NEST-SITE SELECTION OF KITTLITZ'S MURRELETS *BRACHYRAMPHUS BREVIROSTRIS* ON KODIAK ISLAND, ALASKA

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ABSTRACT

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We studied aspects of nest-site selection by Kittlitz's Murrelet *Brachyramphus brevirostris* on Kodiak Island, Alaska, during 2008–2011. We discovered 54 Kittlitz's Murrelet nests on the surface of mountain slopes between 188 and 454 m above sea level, in an area devoid of glaciers. Nests were dispersed across the landscape, with an annual average of 0.09 nests/ha of habitat searched. Four nests were reused in separate study years, and 10 additional nests were located within 60 m of a nest site active in a previous study year. Nest scrapes were most often shallow, circular depressions in gravel situated among larger rocks and immediately downslope of one or more prominent moderate- to large-sized rocks. We compared the habitat characteristics of plots centered on nest sites (nest plots) with those of randomly selected locations within 150 m of nests (near-nest plots) and within the entire area where nest searching was conducted (random plots). Mean percent vegetation cover on nest plots was less than half that of near-nest and random plots (6.6%, 14.0%, 16.3%, respectively). The percent cover of rocks 10–30 cm diameter was higher, and percent cover of rocks >30 cm diameter was lower at nest plots compared with near-nest and random plots. Nest plots were located on steeper slopes (mean 29°) than near-nest and random plots (27° and 25°, respectively) and farther from edges of continuous vegetation (mean 79 m) than near-nest and random plots (mean 64 m and 63 m, respectively). Nest survival was unrelated to selected habitat variables, although our sample size may have been too small to detect an effect. The high dispersion of active nests and sparse vegetation in areas surrounding nest sites suggest that nest-site preference by Kittlitz's Murrelets may reflect an ecological strategy to minimize nest predation.

Key words: Kittlitz's Murrelet, *Brachyramphus brevirostris*, Kodiak, non-colonial seabird, nest-site selection, predator avoidance

INTRODUCTION

The Kittlitz's Murrelet *Brachyramphus brevirostris* is a rare and atypical member of the Alcidae whose nesting habitat requirements are poorly understood. The species and its two congeners, the Marbled Murrelet *B. marmoratus* and Long-billed Murrelet *B. perdix*, are unusual among alcids, as well as seabirds in general, because they nest non-colonially, are cryptically colored during the breeding season, and apparently nest primarily in mainland areas that may support a variety of avian and mammalian predators (Gaston & Jones 1998). These characteristics suggest that predation pressure may have been an important selective force in the evolutionary history of the genus (Piatt *et al*. 1999). Recently, there has been concern about the status and conservation of Kittlitz's Murrelet (USFWS 2011) because of recent suspected population declines in several population centers in Alaska (Kuletz *et al.* 2011a, 2011b; Piatt *et al.* 2011), combined with a small global population largely restricted to a few areas during the breeding season, and the species' potential sensitivity to climate change (van Vliet 1993, Kuletz *et al*. 2003). However, few Kittlitz's Murrelet nests have been described (Day *et al*. 1999, Kaler *et al*. 2009), and associated knowledge gaps relating to nest-site selection may limit our ability to accurately identify suitable nesting habitat to advance future conservation efforts.

Limited data suggest Kittlitz's Murrelets have somewhat narrow requirements for nesting habitat. They appear to nest primarily in mountainous areas, especially among scree and talus (hereafter, broken rock) located on slopes between 20° and 45° (Day *et al*. 1999). In the northern Gulf of Alaska region, an area thought to support the majority of the global population of Kittlitz's Murrelets (van Vliet 1993), individuals tend to aggregate at sea during the breeding season adjacent to glaciated mountainous terrain that supports scant vegetation (Agler *et al*. 1998). Accordingly, nests for many Kittlitz's Murrelets in North America are thought to be associated with barren ground that has been produced by recent glacial activity, including broken rock and consolidated rock outcrops (Day *et al*. 1999, Piatt *et al*. 1999). Nests have been discovered from 0.25 to 75 km inland from the coast and from 140 to 2 000 m above sea level (Day *et al*. 1999). Nests also appear to be widely dispersed, with an average distance between concurrently active nests exceeding 200 m (Kaler *et al*. 2009).

Habitat associations for nesting Kittlitz's Murrelets are known from a small number of scattered nests from across the species' breeding range, but information about nesting habitat selection (i.e., used vs. unused/available habitat) is limited. Kaler *et al*. (2009) conducted the first analysis of nest-site selection based on a sample of 11 Kittlitz's Murrelet nests discovered on Agattu Island, Alaska, where terrestrial

mammals are absent. However, no information is available regarding nest-site selection in areas where terrestrial mammals are present, although a large proportion of the global population of Kittlitz's Murrelets is presumed to nest in such areas, namely mainland regions adjacent to the Gulf of Alaska (van Vliet 1993).

To address data gaps related to nesting-habitat selection, we studied Kittlitz's Murrelet nest sites at Kodiak National Wildlife Refuge, Kodiak Island, Alaska, during 2008–2011. Kodiak Island, like mainland areas where most Kittlitz's Murrelets are presumed to nest, supports a diverse assemblage of possible nest predators, including native mammals, and thus may provide an ecological milieu similar to that experienced by murrelets that nest on mainland habitats. Our objectives were to determine which habitat features differentiate nest sites from unused terrain, and, to the extent possible, test the hypothesis that Kittlitz's Murrelets select nest sites that minimize the risk of detection by potential nest predators.

STUDY AREA AND METHODS

Study area

Kodiak Island lies approximately 50 km south of mainland Alaska and is the largest island in the Kodiak Archipelago, with a land area of 8 975 km^2. The interior of Kodiak Island is mountainous, with a major range extending southwest–northeast across the island's length; several peaks exceed 1 200 m elevation. Kodiak Island's land cover is dominated by shrub, meadow, and dwarf-shrub communities. Approximately 5% of the island's surface area consists of exposed rock (Fleming & Spencer 2007), a ground-cover type associated with many described Kittlitz's Murrelet nests (Day *et al*. 1999).

We studied nest sites of Kittlitz's Murrelets in southwestern Kodiak Island during 2008–2011 (Fig. 1) in mountainous terrain adjacent to the Sturgeon and Ayakulik rivers. Our study area was characterized by mountain slopes of broken rock at relatively low elevation, 60–471 m. Vegetated terrain was interspersed between and surrounding patches of broken rock, both on mountain slopes and in lowlands. The terrain of our study area was somewhat unusual because exposed rock on Kodiak Island is mostly restricted to higher elevations, generally above 610 m. The reason for the scarcity of vegetation over much of our comparatively low-elevation study area is a result of unusual surface exposures of ultramafic rock. These exposures are characterized by high concentrations of heavy metals and scarce nutrients and, thus, support only sparse plant life (Alexander *et al*. 2007). While our study area contained large areas of exposed rock, herbaceous and woody vegetation dominated adjacent, non-ultramafic portions. Although Kittlitz's Murrelets are often associated with glaciated terrain during the breeding season, glaciers were not present near our study area; the nearest glaciated terrain was located approximately 70 km distant. Snow was almost completely absent from the study area by the time our annual field season began in late May and early June.

Vascular vegetation and mosses (hereafter, vegetation) covered an average of approximately 15% of the ground surface in areas where we searched for nests; vascular vegetation consisted of a variety of sedges, forbs, and prostrate shrubs. Exposed rock substrates composed the remainder of ground cover, and ranged from outcrops of unbroken bedrock exceeding 10 m^2, to fine particles <1 cm diameter. Although the range of substrate sizes was broad, approximately 70% of ground cover was composed of rocks ≤10 cm diameter. Vegetation surrounding exposed ultramafic rock was dominated by upland and lowland tundra, mixed forb meadows, and shrub communities composed of Crowberry *Empetrum nigrum*, Sitka Alder *Alnus sitchensis*, and willows *Salix* spp. Areas of exposed rock were generally small relative to the predominantly vegetated surrounding landscape: no point within any of the rocky exposures in the study area was more than 250 m from completely vegetated terrain.

Unlike many islands that support nesting seabirds, Kodiak Island is home to several species of native mammalian predators, of which the Red-tailed Fox *Vulpes vulpes*, Kodiak Brown Bear *Ursus arctos middendorffi*, and Short-tailed Weasel *Mustela erminea* are probably most likely to occur periodically on mountainous terrain. In addition to mammalian predators, Kodiak Island supports a variety of avian species that could potentially depredate Kittlitz's Murrelet adults or nests, including the Common Raven *Corvus corax*, Peregrine Falcon *Falco peregrinus*, and Bald Eagle *Haliaeetus leucocephalus*, among others.

Methods

We systematically and exhaustively searched for Kittlitz's Murrelet nests in alpine terrain generally dominated by exposed broken rock, although we also searched terrain nearly completely covered by

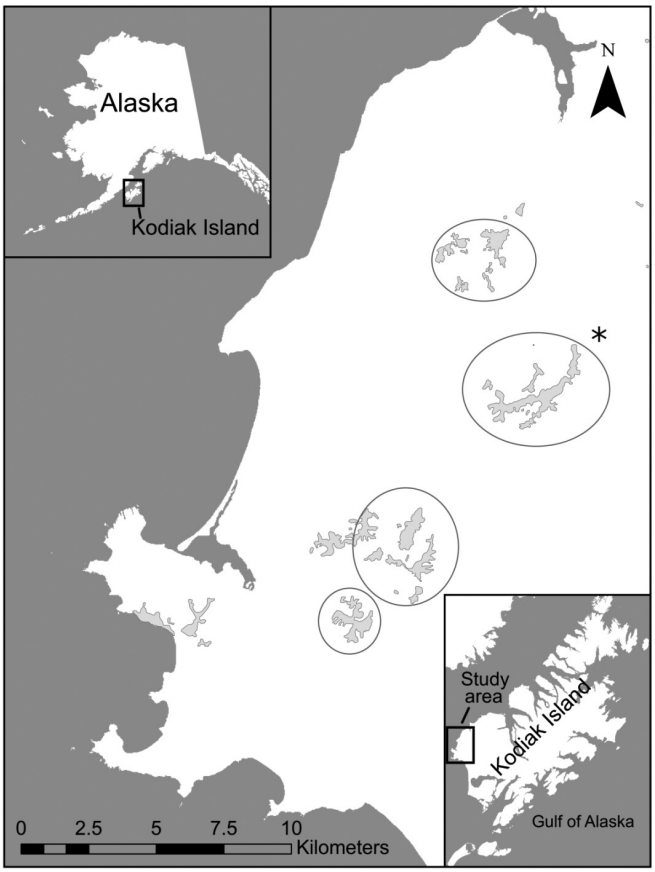

Fig. 1. Map of Kittlitz's Murrelet study area on Kodiak Island, Alaska. Light-gray areas represent ultramafic outcrops dominated by broken rock. Ovals encompass areas where nest-searching was carried out during 2009–2011 and 2008–2011 (asterisk).

vegetation. Two to five persons searched terrain by simultaneously walking transects 5–10 m apart and abreast of each other, generally following a given elevation contour. Following the completion of each transect across the search area, the line of searchers would begin another transect in the reverse direction, either up- or downslope of the previous transect, until an entire area had been searched. We placed pin flags during searches and used track functions on handheld global positioning system (GPS) units to ensure that searches were conducted systematically. Areas within 30–50 m of a known active nest were not searched to avoid disturbing breeding adults. Nest searching extended from late May or early June to mid- or late July. The primary round of nest-searching occurred over a 1 month period during the presumed peak of nesting activity. A second round of nest-searching covered a less expansive search area and lasted 2–3 weeks. Adult Kittlitz's Murrelets were identified after flushing from their nests by confirming presence of their diagnostic white outer rectrices. If species identification could not be confirmed upon discovery, it was determined based on images acquired from nest-monitoring cameras or by observing incubating adults with a spotting scope; we used bill morphology as a field mark in these cases (Day *et al*. 1999).

We collected data on nest-site characteristics at each nest once nesting activity had ceased, typically in late July to mid-August. We collected data each year for nest sites used in multiple study years and treated them as separate nests for analysis. We measured nest dimensions and classified the type and composition of substrate in and adjacent to each nest site. We measured slope aspect at the nest site with a handheld compass. We measured slope pitch to the nearest degree with a clinometer; slope was measured for a 10-m long line segment that extended 5 m above and 5 m below the nest. Nest-site locations were recorded with a handheld GPS, and elevation of the resulting waypoints was obtained from a raster-based digital elevation model with a 10 m resolution in ArcGIS 10. Visibility of the ocean from the nest was determined from a standing position at the nest site and was categorized as either visible or not visible.

We used ArcGIS 10 to determine the location of each nest-site relative to landscape-scale features. We measured the distance of nests to the highest land elevation immediately upslope of the nest to standardize nest distance from the tops of adjacent peaks and ridges. We measured the distance from each nest to the nearest patch of visible vegetation (≥50% vegetation cover; "habitat edge") that was ≥0.5 ha, using high-resolution orthoimagery. Only one set of orthoimages was available, so we used this layer for all years of data; most vegetation within the nest search area was composed of low-lying woody vegetation, the extent of which was assumed to be constant among years. Finally, we measured the shortest straight-line distance from nests to the nearest coastline.

We collected data on habitat characteristics for "nest plots" centered on each nest-site (Table 1). We visually estimated proportional coverage values for 11 classes of ground cover within a 5 m radius of the nest site, as well as total percent cover of vegetation. We also estimated total percent vegetation cover within 25 m and 50 m of the nest site. While small quantities of crustose lichens and trivial amounts of fruticose lichen were present on rocks within the study area, they were not included in percent vegetation cover.

To identify the habitat characteristics of searched areas that were not used by nesting Kittlitz's Murrelets, we collected habitat data for randomly assigned plots at two different spatial scales: near the site of each active nest and across the entire study area. To identify characteristics of habitat near nest sites, we assigned two "near-nest" plots at a random bearing and distance (50–150 m) from each active nest site. Near-nest plots were limited to locations that had been searched during the study year in which the nest was found and were constrained to fall ≥50 m from each other to ensure representative sampling of the area. We generated random numbers to determine bearing and distance from nest sites to near-nest plots and used handheld GPS units to confirm that near-nest plots fell within our nest-search area. To identify habitat characteristics

Fig. 2. Kittlitz's Murrelet nest site, Kodiak Island, Alaska, 16 June 2011. This nest was typical among those discovered during our study: the scrape was composed mostly of rocks 1–5 cm diameter and was located immediately downslope of a moderate-sized rock; this particular nest rock was 24 cm diameter. Photo credit: M.J. Lawonn/USFWS.

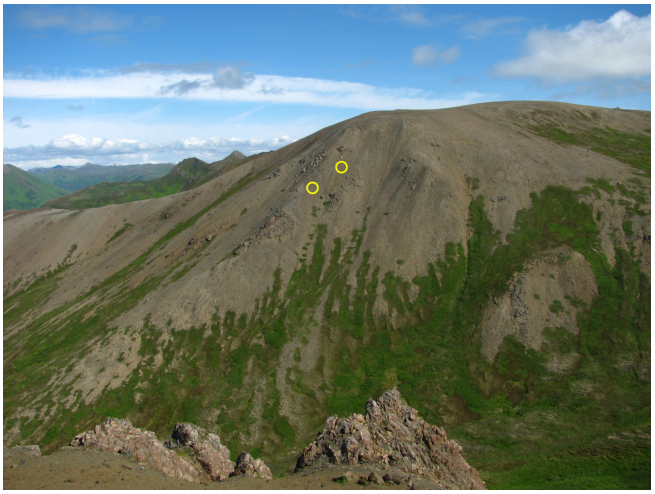

Fig. 3. Active Kittlitz's murrelet nests discovered on an unnamed peak on Kodiak Island, Alaska, in 2008 (right circle) and 2010 (left circle; nest on issue cover). Distance between nests was 45 m. Proximity of these nests to vegetated alpine terrain was typical of nests discovered during this study. Photo credit: M.J. Lawonn/USFWS.

across searched terrain at a broader scale, we surveyed plots randomly located over the entire area where nest searching was conducted. A subset of these "random" plots was assigned each year based on the locations where we carried out nest searching. Random plots were constrained to fall ≥50 m from each other and ≥25 m from any active nest found during a given breeding season. Potential bias in the estimation and measure of habitat variables among years was minimized by thorough training of field-research assistants by the same person throughout the study.

Data analysis

We conducted an analysis of variance (ANOVA) to test for differences among the three plot types (nest, near-nest, and random) for habitat covariates, using appropriate transformations to meet assumptions of normality and homoscedasticity, when necessary. For habitat covariates with significant differences ($\alpha = 0.05$) among plot types, we compared nest plots with near-nest plots and with random plots using *t*-tests. To minimize the possibility of Type II errors, we did not adjust α to compensate for multiple comparisons (Rothman 1990, Gotelli & Ellison 2004). We tested for patterns in nest-site aspect by comparing nest plots with random plots; we simplified aspect to one of the four cardinal directions and performed a pairwise test for each direction using logistic regression. To reduce the number of possible habitat variables for eventual model selection, covariates with *P* values >0.35 were omitted from further analysis for pairwise comparisons. However, to account for possible multicollinearity, we initially retained all covariates related to ground cover for further investigation, except for percent soil cover, which composed only a trivial proportion of total ground cover for all plot types. We conducted a principal components analysis (PCA; Johnson 1998) using the program PCord (McCune & Mefford 2011) to explore patterns in ground cover near nest-sites. We used PCA based on the correlation matrix for data exploration and reduction to account for wide variation in the scale of covariates, and used PCA based on the covariance

TABLE 1
Comparison of habitat variables among three plot types surveyed on Kodiak Island, Alaska, during 2008–2011[a]

Habitat variable	Mean ± SD (range)		
	Nest plots	Near-nest plots	Random plots
Slope (°)	28.8 ± 4.0 (20–37)	26.7 ± 5.3[c] (7–45)	25.1 ± 6.2[d] (0–45)
Elevation (m)	325 ± 71 (188–454)	317 ± 65 (191–450)	307 ± 73 (157–463)
Ocean in view of plot (1 = Y)	0.85 ± 0.36 (0–1)	0.77 ± 0.42 (0–1)	0.70 ± 0.46[c] (0–1)
Distance to ridge top (m)[e]	95 ± 95 (6–409)	107 ± 98 (3–388)	104 ± 106 (1–624)
Distance to habitat edge (m)	79 ± 44 (8–215)	64 ± 42[b] (1–177)	63 ± 44[b] (0–221)
Distance to coast (km)[d]	7.4 ± 1.5 (5.0–10.7)	7.4 ± 1.5 (5.0–10.7)	7.5 ± 1.7 (4.9–11.1)
% Vegetation[f]	6.6 ± 7.0 (1–33)	14.0 ± 18.1[d] (0.1–89)	16.3 ± 23.1[d] (0–100)
% Vegetation, 25 m radius[e]	9.0 ± 8.8 (0.1–45)	17.0 ± 17.6[d] (0–90)	17.8 ± 20.7[d] (0–99)
% Vegetation, 50 m radius[e]	11.5 ± 12.8 (0.1–70)	18.1 ± 17.2[d] (0–92)	19.3 ± 20.5[d] (0–92)
% Dwarf shrubs[e]	3.6 ± 5.5 (0–28)	9.1 ± 15.0[d] (0–79)	11.8 ± 20.6[d] (0–100)
% Moss[e]	2.0 ± 2.4 (0–10)	3.6 ± 6.0 (0–25)	4.4 ± 10.1 (0–90)
% Grass and sedge[e]	1.0 ± 1.0 (0–4)	1.6 ± 1.8[b] (0–8)	1.9 ± 3.1[d] (0–36)
% Forbs[e]	0.3 ± 0.4 (0–2)	0.6 ± 1.0[d] (0–5)	0.8 ± 2.1[d] (0–25)
% Lichens	0.6 ± 1.1 (0–5)	1.0 ± 3.2 (0–30)	1.0 ± 2.4 (0–30)
% Orange crustose lichens	0.1 ± 0.4 (0–2)	0.4 ± 1.6 (0–15)	0.3 ± 1.0 (0–10)
% Rock <1 cm diameter	14.3 ± 7.6 (1–33)	16.0 ± 9.5 (1–50)	16.0 ± 9.8 (0–50)
% Rock 1 to <5 cm diameter	25.6 ± 10.0 (4–50)	26.1 ± 12.6 (1–59)	23.9 ± 12.4 (0–64)
% Rock 5 to <10 cm diameter	23.4 ± 6.2 (10–41)	18.6 ± 10.3[d] (4–70)	18.1 ± 8.9[d] (0–50)
% Rock 10–30 cm diameter	21.5 ± 10.6 (5–60)	14.4 ± 8.3[d] (2–40)	14.4 ± 8.8[d] (0–45)
% Rock >30 cm diameter	8.7 ± 6.9 (0–40)	11.4 ± 11.0 (0–45)	11.0 ± 12.6 (0–95)
% Soil[e]	0.3 ± 0.6 (0–2)	0.3 ± 0.7 (0–4)	0.4 ± 0.9 (0–8)

[a] Plot types: (1) plots centered on Kittlitz's Murrelet nest sites (nest plots), (2) plots centered on randomly selected points 50–150 m from nest sites (near-nest plots), and (3) plots centered on randomly selected points within the area searched for Kittlitz's Murrelet nests (random plots).
[b] $P < 0.05$.
[c] $P < 0.01$.
[d] $P < 0.001$.
[e] Variables dropped from further analysis because of high *P* values or collinearity with other retained variables.
[f] Percent ground cover (e.g., "% Vegetation") for 5 m radius plots unless noted.

matrix for creating principal component (PC) axes for use in the logistic regression model selection described below.

We used logistic regression to determine differences in habitat characteristics among nest, near-nest, and random plots (Hosmer & Lemeshow 2000). We initially conducted logistic regression on retained covariates and PC axes that accounted for ground cover. We then substituted ground cover covariates suggested by significant PC axes in our initial logistic regression model, along with all other retained covariates, into a global logistic regression model. For logistic regression model selection we used the "bestglm" package (McLeod & Changjiang 2010) in the statistical program R (R Core Team 2011), which implements a best subsets procedure that uses Akaike's information criterion (AIC; Burnham & Anderson 2002) to determine the most parsimonious models in a set. We assessed potential multicollinearity of our predictors by calculating variance inflation factors (VIFs) for all covariates in our global models prior to model selection, and used a value of 10 as a cutoff for potential inclusion in models (following Kutner *et al*. 2004). We assessed goodness-of-fit of our final models using the Hosmer–Lemeshow goodness-of-fit test (Hosmer & Lemeshow 2000). We used Wald's test and associated *P* values to determine the significance of predictors.

We used Program MARK (White & Burnham 1999) to determine whether habitat variables had any influence on daily nest survival rates for Kittlitz's Murrelet nests. Program MARK incorporates a maximum-likelihood approach for calculation of nest survival rates and is useful for determining the influence of habitat covariates on nest survival (Rotella *et al*. 2004). We incorporated four habitat covariates suggested by our nest-site selection analyses in models that assumed constant nest survival, and evaluated candidate models using AIC_c. We created a confidence set of models by excluding models with AIC_c weights that were <10% of those of the top model (Burnham & Anderson 2002). We used methods outlined in Burnham and Anderson (2002) to average coefficient estimates for models in our confidence set.

RESULTS

Nest characteristics and spatial distribution

We discovered 53 active Kittlitz's Murrelet nests during the 2008–2011 breeding seasons ($n = 4$ in 2008, 12 in 2009, 15 in 2010, and 22 in 2011), and one nest in 2010 containing a chick that had recently died. Because of the limited number of nests discovered annually, we pooled nests from all years and search areas for analysis. Although we searched terrain supporting varying amounts of vegetation, all nests were located in areas dominated by broken rock (Figs. 2 and 3). Ground cover of non-vegetated rock substrate within 5 m of the nest averaged 93% (standard deviation [SD] 6.9, range 67%–99%, $n = 54$ nests). Only one nest was located within 100 m of a patch of snow at the time of discovery.

The 54 nests in our sample were circular depressions that had a mean diameter of 14.0 cm (SD 1.58, range 9.5–20.0 cm) and depth of 2.7 cm (SD 1.0, range 0–5.0 cm). Substrate composing the interior of the nest consisted mostly of pebbles <1 cm diameter (mean 55.0% cover, SD 29.7, range 0%–95%) and 1 to <5 cm diameter (mean 41.0% cover, SD 28.9, range 0%–98%), with larger rocks situated on nest margins (rocks <1 cm 32.9% cover, SD 21.1, range 0%–80%; rocks 1 to <5 cm 54.2% cover, SD 23.7, range 0%–100%). In three cases, the nest substrate was composed entirely of moss, although small amounts of moss were frequently found at the margins of active nests.

All nests had at least one rock >15 cm diameter, or in two cases a combination of a rock and a moss cushion, situated immediately upslope of the nest. These upslope features were generally large enough to obscure the incubating adult murrelet from the view of an observer directly upslope of the nest (Fig. 2). The average diameter of upslope features was 28.3 cm in their largest dimension (SD 9.6, range 10–63 cm). However, these features were not usually the largest available within 5 m of the nest.

Four different nests were reused once during a subsequent year of the study, but no nest was reused within the same breeding season. Ten additional nests were located <60 m from a nest active in a previous year. Thus, 28 of 54 active nests (the four reused in later years and the 10 nearby nest pairs; 52%) were located within 60 m of an active nest found during a different year of the four-year study. Furthermore, we discovered five inactive nests, apparently used in previous years, <15 m from four different active murrelet nests. These inactive nests contained weathered eggshell fragments, often buried beneath moss or gravel.

Active nests were fairly widely dispersed, with a median within-year nearest-neighbor distance of 344 m (range 13–1 550 m). However, 9 (17%) of 53 active nests were located <100 m from another concurrently active nest. Of these nine, one active nest was located <100 m from two concurrently active nests. The shortest distances observed between pairs of concurrently active nests were 13 and 46 m for two nest pairs; no visual barrier was apparent between nests in either of these pairs.

The mean density of active nests discovered during 2009–2011 was 0.092 nests/ha of searched terrain (SD 0.024, range 0.07–0.12 nests/ha, $n = 3$ years). We did not include 2008 data in this estimate because we searched a smaller area that year and spent more time searching for nests in partially vegetated terrain compared with 2009–2011. Although we believe that we detected nearly all active nests within the areas searched, our estimate of nesting density is nevertheless biased low because it does not include nests that failed before searching commenced, or potential active nests that could have been located in areas we did not search that were 30–50 m from known active nests.

Nest-site selection

There were significant differences for pairwise comparisons among nest, near-nest, and random plots for 11 habitat variables (Table 1). For our test of nest-site aspect, logistic regression analysis indicated that nests were more likely to be located on north-facing slopes ($P = 0.018$) and less likely on south-facing slopes ($P = 0.043$) than randomly selected sites. The percentage of total nests on slopes of various aspects was 48% north, 17% east, 9% south, and 26% west, whereas the percentage of randomly selected sites was 32% north, 16% east, 21% south, and 31% west.

As expected, exploratory PCA of ground cover variables revealed a high degree of correspondence among loadings for covariates related to vegetation cover (Fig. 4). Consequently, we used percent vegetation at the 5 m plot level as a surrogate for all vegetation cover, including percent vegetation cover for both 25 and 50 m

plots. Our final PCA was based on a reduced set of covariates for 5 m plots; PC axes 1–3 accounted for 90.0% of cumulative variance (Table 2).

Initial logistic regression analysis of ground cover variables indicated that PC axes 1 and 3 differed between nest plots and near-nest plots (PC 1, $P = 0.007$; PC 3, $P < 0.001$) and between nest plots and random plots (PC 1, $P = 0.007$; PC 3, $P < 0.001$), but no difference was identified in ground-cover covariates between near-nest and random plots. For our final models, we substituted percent vegetation cover at the 5 m radius scale for PC 1 and percent cover of rocks 5 to <10 cm, 10–30 cm and >30 cm for PC 3. Compared with near-nest plots and random plots, nest plots were more likely to be steeper in slope ($P = 0.003$, $P < 0.001$, respectively; Table 3) and to have lower percent vegetation cover ($P = 0.044$, $P = 0.019$), greater percent cover of rocks 10–30 cm diameter ($P = 0.001$, $P < 0.001$), and lower percent cover of rocks >30 cm ($P = 0.015$, $P = 0.025$). Compared with random plots, near-nest plots were steeper in slope ($P = 0.021$, Table 3), but were not different for ground cover variables.

Nest survival

Covariates entered into our nest-survival models included: (1) percent cover of rock size-class 10–30 cm, (2) slope, and (3) percent cover of vegetation within 25 m of the nest. Although not indicated by our model-selection procedures, we also included as a habitat covariate (4) nearest distance to vegetation-dominated terrain ("Distance to habitat edge"; Table 1), because proximity to habitat edges is known to be a source of reduced nest survival for many ground-nesting birds (Angelstam 1986, Keyser *et al*. 1998).

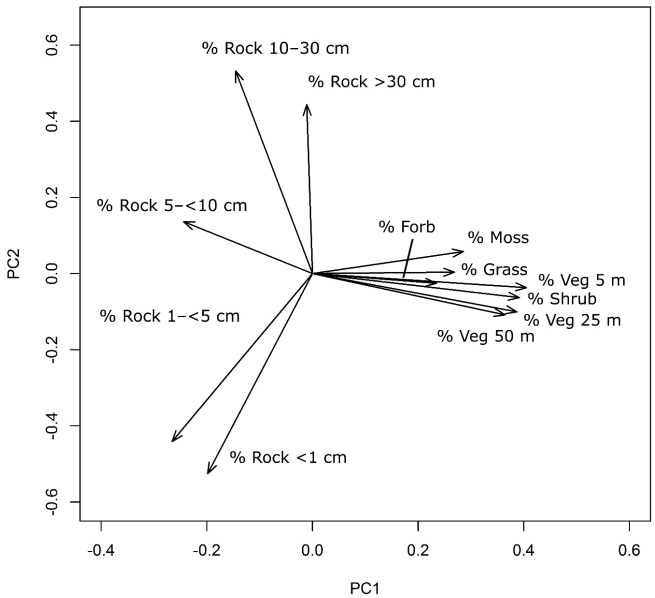

Fig. 4. Vectors of ground-cover covariates for principal component axes 1 and 2 from exploratory principal component analysis (PCA) for plots centered on Kittlitz's Murrelet nests, plots randomly selected near murrelet nests, and plots randomly selected from the total area searched for murrelet nests on Kodiak Island, Alaska, during 2008–2011. Angles between vectors of 0° or 180° represent correlations of +1 and -1, respectively.

For our nest-survival analysis, we tested all possible permutations of the habitat covariates ($n = 16$), including a constant-survival model without habitat covariates (Mayfield estimate). Our confidence set included 15 models with AIC_c weights within 10% of the weight of the top model; all models in the confidence set were within 3.5 ΔAIC_c points of the best model. Confidence intervals (95%) for model-averaged parameter estimates all overlapped zero, indicating no significant influence of habitat covariates on nest-survival rate.

DISCUSSION

Spatial distribution of nests

The reuse of nest sites and the proximity of previously used nest sites to active nests suggests fidelity of breeding Kittlitz's Murrelets to nest sites and nesting areas. Such fidelity is consistent with limited information for both Kittlitz's (Piatt *et al*. 1999) and Marbled Murrelets (De Santo & Nelson 1995, Hébert & Golightly 2006, Barbaree 2011), and the well-documented nest-site and nest-area fidelity of other alcid species (reviewed by De Santo & Nelson 1995). However, in our study, we cannot rule out that the repeated use of areas near previously discovered nest sites was simply a result of a limited amount of high-quality habitat within the study area. In our study area, Kittlitz's Murrelets generally nested in a dispersed manner across the landscape, similar to what has been reported previously (Day *et al*. 1999, Kaler *et al*. 2009). Such apparent dispersion of nests is consistent with an ecological strategy to minimize the probability of nest detection by potential predators. Individuals in a population of cryptic prey appear to have a lower risk of detection by predators when the density of prey individuals is low (Tinbergen 1967). This phenomenon is apparently a result of reduced predator effort and a lower rate of success at finding concealed prey that is widely scattered over a landscape. In a like manner, the concealment of cryptic prey seems to be maximized when its probability of occurrence over a landscape is low (Merilaita *et al*. 1999).

Nest-site selection

Our analysis suggests that vegetation cover may be an important driver for Kittlitz's Murrelet nest site selection on Kodiak Island.

TABLE 2
Axis loadings of covariates from principal component analysis (PCA) of ground-cover habitat variables for 5 m radius plots among three plot types on Kodiak Island, Alaska, during 2008–2011[a]

Ground-cover covariate	PC 1 (58.0%)	PC 2 (20.4%)	PC 3 (12.5%)
% Rock <1 cm diameter	–13	22	–19
% Rock 1 to <5 cm diameter	–23	29	–14
% Rock 5 to <10 cm diameter	–13	–1	32
% Rock 10 to 30 cm diameter	–7	–22	33
% Rock >30 cm diameter	1	–44	–35
% Vegetation	55	14	2

[a] Plot types: (1) centered on a nest, (2) within 50–150 m of a nest, and (3) randomly selected from throughout the area searched. Per axis variance is presented in parentheses.

Logistic regression analysis indicated that the odds of a plot being used as a nest site was inversely related to percent vegetation cover and to percent coverage of rocks >30 cm, but directly related to percent coverage of rocks 10–30 cm (Table 3). However, pairwise comparisons for these variables suggest that vegetation coverage could be of primary importance. Nest plots were characterized by only 6.6% vegetation cover within 5 m of the nest site, while vegetation cover for 5 m radius near-nest and random plots was more than double this amount (14.0%, 16.3%, respectively, $P < 0.001$). Further, the amount of vegetation within 25 and 50 m of nests sites was also significantly lower than equivalent plot sizes for near-nest and random plots. We conclude that low percent vegetation cover may be a major driver of nest-site preference within the study area, and that the importance of low vegetation cover could extend to at least 50 m from a potential nest site.

Our conclusion that Kittlitz's Murrelets may select for poorly vegetated areas on the landscape must be qualified by the fact that a majority of our nest-searching occurred in areas dominated by broken rock rather than vegetation. However, we think that frequent use of vegetated terrain within our study area by Kittlitz's Murrelets is unlikely for several reasons. First, while most of our searched habitat was dominated by broken rock, our searched habitat did include significant areas of highly vegetated terrain adjacent to rocky terrain, including areas with 100% vegetation cover, yet no nests were found in these habitats during four years of searching. Second, our final logistic regression model indicates that Kittlitz's Murrelet nests were more likely to occur as percent vegetation decreased, even within a searched area that averaged only 16.3% vegetation (Table 1). Third, in order to access our searched areas, we daily traversed large areas of predominantly vegetated alpine terrain, and never incidentally encountered a Kittlitz's Murrelet nest in such habitats. Finally, flying Kittlitz's Murrelets within our study area were documented to actively vocalize during early morning hours near broken rock habitats (Lawonn *et al*. 2012), a behavior possibly related to territorial behavior or nest-site prospecting; however, Kittlitz's Murrelets were not heard vocalizing in adjacent habitats where exposed rock was not the dominant ground cover. Taken together, these observations support our conclusion that Kittlitz's Murrelets exhibited a preference for poorly vegetated terrain within our study area.

Percent cover of rocks 10–30 cm was significantly different among plot types for pairwise comparisons, with nest plots characterized by 21.5% coverage compared with 14.4% for both near-nest and random plots ($P < 0.001$). In contrast, pairwise comparisons revealed no difference among plot types for percent cover of rocks >30 cm, suggesting that the actual influence of coverage of this rock size-class on nest-site selection may be low. Percent cover of rocks 10–30 cm may also be an important component of ground cover at the nest site, although the overall heterogeneity in rock sizes observed among nest plots (Table 1) seems to argue against generalizing any one size-class of rocks as a predictor, apart from the context of other size-classes present.

While characteristics of ground cover at nest plots were significantly different from those at near-nest and random plots, habitat characteristics >50 m from plot centers also appeared to be different among plot types. The centers of nest plots were farther from edges of vegetation-dominated terrain than were randomly selected plots, suggesting a possible avoidance of such edges by murrelets, even beyond 50 m from potential nest sites. Further, both nest and near-nest plots were more likely to be steeper in slope than random plots (Table 3), suggesting that areas of steeper slope extend up to at least 150 m from nest sites (since near-nest plots were restricted to this distance) relative to random plots (which were placed across searched terrain regardless of nest presence). Thus, areas of steep terrain ≥300 m diameter seem to have been associated with preferred nesting habitat within our study area.

We were unable to address the potential influence of patch size on nest-site selection because few discrete patches of sparsely

TABLE 3
Results of best-subset multiple-logistic-regression models incorporating ground-cover covariates suggested by principal-component axes for plots centered on nests of Kittlitz's Murrelets found on Kodiak Island, Alaska, during 2008–2011

Model	Predictor	Estimate	Standard error	*P* value
Nest plots vs. near-nest plots	Intercept	4.740	1.333	<0.001
	Slope	0.137	0.046	0.003
	% Vegetation	-0.047	0.023	0.044
	% Rock 10–30 cm diameter	0.075	0.023	0.001
	% Rock >30 cm diameter	-0.057	0.024	0.015
Nest plots vs. random plots	Intercept	6.664	1.110	<0.001
	Ocean view (factor)	0.739	0.415	0.075
	Slope	0.142	0.038	<0.001
	% Vegetation	-0.048	0.021	0.019
	% Rock 10–30 cm diameter	0.053	0.016	<0.001
	% Rock >30 cm diameter	-0.042	0.019	0.025
Near-nest plots vs. random plots	Intercept	2.682	0.532	<0.001
	Slope	0.045	0.019	0.021

vegetated terrain were available to be searched, and these were generally similar in size. However, the overall size of patches of suitable nesting habitat may be an important predictor of Kittlitz's Murrelet nest-site selection in other nesting areas, as it is with other species of ground-nesting birds (Davis & Brittingham 2004, Winter *et al*. 2006). Similarly, all searched habitats were fairly close to the nearest coastline — between 4.8 and 11 km — which likely precluded our ability to detect any effect of distance to the ocean on nest-site selection. It seems likely, however, that the transit distance from the nest to foraging areas at sea could nevertheless be an important driver of nest-site selection, especially given the apparent high energetic cost of provisioning food to chicks (Hatch 2011).

Comparisons with previously described nests

Nesting habitats within our study area were generally similar to those described elsewhere (Day *et al*. 1983, 1999; Day 1995, Piatt *et al*. 1999), although some important differences were observed. Unlike nests described from locations across the species' range by Day *et al*. (1999), most of which were found on south- or east-facing slopes, nests in our study were situated primarily on north- and west-facing slopes. Day *et al*. (1999) hypothesized that the orientation of nests may be related to increased habitat availability resulting from rapid snow melt on south-facing slopes; however, this factor would not apply to our study area because almost no snow was observed during the period when nesting was initiated, owing to the low elevation of nest sites and low winter snowpack typical of the region of Kodiak Island encompassing our study area. While constraints associated with snowpack seem unlikely to have affected nesting habitat availability, the nearest straight-line distance to the ocean was located to the west or northwest of all searched areas, a finding consistent with the slope aspect of most nests. Thus, we speculate that nest-site orientation in our study area may have reflected a tendency for Kittlitz's Murrelets to situate their nests on slopes that face the ocean.

The elevation of murrelet nests in our study area (mean 325 m) was lower than that for nests described from similar latitudes (median 760 m; Day *et al*. 1999). The only nest found on Kodiak Island prior to this study was 901 m above sea level (Stenhouse *et al*. 2008), nearly twice the elevation of the highest terrain available in our study area. Similarly, our study area did not include any glaciers or permanent snow, or any extremely steep (>45°) terrain. The breeding distribution of Kittlitz's Murrelet, however, is clumped in several regions where such steep, high-elevation terrain is common. Nests have been described in patches of broken rock surrounded by permanent snow and glacial ice and on cliff faces (Day *et al*. 1983), and nests are suspected to occur on nunataks adjacent to glaciers in many areas of the species' breeding range (Day *et al*. 1999). It seems likely, therefore, that our models for nest-site selection on Kodiak Island are not wholly reflective of Kittlitz's Murrelet nest-site selection across the species' entire range.

Consistent with many nests previously documented (Day *et al*. 1999), nests within our study area were located in areas dominated by broken rock, with little vascular vegetation, mosses, or lichens near the nest scrape. In contrast, nests described from Agattu Island were characterized by 51% vegetation cover (including mosses and lichens) at the nest site (Kaler *et al*. 2009). Additionally, Kaler *et al*. (2009) reported that the presence of orange crustose lichens and bare ground were the best predictors of whether a given area supported nest sites, while neither of these factors were significant predictors on Kodiak Island. A potential explanation for the variance between nest-site characteristics on Agattu Island and those described in this study could be a function of the difference in predator regimes between the two sites. Agattu Island supports avian predators, yet is free of terrestrial mammalian predators; however, both avian and mammalian predators are abundant on Kodiak Island, and both were commonly observed within our study area. Specifically, the Red Fox was the most commonly observed mammalian predator and was responsible for all identified nest depredations observed by remote camera for a separate study (Lawonn 2012). Since we seldom saw potential alternative prey other than the scattered Kittlitz's Murrelet nests in areas dominated by broken rock, we infer that there were few alternative food sources in such habitat. Such a lack of potential prey is consistent with the scant vegetation cover found near nests, indicating that the area is not capable of supporting significant numbers of primary consumers that would be of interest to potential murrelet predators. Thus, we speculate that risk of predation from both mammalian and avian predators could constrain Kittlitz's Murrelets to select habitats on the landscape, and nest sites themselves, that exhibit a high proportion of rock cover and a concomitantly low proportion of vegetation cover.

Nest survival

While we did not find a relationship between habitat covariates and nest survival, our limited sample size may have precluded detection of any such effect. Moreover, 58% of unsuccessful nests failed due to depredation, with the remainder failing due either to parental abandonment of the egg or death of the nestling due to factors other than predation. Although risk of nest predation might have been influenced by nest-site characteristics, other factors likely accounted for chick death and nest abandonment. Thus, potential habitat factors that influenced the chances of nest predation may have been obscured by the large proportion of nests that failed for other reasons.

Overall nesting success rates within our study area were low during 2008–2011; only 17% of nests discovered during this study resulted in a fledged chick (Lawonn 2012). We hypothesize that low nest survival was partially a result of the limited size of patches of available broken-rock terrain available to nesting murrelets, which may have facilitated access by predators. Additionally, the presence of presumed prey-rich vegetated habitats adjacent to broken rock habitat in our study possibly contributed to the observed high rate of Red Fox encounters with murrelet nests (Lawonn 2012), in spite of the rock-dominated habitat surrounding nests at small and intermediate scales. Density of terrestrial predators is probably lower in regions where vegetation is scarce over large spatial scales, and consequently few sources of alternative prey exist. Such seems likely to be the case for areas of consolidated and broken rock associated with extensive snowfields or glacial ice, areas which are assumed to be core nesting grounds for much of the breeding population of Kittlitz's Murrelets in North America.

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