

Chapter 7

Breeding and Natal Dispersal, Nest Habitat Loss and Implications for Marbled Murrelet Populations

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Abstract: Evidence of breeding and natal dispersal in alcids is typically provided by the resightings of banded birds, the establishment of new colonies, and/or evidence of immigration to established colonies. The difficulties in banding, observing, and censusing Marbled Murrelets at nesting areas preclude using any of these methods for this species. Based on the limited number of nests observed in consecutive breeding seasons, breeding site fidelity (birds breeding in the same nest as the previous year) may be lower than most other alcids. This is likely due to low breeding success associated with high levels of nest predation. By contrast, annual use of nest stands suggests fidelity to a nesting area may be high. Natal dispersal, the breeding at locations away from their fledging site, is likely similar to that of other alcids. Loss or degradation of previously occupied nesting habitat will result in the displaced breeders prospecting for new nest sites. In areas with no unoccupied available habitat, this could result in birds being prevented from breeding, attempting breeding in suboptimal habitat, or increasing the distance dispersed from the previous breeding sites. Each of these is likely to result in a decrease in reproductive output. Dispersal patterns need to be considered when assessing the importance of stands and the status of populations. The small population size and fragmented nature of the remaining breeding habitat could increase the time required for prospecting birds to locate recently matured old-growth forest, resulting in underestimating the importance of a stand. Additionally, birds could be dispersing from regions of high production of young to areas with low production but where recruitment opportunities are higher, partially hiding the low reproduction of the latter population.

The ability of Marbled Murrelets to disperse from natal sites, and their fidelity to breeding sites or stands, has important implications for the potential of the species to respond to habitat loss and colonize or reestablish breeding areas when habitat has been altered. With knowledge of these factors, we could more accurately assess the effects of habitat destruction on the viability of populations throughout the species' range. In the discussion below, we examine what is known about dispersal in other alcid species and the possible implications for the Marbled Murrelet.

Dispersal of birds can occur both by established breeders changing breeding sites (breeding dispersal) and by birds nesting away from their natal nesting area (natal dispersal) (Greenwood and Harvey 1982). The degree of nest-site fidelity by established breeders can be expected to be related to previous breeding success and the frequency of change in availability of suitable nest sites and prey resources. Nest

site availability can be decreased both through the destruction of nest sites and through chronic predation. An increased rate of natal dispersal should be related to the potential to be more successful in finding mates or nest sites away from the natal nest site or colony.

Breeding Dispersal

Breeding site fidelity in a long-lived species, which the Marbled Murrelet is presumed to be (Beissinger, this volume), can provide benefits in increased breeding success and lifetime fitness. Site fidelity can reduce potential reproductive effort by (1) increasing the chances of breeding with the previous year's mate, (2) eliminating or reducing the need to locate a suitable nest site, and (3) allowing the development of familiarity with the marine and terrestrial environment.

The rate of breeding dispersal is low for most alcid species that have been studied. Rates of nest-site fidelity of previously breeding alcids are: 91.5 percent Razorbills (*Alca torda*) (Lloyd 1976); 96 percent Common Murres (*Uria aalge*) (Birkhead 1977); 93.2 percent Atlantic Puffins (*Fratercula arctica*) (Ashcroft 1979), 57-95 percent Black Guillemots (*Cepphus grylle*) (Divoky, unpubl. data; Petersen 1981); 86 percent Pigeon Guillemots (*C. columba*) (Drent 1965); 78 percent Ancient Murrelet (*Synthliboramphus antiquus*) (Gaston 1992).

The degree of breeding dispersal displayed by an alcid should be related to the rate that nesting habitat is created and destroyed, the level of mortality of breeding birds, and the availability of nest sites. Species with a high probability of returning to a nest site destroyed over the winter would have fewer reasons to have evolved site tenacity. Harris and Birkhead (1985) suggested that the Thick-billed Murre (*Uria lomvia*) might show less site tenacity than other Atlantic alcids because rockfalls destroy or create nest sites in their colonies more frequently than for other species. Burrow nesting alcids could be expected to show higher rates of breeding dispersal than talus nesters due to the higher frequency of collapse of burrows.

Annual overwinter mortality could be expected to influence breeding site fidelity. High overwinter mortality would decrease the chances of a surviving bird being able to breed with the previous year's mate and, by creating more vacancies at established nest sites, increase the opportunities for dispersal for species that are nest site limited.

For those alcid species in which breeding site fidelity has been examined, and for birds in general (Greenwood and Harvey 1982), changes in nest site are more frequent after a breeding failure. For Black Guillemots, nest-site fidelity was 92 percent for successful pairs and 48 percent for failed

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pairs (Petersen 1981). For Ancient Murrelets, reoccupancy rates of burrows that supported successful breeding the preceding year was 80 percent, and only about 50 percent for unsuccessful burrows (Gaston 1992). Nest changes caused by simple breeding failure typically result in small scale movements (usually tens of meters) to nearby sites (Divoky, unpubl. data; Petersen 1981).

Chronic disturbance at the nest site can cause established breeders to move to a new breeding location thousands of meters away. A Pigeon Guillemot that experienced persistent disturbance at its nest site was found breeding on an island 7.7 km away 3 years later (Drent 1965). At a Black Guillemot colony where any movement of established breeders is typically to an adjacent nest site (<10 m), one bird moved approximately 1 km and another over 5 km, after Horned Puffins (*Fratercula corniculata*) using the same nest site had repeatedly disrupted nesting (Divoky 1982 and unpubl. data).

Essentially all information on breeding dispersal in alcids has been obtained through the banding and resighting of individuals. The difficulty of capturing and observing Marbled Murrelets at the nest site has prevented the collection of similar information for this species. The old-growth nesting habitat of the Marbled Murrelet is relatively stable. Natural destruction of old growth forests through fire or wind storms is rare enough, and the degradation of nest trees is slow enough, that high site fidelity could have evolved.

Observations of murrelets engaging in "occupied behavior," strongly suggesting nesting (Ralph and others 1993), indicate that Marbled Murrelets, as a species, exhibit high fidelity to a nesting area. Marbled Murrelets have been recorded in the same forest stands for a minimum of 20 years in northern California (Strachan, pers. comm.; Miller, pers. comm.), 18 years in central California (S.W. Singer, pers. comm.), 7 years in Oregon (Nelson, pers. comm.), and 3 years in Washington (Hamer, pers. comm.). These results are in part a function of the duration of survey effort. While these observations indicate that the species exhibits high fidelity to forest stands, no direct information is available on stand or nest-site fidelity of individual birds.

For species having high annual survival and site fidelity, the occupation of the same nest site in consecutive years is strongly suggestive of individual nest-site fidelity. Re-occupation of the same nest site has occurred only once in the 13 instances where Marbled Murrelet nests have been examined in the breeding season following a year of known occupancy (P. Jones, pers. comm.) and nesting occurred in the same tree four times (P. Jones, pers. comm.; Naslund, pers. comm.; Nelson, pers. comm.; Singer, in press). Additional evidence of fidelity to a nest tree is provided by Nelson's (pers. comm.) finding of three nest cups on three platforms in a single tree, although we do not know if it was the same individuals. While the sample size is small, the observed fidelity to the same nest depression in consecutive years appears to be lower than for other alcids. This could be related to the high rate of predation recorded for murrelet

nests (Nelson and Hamer, this volume b). It also indicates that while breeding habitat for this species is reduced (Perry, this volume), and may be limiting, the number of nest platforms apparently is not. If the high predation rate is a recent phenomenon, nest-site fidelity may have been higher in the past. As previously mentioned, breeding dispersal increases with increased rates of nesting failure (Greenwood and Harvey 1982). The high rates of observed nest failure (Nelson and Hamer, this volume b) may explain murrelets not reoccupying a nest site in subsequent years.

Natal Dispersal

The primary benefit that a bird derives from breeding at its natal colony may be that the natal area is a known location where conspecifics of a similar genetic background successfully bred in the past (Ashmole 1962). However if a breeding location is near those of related individuals, there is the possibility of kin selection occurring and a moderate level of inbreeding (Shields 1983).

Philopatry (chicks returning to their natal colony or nesting location to breed) is more difficult to study than the fidelity of breeders to a nest site. It had been assumed that the majority of alcids surviving to breeding are recruited into their natal nesting area (Hudson 1985). More recent information, however, shows that prospecting by prebreeders at non-natal colonies is a regular occurrence in Common Murres (Halley and Harris 1993) and Atlantic Puffins (Harris 1983, Kress and Nettleship 1988). Until recently, the instances of banded birds initiating breeding at a non-natal colony were limited (Asbirk 1979, Lloyd and Perrins 1977). However, recent information indicates that, at least in the Atlantic Puffin, half the chicks that survive to breeding emigrate to a new colony (Harris and Wanless 1991).

Other evidence of natal dispersal is provided by the establishment of new colonies and growth rate of existing colonies that could only be explained by immigration (Divoky, unpubl. data; Gaston 1992; Petersen 1981). The frequency with which new alcid colonies have formed on the west coast of North America in the short period that systematic censusing has been conducted (*table 1*) proves that natal dispersal is common in the alcidae.

The distance that birds will breed from their natal site can be great. Banding returns show that the distance dispersed can be as great as 420 km (by sea) for the Common Murre (Halley and Harris 1993) and over 450 km for the Atlantic Puffin (Harris and Wanless 1991). The rate of increase of some breeding populations, and the establishment of new colonies, indicates that Ancient Murrelets are being recruited into breeding populations at least 30 km from their natal site (Gaston 1992), Black Guillemots from over 500 km, and Horned Puffins from over 200 km (Divoky, unpubl. data).

Because of the difficulties of marking and subsequently resighting Marbled Murrelets, any direct evidence of natal dispersal would have to come from observations of range expansion, occupation of previously unoccupied breeding

Table 1—Alcid species that have recently formed new colonies in western North America

Species	Alaska	British Columbia	Washington	Oregon	California
Common Murre		Campbell and others 1975	Speich and Wahl 1989	USFWS ¹ , unpubl. data Newport, OR	Sowls and others 1980 Carter and others 1992
Thick-billed Murre	Sowls and others 1982	Vallee and Cannings 1983			
Pigeon Guillemot	Sowls and others 1978 USFWS unpubl. data, Anchorage, AK	Campbell 1977	Speich and Wahl 1989	USFWS, unpubl. data Newport, OR	Sowls and others 1980 Carter and others 1992
Black Guillemot	Divoky and others 1974				
Cassin's Auklet					Carter and others 1992
Rhinoceros Auklet		Campbell and others 1975	Speich and Wahl 1989	USFWS, unpubl. data Newport, OR Scott and others 1974	Sowls and others 1980 Carter and others 1992
Tufted Puffin	Byrd and others 1980			USFWS, unpubl. data Newport, OR	Sowls and others 1980
Horned Puffin	Divoky 1982 Divoky, unpubl. data				

¹ USFWS — U.S. Fish and Wildlife Service

areas, or growth of local populations that could only be accounted for by immigration. The nesting habits of the species makes the detection of any of these difficult, as does the short period that the species has been the focus of research. In addition, the high rate of habitat destruction recently experienced (Perry, this volume) adds to these difficulties.

Natal dispersal can be expected to be high in Marbled Murrelets compared with other alcids for several reasons. The winter distribution is extensive, with the species wintering in the nearshore waters of the breeding range, as well as in areas where breeding does not occur. The distance that individual birds disperse from either their breeding or natal area can be great, as murrelets are regularly found in southern California some 300 km south of the closest known breeding area (Briggs and others 1987). Because murrelets attend inland breeding areas during the winter (Naslund 1993b), information on breeding areas is provided to prospecting nonbreeders at all times of the year. The prebreeding period for this species is probably between 2 and 5 years (Beissinger, this volume), allowing sufficient time to prospect for a suitable nesting area. Additionally, the area where Marbled Murrelets might discover suitable nesting habitat is a 60-km band adjacent to the coast. This extensive area of potential breeding habitat may have selected for more extensive

prospecting behavior than in other alcids where potential breeding sites are largely linearly distributed in a narrow shoreline band.

Methods of Dispersal

The manner in which alcids coalesce into breeding pairs can have implications for the level of breeding and natal dispersal. The vast majority of breeding dispersal in alcids consists of birds moving to sites either immediately adjacent, or close to, the previously occupied nest site (Divoky, unpubl. data). This occurs even when an established breeder initiates a new pair bond with another established breeder (Divoky, unpubl. data), indicating that pairing for most, if not all, alcids occurs near the breeding site. If pairing occurs on the water when birds are staging near the breeding location, one would expect to see almost random movement of the established breeders that lose or change mates. Additionally, if established breeders paired on the water, the pair would have affinities to two sites.

Because ownership of a quality nest site or territory is an important prerequisite for breeding, pairing at the nest site allows a bird to find out whether a prospective mate owns a site and to determine the quality of that site. Pairing

with a bird that owns a nest site increases the chances that a bird will pair with an experienced breeder.

Nonbreeding birds, with no previous experience, also probably form pairs near the nest site. Observations of Black Guillemots in northern Alaska (Divoky, unpubl. data) show that nonbreeders are present at the colony throughout the breeding season, and many display a high level of mate and site fidelity. Although nonbreeders form pairs with each other, when one member of an established nest site owning pair dies, the vacancy is typically filled by a nonbreeder of the appropriate sex. Nonbreeding pairs can be recruited as a unit should a new site be created or should two vacancies occur at an established site. However, the low annual mortality rates of breeding alcids indicates that most recruitment occurs through a single vacancy in an established pair. With recruitment occurring at or near the nest site, the established breeder and the individual being recruited, can pair with a familiar bird. Recruitment in murrelets could occur in the same manner. Those birds prospecting new nesting areas could pair on the water before prospecting potential nest sites.

Implications of Habitat Loss and Fragmentation of Populations

The final rule listing Marbled Murrelets as threatened (U.S. Fish and Wildlife Service 1992) regards loss of older forests and associated nest sites as the main cause of decline in murrelet populations. When nest sites are limiting, the loss of nesting habitat has both immediate and long term impacts on the reproductive potential of a murrelet population. While alcid populations have been shown to recover in a relatively short period from episodic anthropogenic mortality events, such as gill net and oil spill mortality (Piatt and others 1991; Carter and others 1992), loss of nesting habitat directly affects the long term reproductive potential of a population. This is especially true for tree-nesting Marbled Murrelet populations where the creation of nesting habitat is extremely time-consuming, perhaps 200 years.

Fragmentation of old-growth also has the potential of reducing murrelet breeding success by increasing the densities of predator populations. Corvids are "edge species" that have been found to increase in numbers with increased forest fragmentation (Andren and others 1985, Wilcove 1985, Small and Hunter 1988). Similar findings have been reported in central Oregon regarding Great Horned Owls (Johnson 1992). In addition, corvid predation on small bird nests has been found to increase with increased forest fragmentation, decreased distance of nests from a forest edge or both (Gates and Gysel 1978, Andren and others 1985, Small and Hunter 1988, Yahner and Scott 1988). Factors that increase fragmentation, such as a wildfire or timber harvest, could reduce murrelet breeding success both through the reduction of cover and the increase in predator densities. This reduced breeding success could be expected to increase the rate, and possibly the distance, of breeding

dispersal. The distances moved would probably relate to the level of disturbance and the threat that the predators pose to adult birds. The reduction and fragmentation of habitat would also act to increase the distance prospecting prebreeders would have to travel to find a suitable nest site.

Habitat loss could be expected to result in the displacement of breeding birds, while fragmentation could lead to both displacement and decreased breeding success. In cases where stands used for nesting are destroyed, the birds previously breeding in the stand would have to locate a new nesting area. If all available nest sites in adjacent habitats are occupied, the displaced birds could attempt to breed in suboptimal sites with a decreased chance of successful reproduction, prospect more distant areas, or not breed at all. There are no conclusive indications of higher densities of murrelet nesting in stands remaining after timber harvests (Ralph and others, this volume). The ease and rapidity with which displaced murrelets seek out new breeding areas could be expected to be related to how frequently murrelets normally change sites. If the level of individual nest-site fidelity is as low as observations indicate, then murrelets may be able to readily move at least short distances to new nest sites. The fidelity birds show to a previously used breeding area or site that no longer can support breeding, should be related to the rate and magnitude of habitat destruction. There is evidence of murrelets visiting remnants of newly harvested stands before disappearing from the area (Folliard, pers. comm.), thus indicating that murrelets might not immediately abandon the unsuitable nest stand. This is consistent with observations in other alcid species. Pairs have shown fidelity to previously occupied, and recently destroyed, nest sites for two years in the Black Guillemot (Divoky, unpubl. data), and a minimum of two years in the Least Auklet (*Aethia pusilla*) (I. Jones, pers. comm.). This type of nest loss would be similar to the loss of a previously used murrelet nest platform branch and not the removal of a nesting stand.

Management Implications of Dispersal

High levels and extensive distances of natal dispersal could result in source areas with high productivity producing young that will be incorporated into sink regions with low productivity, or high adult mortality, or both. This could result in populations in sink areas showing little change in numbers. Without monitoring breeding success, the inability of the sink population to produce enough young to balance adult mortality would not be evident. The maintenance of such a population would be dependent on the continued production of a surplus of young by the source population. The true reproductive status of the sink population would be masked until immigration declines. Such immigration could explain the ability of the central California murrelet population to lose an estimated 150 to 300 birds in the early 1980s (Carter and Erickson 1988) and not show any signs of decline (Carter and others 1992).

The secretive nature of murrelet nesting has precluded the determination of breeding areas solely by the discovery of nests, eggs or chicks. Biologists and managers have had to identify breeding areas based on the birds engaged in activities included in “occupied behavior” as strongly indicative of nesting (Ralph and others 1994). Relying on instances of occupied behavior as an indication of the importance of a stand to Marbled Murrelets has a number of potential weaknesses.

First, recently matured forests that are able to support nesting could not be expected to be immediately discovered and occupied by prospecting murrelets. The ability of alcids to occupy areas where suitable breeding habitat is made available is evident from the rapid colonization of islands in the Aleutian Islands where fox have been eliminated (Bailey and Kaiser 1993). The occupation of newly available suitable habitat by Marbled Murrelets in Washington, Oregon, and California may be delayed by the small stand size, high fragmentation and disjunct distribution of the old growth forest. The small size and apparently low breeding success (Nelson and Hamer, this volume b) of the population can be expected to further slow occupation of newly available habitats. Because almost all prospecting of currently unoccupied suitable habitat would occur through natal dispersal, low productivity would reduce the potential of a population to disperse. This would result in a lack of detections in stands that have the potential of supporting murrelet breeding, but have not yet been discovered by murrelets. The importance of this apparently suitable but currently unoccupied habitat to the future of the species needs to be recognized.

In regions where a large nonbreeding population is prevented from breeding by lack of nest sites, prospecting birds might investigate areas and habitats that do not support breeding. This could result in “occupied” behavior being recorded in areas where nesting is not occurring. Prospecting alcids can be present in apparently suitable habitat (Divoky 1982, unpubl. data; Kress and Nettleship 1988; Carter and others 1992), although no breeding is occurring. If loss of old-growth habitat has both increased the level of dispersal and limited potential nest sites, substantial numbers of murrelets could be displaying “occupied behavior” in habitats where breeding is not currently being attempted or where successful breeding could not occur. Such could be the case in central California where Carter and Erickson (1988) believed that all remaining nesting habitat is occupied and because the population is nest site limited, nonbreeding birds may be present over land and sea in a greater percentage than elsewhere. While this may result in overestimating the use of stands, it is unlikely that murrelets would be repeatedly encountered in stands that do not have some present or future potential for supporting successful breeding.

Discussion

The coastal old-growth forest utilized for breeding by Marbled Murrelets would have selected for relatively high rates of breeding and natal dispersal. Based on the behavior and cryptic coloration of the breeding adults and chicks, and the high rate of nest predation for observed nests (Nelson and Hamer, this volume b), the risk of nest predation appears to be higher than for other alcids. The assumed high rate of nest predation would have selected for frequent short distance movements, while the extensive time required for old growth stands to be destroyed or degraded under natural conditions would have selected for individual fidelity to a nesting stand. There is no indication that the distance that breeding murrelets typically disperse would be any greater than the conservative movements (usually <1 km) that have been observed for other alcids.

Most dispersal in alcids is probably due to natal dispersal, and Marbled Murrelets appear to have the capacity for extensive natal dispersal given the extent of the breeding range, the overlap between the wintering and breeding areas, and the distance individuals are known to move from breeding areas in winter. It would not be unreasonable to assume the percentage of birds that initiate breeding at a non-natal locality (natal dispersal) is as high or higher than has been reported for other alcids (approximately 50 percent) (Harris and Wanless 1991). The ability to prospect for breeding localities should be well developed in Marbled Murrelets. Unlike the potential breeding area of most alcids, which is linearly distributed in a narrow band on the shoreline, murrelet nesting habitat is found in a wide (as much as 60 km) band adjacent to the coast.

Breeding habitat fragmentation and loss can be expected to have affected the rate and extent of murrelet dispersal. In Washington, Oregon, and California, high predation rates apparently associated with fragmentation would select for increasing the rate and extent of breeding dispersal. However, the small size and highly fragmented and disjunct nature of the old-growth remaining in this area can be assumed to have decreased the potential distance for breeding dispersal (at least in areas where stand size is small). Natal dispersal rates and extent may have been increased as habitat in the natal locality was reduced and the distance to the location of suitable habitat is increased. These changes in dispersal may have the overall effect of depressing reproductive output.

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