forest growth patterns (Table 2). Most importantly, none of the definitions was explicitly linked to empirical data on spotted owls needed to support either the stand- or landscape-level components.

Are the management strategies adequate?

To date, there has been no attempt to empirically evaluate the adequacy of the proposed or implemented strategies for management of spotted owl dispersal habitat. Because of the lack of research to investigate or evaluate the dispersal strategies, a full evaluation of the strategies must await research on the topic. A preliminary evaluation, however, can be based in part on the hypotheses posited to explain the spotted owls' general preference for structurally complex older forests (Carey 1985). An evaluation of the factors identified by the original hypotheses may be useful in that the degree of consistency between the factors and the dispersal management strategies might provide an indication of the appropriateness of the strategies. The hypotheses summarized by Carey (1985) addressed habitat use relating to: nesting requirements, amelioration of heat stress, prey abundance, prey availability, predation risk, and ecological adaptation. The first hypothesis, that structurally complex forest is required for nesting, will not be discussed because nesting opportunities are not required by spotted owls during the dispersal phase. It is noteworthy, however, that successfully dispersing California spotted owls (*S. o. occidentalis*) often settled in previously used territories (LaHaye et al. 2001), indicating that juvenile spotted owls were able to use cues that revealed information about aspects of habitat quality when selecting an area in which to settle.

Amelioration of heat stress

Spotted owls are believed to have little tolerance of high temperatures (Weathers et al. 2001). Forests with multiple canopy layers generally provide greater thermoregulation opportunities for owls compared to conditions found in younger forest stands with simple canopy structure (Forsman 1976, Barrows and Barrows 1978, Barrows 1981, Forsman et al. 1984). Juvenile spotted owls in the Pacific Northwest begin dispersal in September and October (Forsman et al. 2002). Temperatures in the autumn are usually rather moderate compared to the summer months, so heat stress may not be an important factor at the beginning of the natal dispersal period. Conversely, because most first- and second-year owls do not breed, and may not hold territories, they, or other nonterritorial owls (i.e., those engaged in breeding dispersal), may disperse

Table 1. Elements of the 18 strategies developed (or proposed) to provide spotted owl dispersal habitat in Washington or Oregon between 1990 and 1999. The strategies are listed in approximately the sequence of their development; strategies described in Washington Forest Practices Board (2002) were developed in 1996.

Definition	Application area	Stand-level attributes	Landscape-level attributes
Interagency Spotted Owl Scientific Committee "50-11-40 rule" (Thomas et al. 1990)	Federal land in Washington, Oregon and California	Mean tree size of ≥28 cm dbh (diameter at breast height); canopy closure ≥40%.	At least 50% of the landscape outside Habitat Conservation Area (HCA) boundaries would meet stand-level conditions. Also, would have retained patches of ≥32 ha of suitable owl habitat at or near former spotted owl site centers, at an average of seven per township, in areas between HCAs.
Beak Consultants (1993)	Murray Pacific HCP; Western Cascade Mountains, Washington	Conifer forest with ≥70% canopy closure; ≥130 and ≤ 300 trees/0.4 ha that were ≥25 cm dbh (or larger trees of an equivalent basal area); where possible, retained ≥2 dominant or co-dominant trees and 3 snags ≥46 cm dbh per 0.4 ha of harvest; retained ≥2 30-cm diameter, 6.1 m logs per 0.4 ha at harvest.	Arranged forest patches such that stands of dispersal habitat were spaced no more than 0.4 km apart. About 43% of the ownership would meet the defined conditions by year 50, and would remain at this approximate amount between years 50 and 100.
Spotted Owl Science Advisory Group (Buchanan et al. 1994)	Unspecified nonfederal lands; Eastern Cascade Mountains, Washington	Supported "50-11-40" rule of the ISC (see above; Thomas et al. 1990) on an interim basis.	Supported "50-11-40" rule of the ISC (see above; Thomas et al. 1990) on an interim basis.
Spotted Owl Science Advisory Group (Buchanan et al. 1994)	Unspecified nonfederal lands; Western Washington	Supported Beak Consultants (1993) definition (see above) on an interim basis.	Supported Beak Consultants (1993) definition (see above) on an interim basis.
Northwest Forest Plan (USDA and USDI 1994)	Federal lands in Washington, Oregon and California	Not addressed.	In matrix areas (landscapes, between reserved areas, where timber harvest was emphasized) retained a) ≥15% of the green trees on each harvest unit, b) 40 ha of habitat around former owl site centers, and c) forest buffers along streams, ponds and wetlands. The remainder of the forest in matrix areas would be managed on a rotation age of ≥100 years.
Washington Forest Practices Rules (Washington Forest Practices Board 2002)	Nonfederal lands; Western Washington	Forest stands with ≥70% canopy closure; At least 70% composition of conifer trees ≥15 cm dbh; ≥130 and ≤300 trees/0.40 ha with a dbh of ≥25 cm or a basal area of 30 m of 25 cm or larger trees; ≥6.1 m of open space (relatively free of dead limbs) between the top of the understory vegetation and the bottom of the live canopy.	Forest stands ≥2 ha in size.
Washington Forest Practices Rules (Washington Forest Practices Board 2002)	Nonfederal lands; Eastern Cascade Mountains, Washington	Forest stands with ≥50% canopy closure; ≥50 and ≤200 conifer trees/0.4 ha with a dbh of ≥15 cm in even-aged stands, or ≥10 cm in uneven-aged stands (or a quadratic mean diameter of ≥23 cm and a relative density of ≥33); an average tree height of ≥20 m; ≥6.1 m of open space (relatively free of dead limbs) between the top of the understory vegetation and the bottom of the live canopy.	Forest stands ≥2 ha in size.

(*Continued*)

[a] HCP not implemented.

[b] Relative density is the basal area divided by $QMD^{0.5}$ (Curtis 1982).

[c] The quadratic mean is the square root of the arithmetic mean of squared values (Curtis and Marshall 2000).

Table 1 (*continued*). Elements of the 18 strategies developed (or proposed) to provide spotted owl dispersal habitat in Washington or Oregon between 1990 and 1999. The strategies are listed in approximately the sequence of their development; strategies described in Washington Forest Practices Board (2002) were developed in 1996.

Definition	Application area	Stand-level attributes	Landscape-level attributes
Longview Fibre Company (1995)[a]	Columbia Gorge, Washington	Conifer-dominated stands of an average height of ≥15 m with 321 – 741 trees/ha of >10 cm dbh.	Not addressed.
Rayonier Wildlife Plan (WFPB 1996)	Rayonier Wildlife Plan Area; Western Olympic Peninsula, Washington	Forest stands ≥30 years old; ≥70% conifer, <400 trees/0.4 ha, a quadratic mean diameter of 23 cm, and a basal area of 28 m^2/0.4 ha.	An estimated 40% of the plan area would meet or exceed the definition of dispersal habitat by 2020; the average amount of dispersal habitat at 5-year increments between 2025 and 2045 was predicted to be 43.8%. Also, a limit on clearcut size of 49 ha, a commitment that no less than 30% of the plan area would be commercially thinned during a rotation, that 3% of the area would remain in fixed reserves and 5% in floating reserves, and that 5% of the stands would be pruned during a rotation.
Weyerhaeuser Company (1995)	Millicoma Tree Farm; Western Oregon	Forest stands with ≥70% dominant or co-dominant conifers; ≥120 and ≤300 trees/0.4 ha with ≥25 cm dbh (or equivalent basal area constituted by fewer but larger trees); co-dominant tree height of ≥21 m; ≥6 m of clear sub-canopy space; ≥2 live trees or snags/0.4 ha, on average, of ≥9 m height and 28 cm dbh; ≥2 hard logs/0.4 ha ≥5 m long and ≥30 cm) in diameter. Possible future modification up to 400 trees/0.4 ha.	Forest stands ≥2 ha in size.
Plum Creek HCP (Hicks and Stabins 1995, Plum Creek Timber Company, Inc. 2000)	"I-90 Corridor", Western Cascade Mountains, Washington	Foraging and dispersal habitat based on Beak Consultants (1993), but including relative density[b] of 30–48 (equivalent to 175–280 trees/0.4 ha) in uplands,relative density of 48 in riparian areas; quadratic mean diameter (QMD)[c] of 25 cm in stands dominated by conifers.	Between 2006 and 2045, 6–10% of the plan area would meet definition of nesting roosting and foraging habitat; 7–34% would meet definition of foraging and dispersal habitat (combined totals would range between 17 and 42%). These goals will have been considered met if actual values are within 10–20% of the incremental or final targets.
Plum Creek HCP (Hicks and Stabins 1995, Plum Creek Timber Company, Inc. 2000)	"I-90 Corridor", Eastern Cascade Mountains, Washington	Foraging and dispersal habitat based on Beak Consultants (1993), but including forest stands dominated by Douglas-fir, ponderosa pine, and true fir, with a relative density of 33 and a QMD of 23 cm.	See above.
Weyerhaeuser Willamette (Weyerhaeuser Company 1996)[a]	Willamette Tree Farm; Central-western Oregon	At least 4 snags or green trees/0.4 ha of ≥30 cm dbh and ≥9 m height (snags and leave trees could be retained within riparian areas); would retain one live conifer ≥81 cm dbh (9 m tall), if possible, per 8 ha of harvested timber. Foraging habitat (used in landscape definition) defined as stands with ≥30% conifers, ≥70% canopy cover, 115 – 280 stems ≥10 cm dbh/0.4 ha, and dominant and co-dominant trees of ≥26 m (except in thinned stands, where trees could be shorter).	Would maintain ≥40% of the landscape, beyond 2025, in stands of ≥pole timber, including ≥20% foraging habitat (see stand-level attributes) in "zone 1" and ≥10% foraging habitat in "zone 2"; ≤20% of the landscape would be > 0.4 km from reserved areas or stands of ≥pole timber; would maintain approximately 243 ha of suitable habitat in connectivity patches, and temporarily maintain about 486 ha of habitat until equivalent new habitats developed on adjacent federal lands. A 28-ha core around known spotted owl site centers would be protected until the site became inactive, at which point the core could be harvested.

(*Continued*)

[a] HCP not implemented.
[b] Relative density is the basal area divided by $QMD^{0.5}$ (Curtis 1982).
[c] The quadratic mean is the square root of the arithmetic mean of squared values (Curtis and Marshall 2000).

Table 1 (*continued*). Elements of the 18 strategies developed (or proposed) to provide spotted owl dispersal habitat in Washington or Oregon between 1990 and 1999. The strategies are listed in approximately the sequence of their development; strategies described in Washington Forest Practices Board (2002) were developed in 1996.

Definition	Application area	Stand-level attributes	Landscape-level attributes
Crown Pacific (Biota Pacific Environmental Services 1999) [a]	Crown Pacific lands; North-western Cascade Mountains, Washington	Basic definition from Beak Consultants (1993) was adopted. In addition, ≥30% coniferous species, co-dominant trees ≥26 m tall, minimum tree diameter (counting trees ≥10 cm dbh) of 25 cm, tree density (of trees ≥10 cm dbh) of 115–280/0.4 ha, and ≥70 canopy closure. Would retain all safe snags >38 cm dbh along with ≥6 retention trees/0.4 ha (≥25 cm dbh and of which 3 are ≥38 cm dbh) of the harvest area.	Basic definition from Beak Consultants (1993) was adopted. In addition, stand-level definitions would apply to 50% of dispersal habitat on Class I-IV lands; minimum stand size of ≥8 ha and minimum stand width of ≥61 m. All snags or retention trees could be situated in riparian management zones and unstable slope areas.
Oregon Department of Forestry (1995)	Elliot State Forest; Oregon Coast Range	Essentially adopted the "50-11-40 rule" at the scale of quarter-township management areas. For other state lands defined dispersal habitat as forests with a QDBH of 28 to 45 cm.	Essentially adopted the "50-11-40 rule" at the scale of quarter-township management areas. For the North Coast Region, retained 70% of the landscape as dispersal habitat in areas outside breeding clusters; these landscapes would also contain 70% forests older than 50 years (including ≥10% with older forest structure) by year 50 of the plan.
Washington Department of Natural Resources (WDNR 1997)	DNR lands; Western Cascade Mountains, Washington	Forest stands with ≥70% canopy cover; ≥28 cm QDBH for the largest 100 trees/0.4 ha; the 40 tallest trees/0.4 ha ≥26 m tall; retention of ≥4 trees of the largest diameter class at harvest.	Dispersal landscapes would be managed such that 50% of the stands met the stand-level criteria.
Washington Department of Natural Resources (WDNR 1997)	DNR lands; Eastern Cascade Mountains, Washington	Forest stands with ≥50% canopy closure; ≥40 overstory trees/0.4 ha of ≥28 cm dbh; tree height of ≥18 m; retention of ≥4 trees of the largest diameter class at harvest.	Dispersal landscapes would be managed such that 50% of the stands met the stand-level criteria.
Weyerhaeuser-U.S. Forest Service land trade (Foster Wheeler Environmental Corporation 1996, U.S. Fish and Wildlife Service 1997)	Weyerhaeuser lands; Western central Cascade Mountains, Washington	From Washington Forest Practices Rules (Washington Forest Practices Board 2002). Foraging habitat defined as stands with ≥30% conifer stems, ≥70% canopy closure, 115 – 280 stems/0.4 ha of ≥10 cm dbh, and dominant/co-dominant trees of ≥26 m height, except for commercially-thinned stands where minimum tree height was 21 m. Snags would be retained where feasible and safe.	At least 40% of the plan area would meet the definition of dispersal habitat used in the land trade agreement. At least 37.5% of the dispersal habitat would be foraging habitat. Also, ≤20% of the area (roughly 5,261 ha) would be more than 0.4 km from patches ≥2 ha of dispersal habitat, with wildlife reserve trees (≥3/0.4 ha), if available, that were ≥3 m tall and ≥30 cm dbh, and green retention trees (2/0.4 ha; ≥25 cm dbh, ≥9 m tall, and at least 1/3 of height in live crown) would be retained in harvest units. The reserve and recruitment trees could be clumped in riparian or wetland management zones or across the landscape. In each 0.4 ha of forest harvested 2 downed logs (30 cm dia. at small end and ≥ 6.1 m in length, or an equivalent volume of larger logs) would be retained. A 28-ha core centered on any current spotted owl site center would be retained until site abandonment, at which time the core could be harvested.

[a] HCP not implemented.

[b] Relative density is the basal area divided by $QMD^{0.5}$ (Curtis 1982).

[c] The quadratic mean is the square root of the arithmetic mean of squared values (Curtis and Marshall 2000).

Table 2. Rationale for inclusion of specific required elements in the definition of spotted owl dispersal habitat developed for the Murray Pacific Habitat Conservation Plan (from Beak Consultants 1993). This plan, the first HCP in the Pacific Northwest, was developed for a 21,000+ ha tree farm in the western Cascade Mountains foothills in Washington. The rationale for snags and leave-trees was not provided because snags were not a required element of the plan. See Table 1 for the specific values of the elements included in the definition.

Element	Rationale
Tree species composition	Coniferous forests provide thermal cover and protection from precipitation, particularly during autumn and winter periods.
Tree size and density	25-cm trees provide perch opportunities in and below the canopy because such trees have branches of suitable size (3.8 cm at the base) for an owl to use. Stands grown at a density of ≥130 trees/0.4 ha would self-prune and provide open space for spotted owls flying through the understory. An upper limit of 300 trees/0.4 ha was identified as a compromise density at which tree mortality occurs due to competition.
Canopy "lift"	Spotted owls must be able to fly in the forest understory. An open area of 6.1 m between the ground and the canopy would occur on the plan area when trees were about 25 cm dbh and were able to self-prune if grown at a density of more than 130 trees/0.4 ha.
Canopy closure	This amount of canopy closure would occur at a density of 130 trees/0.4 ha.
Downed wood	The level of retention at harvest reflected current Forest Practices Rules.
Size of and spacing between patches	On average, a stand of 16 ha had an edge-to-interior ratio of 1:1; therefore, the average harvest size in the HCP would be 16 ha, and ranged from 2–49 ha. No rationale was given for using a 0.4-km spacing between patches, but it was inferred to reduce the number of crossings an owl would make over openings or areas of unsuitable habitat.
Percentage of landscape	It was inferred that a landscape with a high proportion of dispersal habitat would reduce the likelihood of predation by creating more cover and reducing the number of times owls would cross open areas where predation risk would be higher.

during subsequent summers (in either transience or colonization mode). These owls would benefit by the presence of structurally complex forest during those periods.

Prey abundance

The spotted owl's primary prey in much of the Pacific Northwest is the northern flying squirrel (*Glaucomys sabrinus*) (e.g., Forsman et al. 1984, 2001). Carey et al. (1999) found that capture rates of squirrels were higher in "niche diversification" (4.0±0.3 /100 trap nights) and old-growth (3.2± 0.1) stands compared to forests in the younger, competitive-exclusion phase of development (2.6± 0.2). They also found that capture rates of squirrels were positively associated with the amount of coarse woody debris in the stand. In fact, presence and amount of coarse woody debris explained 40% of variance in the carrying capacity of flying squirrels. Feen (1997) found that squirrel winter den sites were in areas with a greater basal area of dead conifer trees as compared to random sites. Carey et al. (1997) reported a strong positive association between abundance of large snags and population size of flying squirrels throughout the Pacific Northwest. Among the likely reasons for this relationship were 1) flying squirrels tended to den communally and therefore required larger-diameter snags (Carey et al. 1999), and 2) flying squirrels change dens often and therefore require a good number of snags or cavity trees within the home range (Carey et al. 1997). Also, Amaranthus et al. (1994) found that the abundance of truffles, an important food source for flying squirrels, was 20–30 times higher in 180-year-old forest than in 4–27-year-old forests with 11–14% cover of downed wood. It is unknown at what stage of forest development the abundance of truffles begins to approach levels noted in older forests.

Spotted owls also prey on a wide range of other small-mammal species (Forsman et al. 2001), and the collective abundance of these species may vary as a function of forest structure. Research conducted in the southern Cascade Mountains of Washington found that the combined total number of captures (per 100 trap-nights) of all small mammals was higher in old-growth stands than in fire-regenerated younger stands in both years of study. Capture rates (per 100 trap nights) in young stands were 5.07 and 5.88 in 1984 and 1985, respectively (West 1991). In contrast, capture rates of all small mammals in an intensively managed younger forest in southwestern Washington averaged 2.08/100 trap-nights (Stinson et al. 1997). Similarly, the total abundance of small mammals was nearly 1.7 times higher in old growth than in managed second-growth forest on the Olympic Peninsula, Washington (Carey and Johnson 1995). In that study the variance in abundance of numerous small-mammal species in managed stands was positively related to the amount of coarse wood debris on the forest floor (Carey and Johnson 1995).

The relationship between prey availability in and owl use of particular cover types is obviously important. Owls that fail to consume an adequate amount of prey will starve to death (Miller et al. 1997), and those that struggle to secure adequate prey will experience nutritional stress, may become more susceptible to predation (Hirons et al. 1979), and may have lowered reproductive success (Newton 1779). The relationship between prey abundance and complex forest structure was consistent with the spotted owl's use of old-growth forest during transience and colonization phases of dispersal (Miller et al. 1997).

Prey availability

The spotted owl is a sit-and-wait predator, in that it scans its surroundings from a perch before locating and attacking prey. The relevance of this predatory behavior to the prey-availability hypothesis involves the availability of hunting perches (Forsman 1976, Forsman et al. 1984) and the susceptibility of prey present in the forest. Forests with complex structure provide perch locations at various locations in the canopy and subcanopy that likely provide more opportunities for owls to locate prey, and this likely equates to a greater availability of prey. In addition, the varied structure in the canopy, subcanopy, and forest floor in these forests likely provides a more diverse array of niches that serve as prey refugia interspersed with areas where the prey are vulnerable to predators (Carey 1985). Second-growth forests are in comparatively early stages of successional development and typically have less complex structure and provide less of this dispersion of within-stand patches, and fewer perch sites low in the sub-canopy (Oliver 1981). The ecological significance of these supposed differences in forest structure relative to prey availability to the spotted owl has not been evaluated, but the apparent relationship between structural complexity and a greater availability of prey is consistent with the preference for old-growth forests during dispersal (Miller et al. 1997).

Predation risk

The chief predators of the spotted owl are the northern goshawk (*Accipiter gentilis*), red-tailed hawk (*Buteo jamaicensis*), and great horned owl (*Bubo virginianus*) (Forsman et al. 1984, Miller and Meslow 1985, Carey et al. 1990). Northern goshawks are rather uncommon in substantial parts of the northern spotted owl's range (Watson et al. 1999), and appear to be rare in some designated spotted owl dispersal areas, probably due to the lack of suitable habitat in managed-forest landscapes (DeStephano and McCloskey 1997). In other areas they are more common, nest in the same cover types used by spotted owls, and build nests that may eventually be used by spotted owls (Forsman et al. 1984, Buchanan et al. 1993). Red-tailed hawks nest in forest and forage in clear-cuts and other open cover types. Anecdotal information suggests that goshawks and red-tailed hawks occasionally kill spotted owls, but their significance as predators of the owl is unknown (Gutiérrez et al. 1995, Forsman et al. 2002).

The great horned owl is a common and widespread species of forested landscapes within the range of the northern spotted owl (e.g., Irwin et al. 1991). In some areas, such as southwestern Washington and the Oregon Coast Range, it is much more numerous than the spotted owl (USDI 1992), and in some areas it may be the primary predator of spotted owls (Forsman et al. 1984, 2002; Gutiérrez et al. 1995). In the central Cascade Mountains in Oregon, 500-ha areas around great horned owl locations contained forests with a greater edge-to-old-forest area ratio, greater areas of shrub and forb vegetation, and lesser amounts of old and interior forest, compared to comparable areas around spotted owl locations (Johnson 1993). Compared to spotted owls, great horned owls were more often detected in landscape areas with only 10–20% old forest and were less commonly detected than spotted owls as the amount of old forest in the landscape increased beyond about 60% (Johnson 1993). Consequently, landscapes with high amounts of old forest will support fewer great horned owls, and landscapes with little old forest will support high densities of great horned owls. The landscapes being maintained or created for spotted owl dispersal were characterized by conditions that will support comparatively high densities of great horned owls (see Table 1), and this could result in higher mortality rates than in landscapes with fewer great horned owls.

Ecological adaptation

Prior to European settlement, the coniferous forests of the Pacific Northwest were dominated by older forests and fire-regenerated younger-aged stands (Wimberly et al. 2000). At any given time, perhaps 30–45 percent of landscapes in western Washington and Oregon were generally unsuitable for spotted owls because of an incompatible vegetation association or the presence of forests lacking complex structure due to regeneration following wildfires (Eby and Snyder 1990, Wimberly et al. 2000). The remaining 55–70 percent of the region consisted of fire-regenerated young-, mature-, and old-forest cover types that would have been suitable for spotted owls. The owls likely dispersed through these forests and through a mosaic of remnant patches of old forest scattered throughout landscapes otherwise converted to the stand-regeneration phase (Oliver 1981) by stand-replacing fires. A preference for old-forest cover types (Gutiérrez et al. 1995) suggests that spotted owls adapted to disperse through landscapes dominated by structurally complex forest, although it is unclear whether juveniles seek old-forest cover types innately or as a learned response, perhaps to conditions at the natal site or foraging areas that support an abundance of prey (Carey 1985, E. Forsman personal communication). Given the reduction in both amount of old forest and abundance of snags on the landscape over the past century (e.g., Spies and Cline 1988, Thomas et al. 1990), the condition of forest landscapes currently available for spotted owls certainly is unprecedented.

Overview of the dispersal management strategies

Examination of the hypotheses associating spotted owls with various forest attributes and ecological conditions indicate inconsistencies between the function of forest attributes associated with dispersal management plans and the habitat attributes identified as important to spotted owls. Given the lack of understanding about dispersal habitat needs at the landscape level, this should be cause for concern. The greatest potential shortcoming in management strategies for dispersal habitat is the general lack of structurally complex forest conditions. For example, definitions of dispersal habitat generally have not required substantive retention of snags or downed wood following timber harvest. Although several of the management strategies recommended protection of snags at the time of harvest, these provisions essentially were voluntary and did not *require* retention of snags (i.e., snags generally could be removed for safety and operational reasons). Intensively managed forests are characterized by a dearth of snags (Spies and Cline 1988), and the requirement of snag retention is therefore unlikely to be achieved in most cases without dedicated management. Furthermore, with only one exception (and in a plan that was not implemented), strategies that retain green trees have not *required* that these trees become snags at any time during the life of the plan, typically a period of 50–100 years. Therefore, most of the implemented dispersal management strategies will result in landscapes dominated by younger, second-growth forests. These forests are managed on short rotations (e.g., 50 years) and typically lack the structural components (e.g., snags; Spies and Cline 1988, Wilhere 2003) of forests used by spotted owls.

Although Thomas et al. (1990) were unable to identify a threshold value of foraging habitat that would facilitate dispersal, they clearly recognized the importance of foraging requirements during dispersal. In addition, as a guiding principle Thomas et al. (1990) cited Wiens (1989:227), in stating "To establish reserves according to ecological insights requires both a consideration of broad-scale landscape configurations and knowledge of the ecological requirements of the species that are important in particular situations." Although many dispersal management plans required that 40–50% of the landscape meet a stand-level definition of dispersal habitat, it is unknown whether these targets are sufficient to support dispersing spotted owls, particularly given the lack of structural complexity in the vast majority of stands in dispersal landscapes. In Washington there are several regulatory definitions of suitable spotted owl habitat (WAC 222-16-085), including foraging habitat, and these or similar definitions do not appear in most of the 18 dispersal habitat plans. It is not evident that the majority of dispersal management plans have adhered to this guiding principle. Unfortunately, almost none of the plans contain an adaptive management element that would initiate different management practices to achieve a different target condition based on new knowledge. Therefore, in both the near term and the long term, the proposed and implemented strategies for management of spotted owl dispersal habitat may not produce conditions preferred by spotted owls and may result in dispersal-related mortality (due to starvation or predation) or other consequences that negatively influence juvenile recruitment.

Potential competition with barred owls

Although direct evidence demonstrating competition between the barred owl (*Strix varia*) and spotted owl is lacking, there is a growing concern that the barred owl, now sympatric with the northern spotted owl (Dark et al. 1998), is a superior competitor for resources (Kelly and Forsman 2003, Pearson and Livezey 2003). This potential competitive advantage is likely to occur in all seasons, including during dispersal.

Barred owls differ ecologically from spotted owls in a number of ways. Barred owls are habitat and prey generalists (in the Pacific Northwest), they appear to have greater reproductive output, and they disperse substantially longer distances (Mazur and James 2000) than is typical for spotted owls (Forsman et al. 2002). Consequently, if spotted owls compete with barred owls for resources during the nesting season, they may face an even greater challenge as they move across large dispersal landscapes dominated by younger forests of arguably lower-quality habitat. These dispersal forests provide nesting (e.g., in riparian hardwoods; J. Buchanan, personal observation) and foraging opportunities not exploited by spotted owls. Consequently, barred owls (local adults and their young as well as dispersing birds from adjacent areas) likely are present in dispersal landscapes when spotted owls begin dispersing. Given the generalist nature of prey selection by barred owls (Mazur and James 2000), these owls can persist in such landscapes and may well reduce populations of prey species that in many cases were probably marginal but otherwise available for spotted owls. Research will be required to understand the relationship between these 2 species during dispersal.

Recommendations

An empirical evaluation of the effectiveness of the current dispersal management strategies will be a complex task. A complete assessment of dispersal efficacy in intensively managed forest landscapes will require evaluation of both the suite of ecological conditions and relationships experienced by spotted owls and the influence of dispersal on the demographic health of the population (McPeek and Holt 1992). This is a daunting challenge because an investigation to identify stand- or landscape-level habitat conditions experienced by dispersing spotted owls that eventually influence population performance will be substantial and expensive. Addressing the relationship between dispersal and population demography likely would require that the demography and dispersal landscapes be contiguous, or approximately so.

Cost and logistical constraints are not the only barriers to a better understanding of the habitats used by spotted owls during dispersal. With the exception of a dispersal management strategy implemented by the Washington Department of Natural Resources (WDNR 1997), all other management strategies within HCPs are static and not subject to modification based on new information on spotted owl habitat requirements or the effectiveness of the original strategy. For this reason, the absence of adaptive management provisions seriously limits motivation to evaluate or modify the strategies. Evaluating and subsequently modifying dispersal management strategies, if necessary, may require using adaptive management principles in future Habitat Conservation Plans or other forest management planning efforts. In addition, it may be possible to employ tools such as conservation easements to offset costs that would otherwise be imposed on the United States Fish and Wildlife Service to modify existing HCPs on nonfederal lands.

Significant ecological factors that influence, or have the potential to influence, behavior and survival of spotted owls include the amount, quality, and distribution of suitable habitat, the availability and abundance of prey, and the presence of predators or competitors. It would be insightful to associate the ecological factors with assessments of survival, physiological condition (e.g., mass loss or rate of mass change; see Williams et al. 1999), and behavior (e.g., rate of movement, amount of colonization activity; Forsman et al. 2002). Radiotelemetry would be required to accurately link spotted owl area use with specific stand- and landscape-level attributes. In addition, measures of prey and predator abundance and the habitats they use could be obtained to evaluate the potential importance of these factors. A variety of modeling efforts could be applied (Mooij and DeAngelis 2003), and models could be generated that improve the management strategies currently in use (see Peterson et al. 2003).

There are certainly limitations in conducting the type of research described above. Every landscape or landscape segment is unique in some way, and this will influence predator and prey densities and habitat functionality. These conditions will place certain limitations on the types of study designs and analytical procedures that can be applied. On the other hand, it should be possible to determine the ecological or environmental factors that influence the success of dispersing spotted owls. Research design should allow for credible investigation, and the information derived from research should be used to develop better dispersal management plans for spotted owls. We should learn from the example of the red-cockaded woodpecker and avoid relying on strategies that may not deliver.

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