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Note

Habitat as a Potential Factor Limiting the Recovery of a Population of Nocturnal Seabirds

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ABSTRACT We asked whether the lack of a population response by ancient murrelets (*Synthliboramphus antiquus*) to eradication of rats (*Rattus* spp.) at Langara Island could be due to a change in vegetative cover. We quantified ancient murrelet habitat associations on 12 islands and assessed changes in vegetation at Langara Island between 1981 and 2007. We found that ancient murrelets exhibit a high degree of flexibility in their use of available breeding habitats, and we noted no changes over time. Thus, recovery of ancient murrelets at Langara Island is unlikely to be limited by habitat quality. We propose artificial social attraction as a method to speed recovery. © 2011 The Wildlife Society.

KEY WORDS ancient murrelets, British Columbia, habitat, Haida Gwaii, island restoration, Langara Island, recovery, *Synthliboramphus antiquus*.

Understanding how and why animals choose different habitats is a necessary step to preserve and manage populations (Manly et al. 1993). In many theoretical studies, habitat or resource selection is addressed in terms of Allee effects, settlement costs, and ideal distributions (Brown 1969, Fretwell and Lucas 1970, Pulliam and Danielson 1991, Greene and Stamps 2001), all of which assume that individuals select the highest quality habitat available. How individuals, especially those that are young and inexperienced, recognize high quality habitat has been the focus of much research (Parejo et al. 2006, Betts et al. 2008, Harrison et al. 2009) and is a key aspect in restoration and recolonization work.

Introduced species have caused declines and extirpations of many native insular populations, altered the flow of nutrients from sea to land, and changed vegetative structure (Martin and Joron 2003, Croll et al. 2005, Fukami et al. 2006, Grant-Hoffman et al. 2010). These changes can cause a shift in ecosystem states, where vegetative structure is changed and the island may no longer contain high quality habitat. The eradication of introduced predators from seabird breeding islands may not be sufficient to facilitate ecosystem recovery and these systems may become locked into a non-seabird state (Jones 2010). Norway rats (*R. norvegicus*) introduced to Langara Island, Haida Gwaii, British Columbia (Fig. 1), decimated one of the world's largest ancient murrelet (*Synthliboramphus antiquus*) breeding colonies (Bertram and Nagorsen 1995). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists ancient murrelets as a species of Special Concern because of impacts by introduced mammalian predators. The eradication of rats from Langara Island in the mid-1990s (Taylor et al. 2000) has resulted in a gradual increase in ancient murrelet burrow occupancy, but only within a relatively small area; large areas of the island remain unoccupied (Regehr et al. 2007).

This localized effect has 2 possible explanations. First, rats have been shown to act as ecosystem engineers, altering the flow of nutrients through island systems and changing vegetative structure (Fukami et al. 2006, Grant-Hoffman et al. 2010). During the 20–30 years that ancient murrelets have been absent from much of Langara Island, dramatic changes in vegetation have occurred on other islands in British Columbia, in both the presence and absence of introduced mammals, negatively affecting habitat quality for seabirds (Hipfner et al. 2010). On the other hand, some animals use conspecifics as cues to habitat selection (Stamps 1988, Doligez et al. 2003), which results in clustering of individuals within occupied habitat (Danchin and Wagner 1997, Greene and Stamps 2001). Experiments have shown that prospecting ancient murrelets are more likely to visit areas where conspecifics are vocalizing (Major 2011, Major and Jones 2011), suggesting that they use public information when locating potential nesting sites. Therefore, abandoned colony sites may remain unused irrespective of habitat quality.

Our objective was to test whether vegetative cover is limiting recovery at Langara Island. We quantified ancient murrelet breeding habitat on 12 islands in Haida Gwaii free of introduced predators, and used this information to estimate the extent of breeding habitat at Langara Island. We also assessed how changes in vegetative cover at Langara Island over 26 years (1981–2007) might affect the expected distributional pattern of ancient murrelet recovery.

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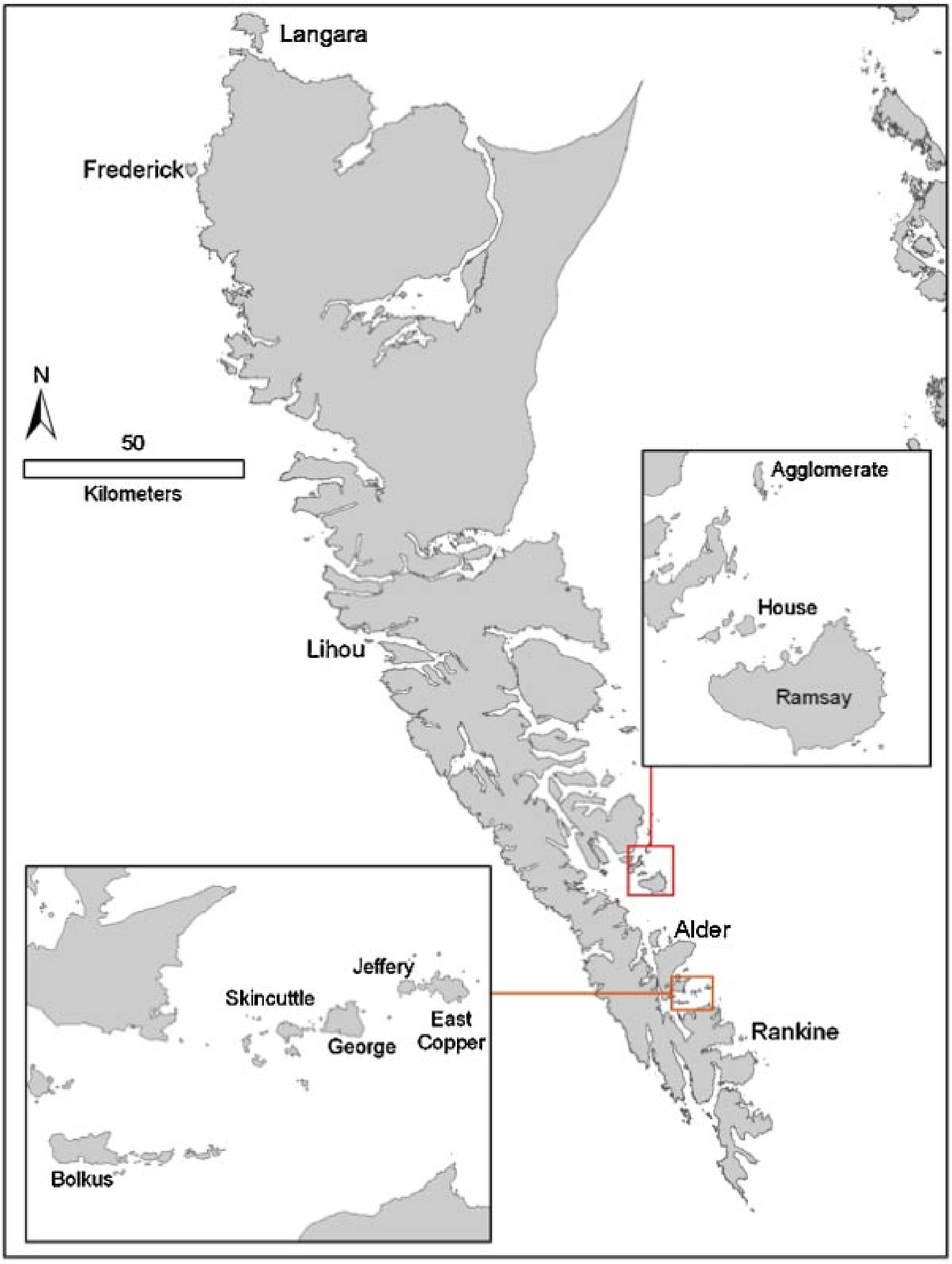

Figure 1. Map of Haida Gwaii showing locations of each of the 12 introduced predator-free islands used to analyze ancient murrelet habitat at Langara Island.

STUDY AREA

We conducted our study on 13 islands in Haida Gwaii, British Columbia (Fig. 1) ranging in size from 7.3 ha to 3,105.0 ha. All islands were forested; the dominant tree species were Sitka spruce (*Picea sitchensis*) and Western hemlock (*Tsuga heterophylla*) with Western red cedar (*Thuja plicata*) in the interior. Ground cover was mainly moss and mossy stumps and logs (Rodway et al. 1988, 1994). Ancient murrelet breeding colonies occurred on all 13 islands but surveys included both occupied and unoccupied areas. Langara Island was the only island where introduced Norway rats were present, and they were successfully eradicated in 1997 (Taylor et al. 2000).

METHODS

We used published information to develop a suite of variables that could predict breeding habitat for ancient murrelets based on specific features of their biology; notably their habit of precocial nest departure (Gaston 1992). Specifically, we hypothesized that ancient murrelets will nest where the easiest land-to-ocean travel route and cover from predation occur. If true, then we could predict that ancient murrelets would: 1) select breeding habitat close to the sea, as this minimizes the travel distance for the 2 precocial chicks; 2) nest on moderate slopes, as adults increase their susceptibility to predators on flat ground where they must accompany chicks further towards the sea (Jones et al. 1987); 3) nest in locations with moderate canopy cover, balancing the antipredator benefits of increasing canopy cover against the increased danger in having more obstacles (i.e., branches and trunks) to avoid when flying into colony sites (Heath 1915); 4) avoid dense shrub cover, as increasing shrub cover increases the risk of colliding with obstacles while flying through the area to attend the colony (Heath 1915); and 5) favor areas with mossy ground cover (Vermeer and Lemon 1986). Finally, as larger islands in Haida Gwaii support larger colonies (Gaston 1992), likely because of the amount of shoreline and subsequently breeding habitat close to shore, we predicted that ancient murrelets would: 6) be more likely to breed on islands with greater shoreline perimeters.

Habitat on 12 islands in Haida Gwaii free of introduced predators was quantified by the Canadian Wildlife Service (CWS) branch of Environment Canada using distance sampling with transects and quadrats between 1980 and 1986 (Fig. 1). Island area, number of transects, transect lengths, distance between transects, quadrat size, and distances between quadrats varied among islands (Table 1). Specific details of sampling methods are available elsewhere (Rodway et al. 1988, 1990, 1994). The survey design required transects to run through the extent of the colony and up to 2 quadrats beyond the colony boundary. On small islands this meant transects ran across the island and therefore sampled habitat throughout the island, whereas on larger islands transects ended before reaching the center of the island, meaning the interior habitat of the island was not sampled. Within each quadrat, measures of habitat (including slope, ground cover species, and shrub and canopy cover percent) were noted. For this analysis, we simplified our habitat data to reflect dominant ground cover species (i.e., species with >50% cover and classified them as moss, grass, or other), and percentage total shrub and canopy cover. We calculated distance to nearest shoreline using a map with plotted transect lines. We estimated shoreline perimeter using a Geographic Information System (GIS), and modeled shoreline using a Terrain Resource Information Management (TRIM—1:20,000) digital data set that delineated coastal island boundaries as "the apparent high water mark," and was digitized from ortho-photographs.

We based presence of breeding birds within each quadrat on the presence of adults, eggs, hatched eggshells, eggshell membranes, and/or chicks in burrows. We searched all burrows within a quadrat by hand and noted the contents, including bird sign at the entrance (i.e., worn tunnels, feathers, and droppings). We controlled for differences in quadrat size by assigning each quadrat as either occupied by ancient murrelets or not, as opposed to using the number of occupied burrows within each quadrat.

At Langara Island, habitat surveys were conducted in 1981 by CWS personnel using the same methods (Rodway et al. 1994). We repeated these surveys and quantified habitat along 28 transects, excluding 6 transects on the northwestern coast, which was inaccessible during May and June 2007. For consistency, we did not use 1981 data from these transects in our analysis (Table 1). Our research was completed under Simon Fraser University Animal Care permit #782B-06.

To quantify ancient murrelet breeding habitat and change in vegetative cover at Langara Island between 1981 and 2007, we used a repeated measures logistic regression with a maximum pseudo-likelihood fitting method (allowing for inter-model comparisons), a binomial distribution, and a log link function in SAS 9.2 (Proc GLIMMIX; SAS Institute, Cary, NC) for both analyses, where quadrat was nested within transect and included as a random factor in all models, including the null. We used an information theoretic approach and considered 70 a priori candidate models composed of biologically plausible combinations of 6 explanatory variables of interest (dominant ground cover, percent shrub cover, percent canopy cover, slope, shoreline perimeter, and distance to nearest shore) including a null model to assess ancient murrelet breeding habitat. We then considered 10 a priori candidate models composed of biological plausible combinations of 3 explanatory variables of interest (dominant ground cover, percent shrub cover, and percent canopy cover) including a null model to assess change in vegetation at Langara Island between 1981 and 2007. We ranked our

Table 1. Summary of island area and survey parameters potentially affecting ancient murrelet habitat selection for 12 introduced predator-free islands in 1980–1987 and introduced predator-impacted Langara Island in 1981 and 2007.

Island		Area (ha)	No. of transects	Distance between transects (m)	Max. length of transect (m)	No. of quadrats	Quadrat size (m^2)	Distance between quadrats (m)
Agglomerate		22.9	2	200	200	20	25	20
Alder		56.5	6	200	600	86	49	30
Bolkus		62.1	4	200	510	38	49	30
East Copper		29.9	4	200	420	38	49	30
Frederick		492.1	28	80–500	1,170	250	25	45
George		38.5	4	150	660	65	49	30
House		32.9	5	138	560	43	49	40
Jeffrey		7.3	1	n/a[a]	240	8	49	30
Langara	1981	3,105.0	30	600–1000	400	163	25	40
	2007		28	600–1000	400	131	25	50
Lihou		73.3	14	100 and 200	240	80	25 and 49	30
Ramsay		1,622.8	44	200	960	372	49	30
Rankine		55.2	6	150	810	102	25	30
Skincuttle		11.9	3	150	180	16	49	30

[a] Only 1 transect across island

models using Akaike's Information Criterion for small sample sizes correcting for overdispersion (QAIC$_c$) by including an estimate of model deviance ($\hat{c}$ = model deviance/df) for the global model, and used QAIC$_c$ weights (w_i) to evaluate model likelihood (Burnham and Anderson 2002). We present models with a difference in QAIC$_c$ value, relative to the smallest value, $\Delta QAIC_c > 10$ and a $w_i \geq 0$.

RESULTS

During 1980–1986, 1,118 quadrats were surveyed along 121 transects on 12 islands free of introduced predators. Quadrats ranged in size from 25–49 m^2 for a total of 45,854 m^2 surveyed, of which 18% (8,463 m^2) was occupied by ancient murrelets. Overall, we observed little difference in physical habitat feature use and availability (Fig. 2). Similarly, our analysis did not reveal selection for any of the habitat variables used in this analysis; the top-ranked model was the null model. This model received virtually all the support among the candidate models and over 5 times more support than the second best supported model (Table 2). Further, all of the habitat parameters included in the analysis had parameter estimates of 0.

Table 2. Candidate models with a difference in quasi-Akaike's Information Criterion corrected for small sample size ($\Delta QAIC_c$) < 10 and an Akaike weight (w_i) ≥ 0 describing ancient murrelet presence at 12 islands without introduced predators located in Haida Gwaii, British Columbia in relation to distance to nearest shore, slope (Slope × Slope2), percent canopy cover, percent shrub cover (SC × SC2), dominant ground cover (grass, moss and other), and shoreline perimeter (n = 1,118; $\hat{c}$ = 0.79). *K* represents the number of parameters in the model.

Candidate model	*K*	$\Delta QAIC_c$	w_i
Null	3	0.00	0.73
SC × SC2	4	3.34	0.14
Slope × Slope2	4	3.81	0.11
Slope × Slope2 + SC × SC2	5	7.35	0.00

Researchers surveyed 160 and 134 quadrats along 58 transects on Langara Island in 1981 and 2007, respectively. All quadrats were 25 m^2 in area for a total of 4,000 m^2 and 3,350 m^2 surveyed in 1981 and 2007. We noted no differences in vegetative cover of any type between 1981 and 2007 (Fig. 3) as the null model was the best supported model in the candidate set receiving 3 times more support than the second best supported model which included the term canopy cover (Table 3). The parameter estimate and standard error for the

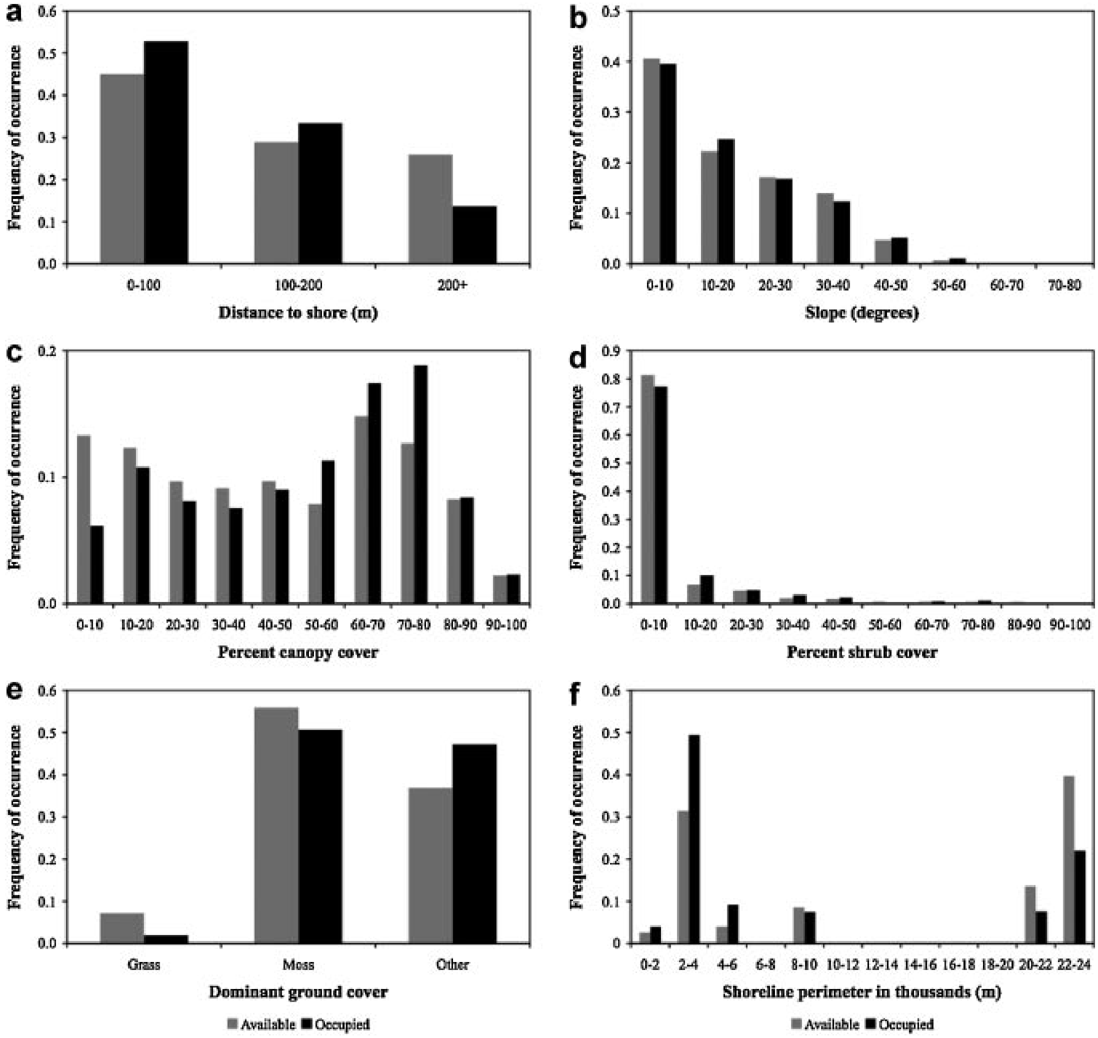

Figure 2. Ancient murrelet use (black bars) and availability (gray bars) of (a) distance to shore, (b) slope, (c) percent canopy cover, (d) percent shrub cover, (e) dominant ground cover, and (f) shoreline perimeter at 12 introduced predator-free islands in Haida Gwaii, British Columbia, 1980–1986.

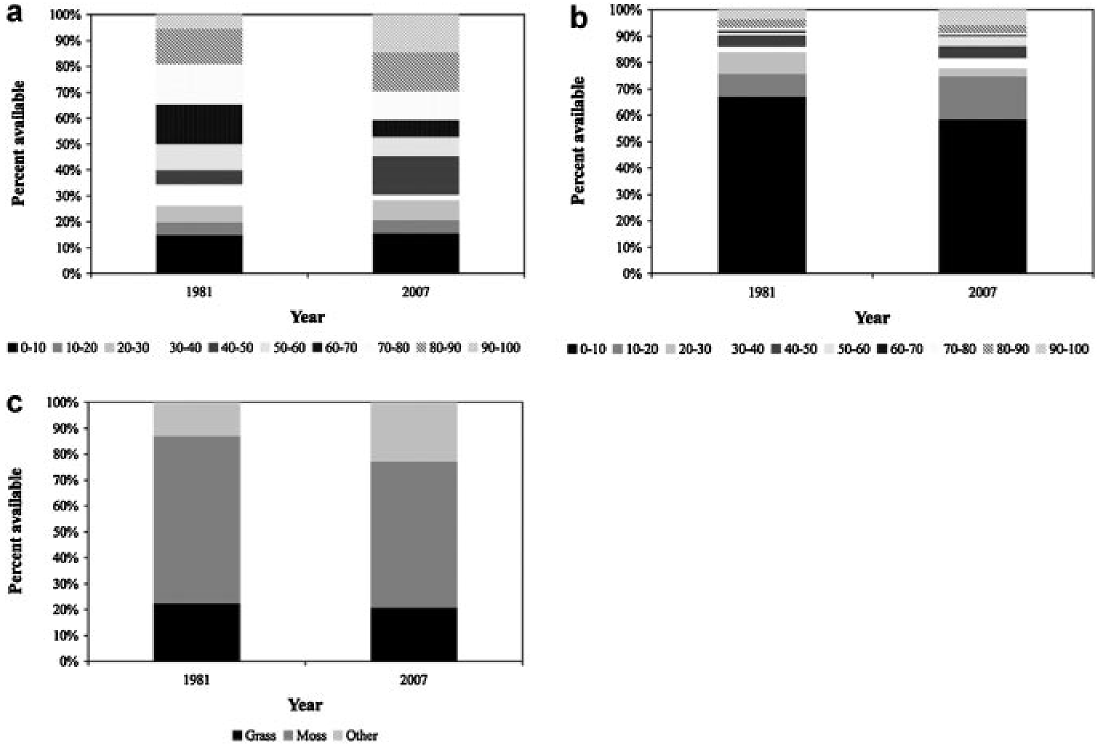

Figure 3. Summary of the percent available (a) canopy cover, (b) shrub cover, and (c) dominant ground cover at Langara Island in 1981 and 2007 in ancient murrelet habitat.

canopy cover term ($3.33 \times 10^{-4} \pm 1.24 \times 10^{-3}$) suggests that canopy cover increased between 1981 and 2007, but the estimate is very small and bounds zero, suggesting this effect is weak.

DISCUSSION

We found that ancient murrelets exhibit considerable flexibility in their choice of breeding habitat, as none of the habitat variables we selected based on preexisting information appeared to strongly influence breeding habitat use. Given this flexibility and lack of long-term change in vegetative cover at Langara Island, we conclude that breeding habitat availability is not limiting recovery. Our results run counter to published accounts suggesting that ancient murrelets preferred to nest in mossy habitat between 40 and 450 m inland when Cassin's auklets (*Ptychoramphus aleuticus*) were present (Vermeer and Lemon 1986). However, the earlier study considered just a single island with high nesting densities of both auks, whereas our study included islands with and without breeding Cassin's auklets. Vermeer and Lemon's suggestion that ancient murrelets will nest closer to shore in the absence of Cassin's auklets and the fact they also nest at the base of grass tussocks on treeless islands in the Aleutian archipelago (Byrd and Day 1986) further hints at flexibility in habitat use.

Table 3. Candidate models with a difference in quasi-Akaike's Information Criterion corrected for small sample size ($\Delta QAIC_c$) < 10 and an Akaike weight (w_i) ≥ 0 describing change in ancient murrelet habitat at Langara Island between 1981 and 2007 in relation to percent canopy cover (CC), percent shrub cover (SC), and dominant ground cover (grass, moss, or other; $n = 294$; $\hat{c} = 0.48$). K represents the number of parameters in the model.

Candidate model	K	$\Delta QAIC_c$	w_i
Null	3	0.00	0.68
CC	4	2.28	0.22
SC	4	4.31	0.08
SC + CC	5	7.40	0.02
SC + CC + SC × CC	6	9.73	0.01

In comparison with other *Synthliboramphus* species, ancient murrelets have a relatively vast geographical breeding distribution, ranging from Haida Gwaii through the Aleutian chain and into Southeast Asia (Gaston and Shoji 2010). Their populations on 3 introduced predator-free islands in Haida Gwaii (Frederick, East Copper, and George islands) are estimated to be stable or increasing (Gaston et al. 2009), and among pelagic seabirds, ancient murrelets have relatively low adult survival and high reproductive output (Gaston 1990). Given the proximity to a stable or increasing source population (Frederick Island), the presence of a residual colony, a presumed stable prey base, apparent high intercolony dispersal (Gaston 1990, 1992; Pearce et al. 2002), and flexibility in breeding habitat (this study), ancient murrelet recovery at Langara Island is highly plausible, given sufficient time. Therefore, management actions to recover ancient murrelets at Langara Island are expected to be effective.

Recolonization may additionally depend upon behavioral factors relating to breeding site selection. Ancient murrelets congregate at offshore gathering grounds before sunset, flying into colony sites 1–2 hours after sunset (Gaston 1992). Prospectors may use these gathering grounds as a first indication to the locations of breeding sites, in the same manner that other species use conspecific aggregations as a compass when searching for foraging patches (Weimerskirch et al. 2010). Furthermore, ancient murrelets in Haida Gwaii do not necessarily dig burrows but rather compact the ground and make use of natural openings or cavities (Gaston 1992). We did not have data on soil properties, but believe this could be an influential factor related to breeding site selection that merits further study. The possibility that individual fitness (i.e., reproductive success and adult survival) varies among habitat types, which we did not consider, also merits further study.

Campomizzi et al. (2008) assert that models of habitat selection should account for the use of conspecific cues in breeding site selection. Public information is a beneficial aspect of sociality, and obtaining and using information from others allows an individual to increase its fitness (Valone 2007). Ancient murrelet prospectors are highly attracted to the vocalizations of conspecifics, and may use vocalizations as a locator cue when searching for potential breeding colony sites (Major 2011, Major and Jones 2011). Therefore, the presence of conspecifics might outweigh the benefits of specific physical habitat types.

MANAGEMENT IMPLICATIONS

We found that terrestrial habitat features alone are unlikely to identify potential colony areas or ancient murrelet breeding locations. Managers and researchers must therefore complete surveys for ancient murrelets to identify areas that can support healthy murrelet populations. Further, the identification of specific physical habitat features again cannot be used to lead restoration efforts, but given that vocalization activity is integral to ancient murrelet prospecting behavior, using artificial playback can be a potentially effective method to induce recolonization and enhance recovery. Researchers and managers need further study to identify whether smaller scale habitat features (e.g., soil properties, availability of natural burrows) are influential factors in habitat selection by ancient murrelets. We advise managers to evaluate the foraging landscape and predator abundances prior to implementing any restoration actions, so that a breeding colony is not established in a risky environment.

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