

ECOLOGICAL CORRELATES OF REPRODUCTION FOR A BET-HEDGING SEABIRD, THE KITTLITZ'S MURRELET *BRACHYRAMPHUS BREVIROSTRIS*

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ABSTRACT

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For longer-lived species, individuals hedge their bets by skipping breeding when conditions are poor to preserve the opportunity for future breeding attempts. Thus, understanding the ecological drivers behind the 'choice' to reproduce or not is a key step in identifying and diagnosing causes of population change. We investigated both marine and terrestrial factors that might influence whether Kittlitz's Murrelets *Brachyramphus brevirostris*—a long-lived seabird of conservation concern that is often associated with glacially-influenced habitats—choose to breed in a given year. We used a suite of proxies to explain variation in reproductive metrics of radio-tagged Kittlitz's Murrelets, exploring three hypotheses related to prey availability, nest depredation risk, and energetic costs of nesting in Icy Bay, Alaska, 2007–2012. In two of the years, we compared results with the locally co-occurring, closely-related Marbled Murrelet *B. marmoratus*. Across the six-year period of our study, the posterior mean breeding propensity of Kittlitz's Murrelets was 0.21 (95% credible interval [CrI] = 0.15–0.27), nesting success was 0.41 (CrI = 0.25–0.57), and fecundity was 0.04 (CrI = 0.02–0.06). Although none of our three hypotheses were strongly supported by the data, our results collectively suggest that successful nesters expended greater effort than failed nesters and non-nesters to acquire sufficient prey—they stayed longer in the study area, had larger marine core use areas, spent slightly less time diving, and had shorter commuting distances and longer incubation shifts. Also, in years when fecundity was highest, overlap of individual marine core use areas was greatest, suggesting predictable foraging hotspots for murrelets in those years. Importantly, when comparing *Brachyramphus* species, we found that Marbled Murrelets outperformed Kittlitz's Murrelets reproductively by three to four times in overlapping years, suggesting different drivers of reproduction. From our collective results, we posit that the limitation to reproduction of Kittlitz's Murrelets may not be prey abundance or quality, but instead efficient access to prey. While our associations with indices of prey availability, depredation risk, and energetic costs to nesting did not explain much of the variation in fitness metrics, our study demonstrates the value of using a comparative approach and multiple metrics to diagnose factors limiting a population, especially when data are sparse. For bet-hedging species with complex life histories, we recommend using a combination of integrated modeling and a monitoring framework designed to accumulate evidence across studies to estimate population dynamics and improve inferences about ecological drivers.

Key words: *Brachyramphus*, murrelet, Alaska, skipped breeding, prey availability, nest depredation risk, energetic costs of nesting

INTRODUCTION

Species display a wide array of life histories that represent trade-offs in allocation of individual resources to maximize their fitness or lifetime reproductive success (Lack 1954, Stearns 1992, Roff 2002). For longer-lived species, individuals hedge their bets by skipping breeding when conditions are poor, so as not to incur unnecessary costs and jeopardize the opportunity for future breeding attempts (Stearns 1976). Thus, understanding the ecological drivers of reproduction that contribute to maximizing fitness is a key step in identifying and diagnosing causes of population change.

Gathering sufficient information on reproduction of species that breed intermittently can be inherently difficult, especially if the potential drivers are unknown, confounded, or interact. A long-term data series relative to a species' lifespan is needed to capture the range of conditions that determine breeding attempts by individuals and the specific conditions required for successful

breeding (White 2019). Intuitively, if population changes are suspected or underway, an even longer-term data series is required, as skipped and failed breeding attempts are likely to occur more frequently. Those species whose populations appear to be decreasing warrant the greatest conservation concern, and this concern may be urgent depending on the underlying circumstances of the decline; paradoxically, these populations may be fundamentally more challenging to investigate.

This conservation conundrum is well-illustrated by the Kittlitz's Murrelet *Brachyramphus brevirostris*, a relatively long-lived seabird that is patchily distributed across coastal Alaska and eastern Russia. During the breeding season, this species is often found in glacially-influenced habitats where it nests in low densities on scree slopes, cliff ledges, glacial moraine, and nunataks, and where it feeds in cool, turbid waters on small forage fish such as Pacific Sand Lance *Ammodytes hexapterus* and Pacific Capelin *Mallotus catervarius* (Day *et al.* 2020).

The Kittlitz's Murrelet, along with its congeners, the Marbled Murrelet *B. marmoratus* and Long-billed Murrelet *B. perditus*, is thought to have evolved solitary- and inland-nesting habits to take advantage of habitats that are under-utilized by colony-nesting seabirds (Gaston 2004). This life-history strategy likely reduces competition for food resources by allowing individuals to scatter along unused portions of the shoreline. However, it also means they forgo the benefits of colonial nesting, such as protection from predators, and incur higher energetic costs to access inland nest sites. Consequently, non-breeding appears to be common for Kittlitz's Murrelets, presumably because individuals skip breeding in some years, a decision that is likely influenced by intrinsic and extrinsic factors (Kissling *et al.* 2016).

Owing to concerns about apparent population declines, thought to be related to loss of tidewater glaciers, the Kittlitz's Murrelet was listed as a candidate for protection under the U.S. Endangered Species Act in 2003 (USFWS 2004). A decade later, after considerable new research was conducted, a not-warranted finding was published based on recent stabilization of populations, low probability of extinction (< 1% in 25 years), and lack of a mechanistic link to identified stressors (USFWS 2013). Although the species was not ultimately listed as threatened or endangered, the finding highlighted concerns about the chronically low reproductive output across its range, as reported by studies spanning southeastern Alaska (Kissling *et al.* 2015a), Prince William Sound (Day & Nigro 2004), Kodiak Island (Lawonn *et al.* 2018a), the Aleutian Islands (Kaler *et al.* 2009), and locations farther north in the Arctic (Kissling & Lewis 2016). However, none of these studies were able to identify the driver(s) of reproduction and, therefore, could not assess them as threats to the species' survival.

Several explanations for the purported poor reproductive performance of Kittlitz's Murrelets have been investigated, but none has been supported with clear and consistent evidence. Breeding propensity has been weakly correlated to spring phytoplankton bloom dynamics (Kissling *et al.* 2016) and indices of fall ocean productivity, suggesting possible carryover effects (Schaefer 2014). Low nesting success also has been attributed to high levels of depredation, unstable terrain, starvation, and inclement weather (summarized in Day *et al.* 2020). However, changes in the availability and quality of prey are often surmised to be the ultimate, though undocumented, cause (Kaler *et al.* 2009, Lawonn *et al.* 2018a). Importantly, most nests fail during the egg stage (a 30-day period), not the nestling stage (~25 days; USFWS 2013), suggesting either energetic constraints of incubating adults or the ability of incubating adults to predict insufficient prey resources for the upcoming chick rearing period. Lawonn *et al.* (2018a) hypothesized that the risk of nest depredation coupled with the high energetic cost of breeding may make the reproductive success of Kittlitz's Murrelets more sensitive to prey variability than other pursuit-diving seabirds. While entirely plausible, testing this hypothesis is difficult because of the complex life history of this species, notably intermittent breeding and dispersed nesting in remote areas, and the challenges in accurately assessing prey abundance, distribution, and utilization.

Here, we developed a set of hypotheses to explore the relationships between prey availability, nest depredation risk, and energetic costs of nesting using radio-tagged Kittlitz's Murrelets in Icy Bay, Alaska, 2007–2012. Following Peery *et al.* (2004), we used a weight of evidence approach having multiple competing hypotheses and reproductive metrics, and, for the first time, ecological comparisons

with radio-tagged Marbled Murrelets in the same study area. In addition, we investigated the amount of data, including the number of years, needed to identify ecological drivers of reproduction for this bet-hedging species. Our final goal was to leverage our comprehensive but sparse dataset to inform development of testable hypotheses for future studies of the Kittlitz's Murrelet.

METHODS

Study area

Our study was centered in Icy Bay, Alaska, USA, located in the northeastern Gulf of Alaska, ~110 km northwest of the town of Yakutat (Fig. 1). Icy Bay is a highly dynamic glacial fjord system that includes a shallow outer bay and a deeper inner bay. The outer bay is adjacent to the Gulf of Alaska and measures 6 km in width at the mouth. The inner bay is divided into four distinct fjords, each of which terminates at an active tidewater glacier. The Malaspina Glacier, the largest piedmont glacier in North America (Molnia 2008, Loso *et al.* 2014), is situated to the east and empties meltwater and glacial sediment into Icy Bay via the Caetani River system. The total surface of Icy Bay is approximately 263 km², but typically the upper half of the bay is covered in thick ice floes and large icebergs, resulting in an open water surface area of ~160 km².

Substantial variability is apparent in the relief and vegetative cover of the uplands surrounding Icy Bay. Low relief forelands are adjacent to the outer bay and are composed primarily of coastal and glacial deposits that are now heavily vegetated with Sitka Spruce *Picea sitchensis*, Western Hemlock *Tsuga heterophylla*, and Mountain Hemlock *T. mertensiana*. As one moves toward the inner bay, deciduous, early successional trees such as Black Cottonwood *Populus trichocarpa* and Sitka Alder *Alnus sinuata* are more common. The uplands adjacent to the inner bay are dominated by the high peaks of the St. Elias and Robinson mountains, most of which are 1000 to 2000 m in elevation. Permanent snow and ice are present and are associated with the four tidewater glaciers, the Malaspina Glacier, and other glaciers extending from the Bagley Icefield (~30 km from tidewater). The highest peak in the area is Mt. St. Elias, which reaches 5489 m in elevation only 20 km from tidewater. Indeed, the terrain in the area is very steep.

In our study area, the most likely mammalian predators to occur periodically on mountainous terrain where Kittlitz's Murrelets nest were Red Fox *Vulpes vulpes*, Brown Bear *Ursus arctos*, Black Bear *Ursus americanus*, Gray Wolf *Canis lupus*, Mountain Goat *Oreamnos americanus*, Wolverine *Gulo gulo*, and Short-tailed Weasel *Mustela erminea*. Possible avian predators included Peregrine Falcon *Falco peregrinus*, Common Raven *Corvus corax*, Bald Eagle *Haliaeetus leucocephalus*, and Glaucous-winged Gull *Larus glaucescens*.

Field methods

We summarize our field methods here, but for a full description, see Kissling *et al.* (2015a, 2016). We captured Kittlitz's and Marbled murrelets on the water using the night-lighting method (Whitworth *et al.* 1997) in and near Icy Bay between 08 May and 03 June each year for six years, 2007–2012. This period generally corresponded to the pre-breeding arrival of Kittlitz's Murrelets in the nearshore waters of Icy Bay (Day 1996). Following capture, we placed the bird into a mesh bag and then a water-resistant cardboard pet

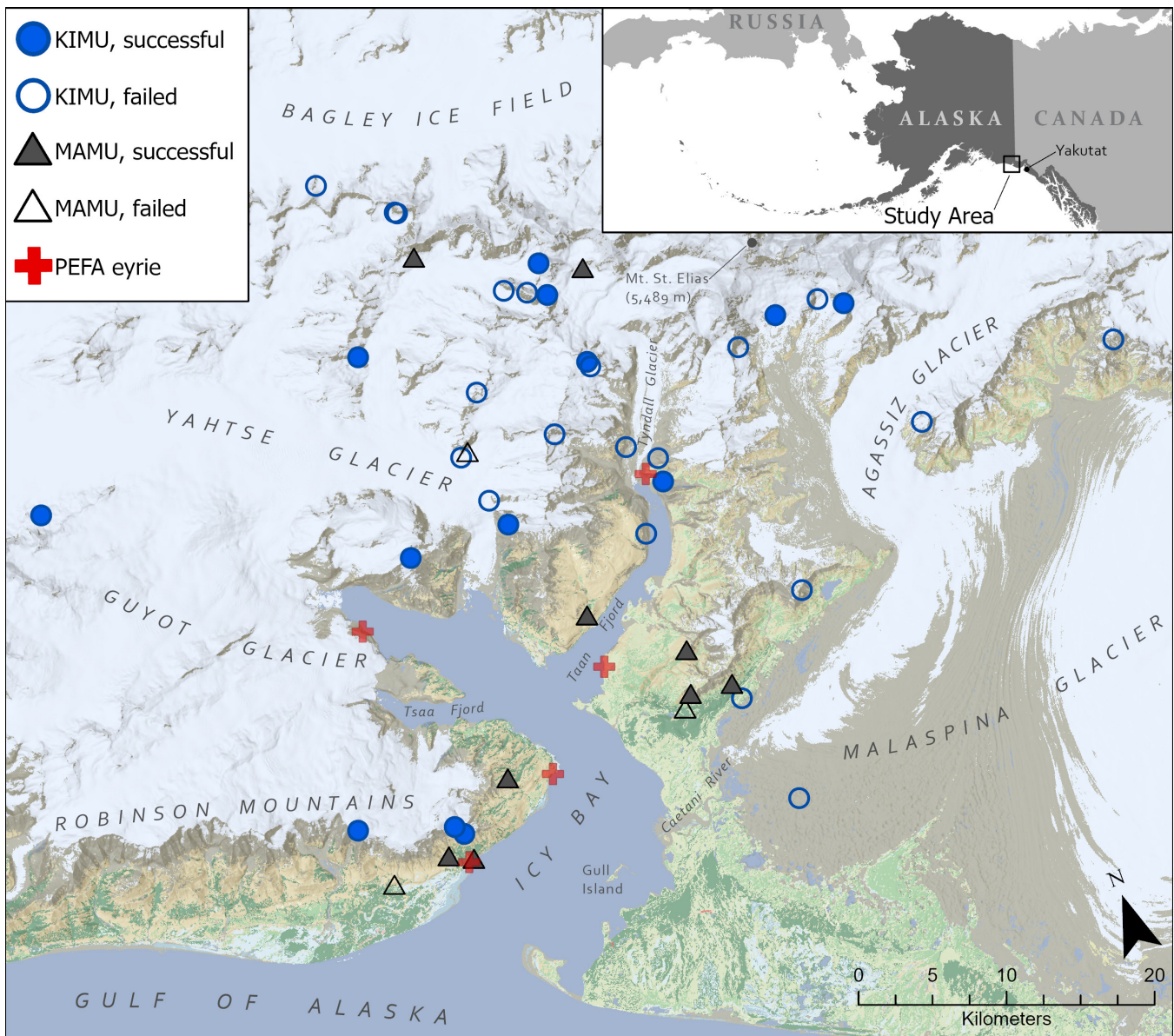


Fig. 1. Map of study area with *Brachyramphus* murrelet nest locations and fate by species (KIMU: Kittlitz's Murrelet *B. brevirostris*; MAMU: Marbled Murrelet *B. marmoratus*), and Peregrine Falcon *Falco peregrinus* eyrie locations.

carrier and transported it to a larger vessel for processing. For each captured bird, we recorded standard morphometric measurements, scored brood patch development, attached a leg band, and drew a blood sample for sex determination. We also examined the underwing plumage to distinguish second-year birds from after-second-year (ASY) birds (Pyle 2008).

Each year, we deployed very-high-frequency radio-transmitters on a subset of captured ASY murrelets (range = 24–44 murrelets annually) for a total of 191 murrelets (95 females, 96 males) across the six-year period of our study. We attached transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA; model number A4360, < 3.2 g in weight, ~1.5% of bird's mass, 28 mm [l] × 14 mm [w] × 7 mm [h]) using a subcutaneous anchor and suture on the bird's back between the scapulars following Newman *et al.* (1999). Birds were released immediately afterwards from the processing vessel. In the earlier years of the study (2007–2009), we

focused capture efforts on Kittlitz's Murrelets. However, beginning in 2010, we aimed to capture a small number of Marbled Murrelets to provide context to our study of Kittlitz's Murrelets, and in 2011 and 2012, we radio-tagged 16 of them (6 females, 10 males).

We attempted to locate radio-tagged murrelets two to five times per week (mean = 3.5; standard deviation [SD] = 1.5) for at least eight weeks using fixed-wing aircraft equipped with H-style antennas mounted on the wing struts. Generally, we began flying to locate radio-tagged murrelets immediately following capture. First, we attempted to locate all radio-tagged murrelets on the water in or near Icy Bay. If birds were not detected at sea, we flew over all assumed potential nesting habitat, within reason (e.g., fuel constraints), to locate incubating birds. In a separate analysis (Kissling *et al.* 2015b), we determined that the probability of detecting a murrelet on the water was high (0.972–0.999); at a nest, following initial discovery, the probability of detecting a murrelet was moderately

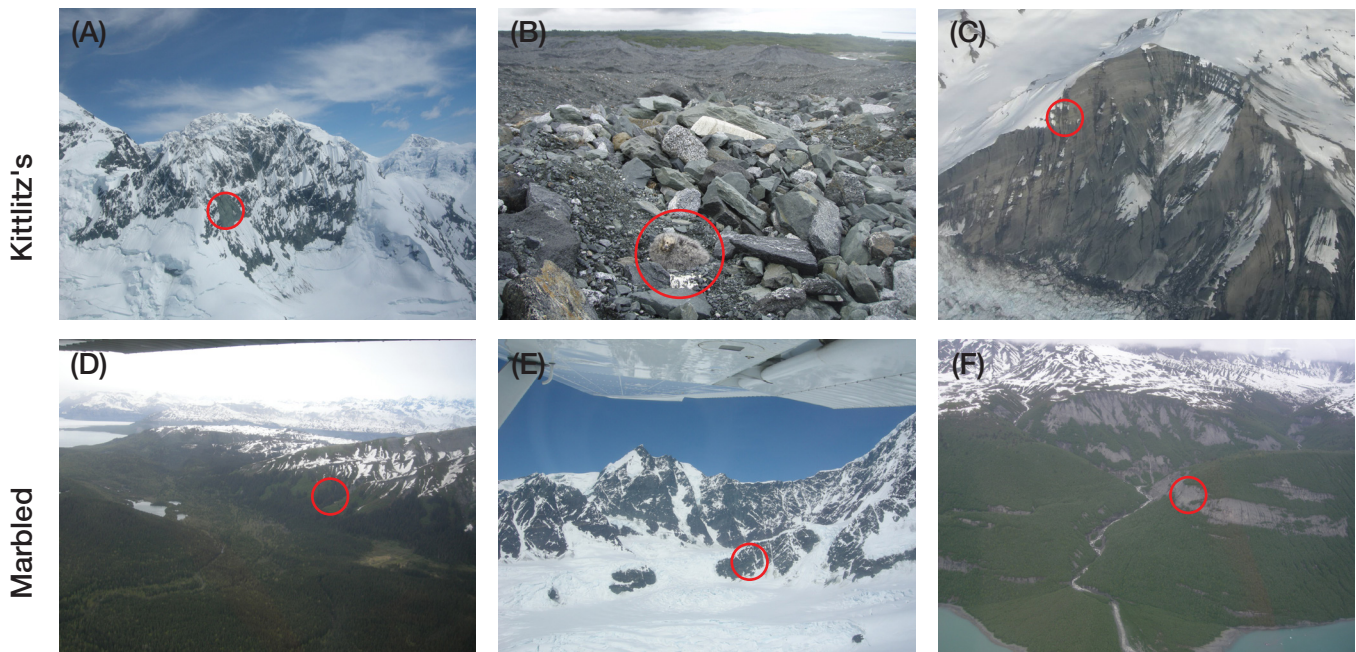


Fig. 2. Photographs of Kittlitz's Murrelet *Brachyramphus brevirostris* (top row; A–C) and Marbled Murrelet *B. marmoratus* (bottom row; D–F) nest (red circles) locations found in Icy Bay, 2007–2012. Of these nests, only (B) and (D) were accessible on foot. Note that (B) shows a Kittlitz's Murrelet chick in the nest.

high (0.700), but its presence could also be inferred. That is, when a nesting murrelet was not found on the water, but the nest could not be reached for safety reasons, we deduced it was on the nest provided that it was subsequently detected on the water. When possible, we used dataloggers to verify these instances (see below). For each radio-tagged murrelet that we located from the air, we recorded a GPS location, time of location, and, for birds on the water, whether the bird was diving.

If a nest was located during an aerial survey and was deemed accessible on foot, we immediately searched for the incubating radio-tagged murrelet using handheld receivers and antennas. If we found the nest, we attempted to deploy a remote video camera system with an infrared camera for night recording as soon as possible thereafter (SeeMore Wildlife Systems, Homer, Alaska, USA, or similar). However, the majority (91%) of nests were not accessible on foot, even with the assistance of a fixed-wing aircraft and helicopter (Fig. 2). Therefore, when possible, we monitored attendance at nearly all nests remotely using dataloggers (ATS, model R4500S, and Telonics, Mesa, Arizona, USA, model TR-5) with 4-element antennas set up within 5 km of the nest. To preserve battery life, dataloggers were programmed to scan for the frequency of the nesting bird once every 10 min for 30 s, which was less than the mean time that provisioning adults remained at nests on Kodiak Island (12.6 min; Lawonn *et al.* 2018a). We downloaded data from the dataloggers and swapped batteries as often as possible; in some cases, we could not revisit the system until after the nesting period. We determined incubation patterns and nest fate directly from cameras or indirectly from dataloggers, in addition to aerial- and ground-based telemetry locations of breeding adults. Because most of our nests were not accessible for camera deployment, we had to infer fate at the nest from dataloggers with the assumption that a murrelet would not travel repeatedly to a nest site unless it was actively incubating an egg or rearing a chick. This assumption

was largely confirmed by our cameras and other nesting ecology studies of Kittlitz's Murrelets (Kaler *et al.* 2009, Lawonn *et al.* 2018a, Kissling 2023). A complete description of our approach to determining nest fate is detailed in Kissling *et al.* (2015a).

Explanatory factors

We lacked explicit data on prey availability, nest depredation risk, and energetic costs of nesting. Therefore, we used proxies to represent these variables in our analyses. We started by generating a list of potential proxies based on our knowledge of the species and system, and on information obtained from the literature. Then, to reduce the number of proxies for analysis, we removed those that were moderately correlated ($r \geq 0.60$) and that were found to be inconclusive in prior murrelet studies (e.g., sea surface temperature, chlorophyll-*a*; Kissling *et al.* 2016). Ultimately, we used five marine factors that might represent prey availability during the breeding season, two terrestrial factors to characterize risk of nest depredation, and three combined factors that linked marine and terrestrial elements to approximate energetic costs (Table 1).

Prey availability

We assumed reproduction was positively associated with prey availability. As proxies, we used departure date, proportion of time diving, prevalence index of Pacific Capelin, and marine core use area size and overlap during the breeding season (mid-May through August).

We considered departure date from Icy Bay as a proxy of prey availability, reasoning that murrelets would remain in Icy Bay until prey resources became insufficient. Nesting murrelets are central place foragers, and although non-nesters and failed nesters are not geographically constrained, they often remained in Icy Bay, though less

TABLE 1
Marine, terrestrial, and combination factors used to explain variation in reproduction of Kittlitz's *Brachyramphus brevirostris* and Marbled *B. marmoratus* murrelets and their predicted effects, Icy Bay, Alaska, USA, 2007–2012

Reproductive metric	Response variable	Level	Hypothesis					
			Prey availability		Nest depredation risk		Energetic costs to nesting	
			Marine	Effect	Terrestrial	Effect	Combined	Effect
Breeding propensity	Reproductive status ^a (<i>n</i> = 142)	Individual	Departure date	Positive	–	–	–	–
			Marine core use area size	Negative	–	–	–	–
			Proportion time diving	Negative	–	–	–	–
Nesting success	Nest fate ^b (<i>n</i> = 32)	Individual	Departure date	Positive	Percent nest vegetated	Negative	Commuting distance	Negative
			Marine core use area size	Negative	–	–	Incubation shift length	Negative
			Proportion time diving	Negative	–	–	–	–
Fecundity	Annual fecundity ^c (<i>n</i> = 6)	Population	Marine core use area overlap	Positive	Raptor productivity	Negative	Precipitation	Negative
			Proportion of capelin in diet	Positive	–	–	–	–

^a Binomial response: non-nester (0) and nester (1)

^b Binomial response: failed (0) and successful (1)

^c Defined as annual production of females per after-second-year female in the population

frequently than nesters (Fig. 3). Given that *Brachyramphus* murrelets are not known to be territorial (Day *et al.* 2020, Nelson 2020), we assume that their departure signaled scarcity of prey; otherwise, it is not clear why they would choose to leave Icy Bay. Thus, we assumed Julian departure date to be positively associated with prey availability and calculated it as the last day a radio-tagged murrelet was located in our study area via telemetry or nest monitoring.

Next, we calculated the proportion of time diving as the number of our telemetry flights in which a radio-tagged murrelet was detected as diving divided by the number of flights it was found on the water. While this metric was a brief snapshot, the values were comparable to time activity budgets of Kittlitz's Murrelets estimated directly by Hatch (2011), so we think this method of estimation provided a reasonable approximation of proportional time murrelets spent diving. We hypothesized that the proportion of time diving was negatively associated with prey availability, assuming that if prey was readily available, murrelets would spend less time in prey pursuit, as has been found in other seabird studies that quantified activity budgets directly (Cairns 1987, Litzow & Piatt 2003, Stephens *et al.* 2007).

We used an index of annual abundance of Pacific Capelin, an important forage fish species for Kittlitz's Murrelets in Icy Bay (Hatch 2011) and elsewhere (Day *et al.* 2020 and references therein), as a proxy of prey availability. Although sand lance are also regularly consumed by murrelets (e.g., Day *et al.* 2020), we chose to use capelin as a proxy because this species is associated with cold water (McGowan *et al.* 2020), which is preferentially used by Kittlitz's compared to Marbled murrelets (Day *et al.* 2003). Moreover, capelin was significantly more abundant than sand lance during fish surveys in Icy Bay in 2011 (Arimitsu *et al.* 2016). Because we lacked explicit forage fish data

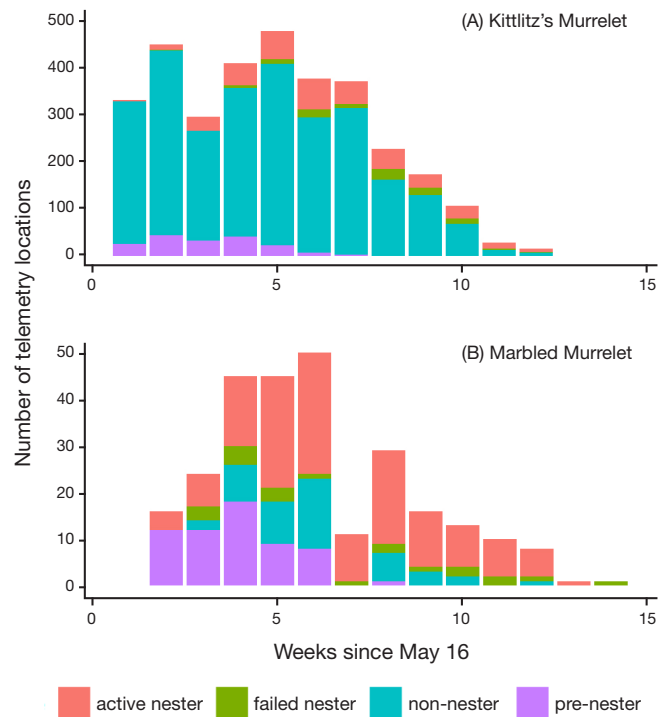


Fig. 3. Number of telemetry locations of (A) Kittlitz's Murrelets *Brachyramphus brevirostris* and (B) Marbled Murrelets *B. marmoratus* by reproductive class across all years, Icy Bay, Alaska, USA, 2007–2012. For presentation purposes, we tallied locations by week starting on 16 May when the earliest telemetry flight occurred.

for all years of our study, we used the annual proportion of capelin by biomass in the chick diet of pursuit-diving Rhinoceros Auklets *Cerorhinca monocerata* nesting at Middleton Island, roughly 275 km west of Icy Bay (Hatch *et al.* 2023). Although the distance from Icy Bay is notable, Middleton Island hosts the closest seabird colony where diet is monitored regularly and is presumed to be a reliable indicator of forage fish dynamics in the northeastern Gulf of Alaska (e.g., Cunningham *et al.* 2018, Piatt *et al.* 2018, Arimitsu *et al.* 2021).

Lastly, we considered marine space use by murrelets as a proxy for prey availability. Seabirds are expected to maximize foraging efficiency by increasing consumption of high energy-dense prey and reducing energy spent to find it (Pyke *et al.* 1977, Stephens *et al.* 2007). Therefore, we predicted that if prey availability was high, murrelets would require less marine space to acquire sufficient prey. We calculated marine home range utilization distributions (km²) using 50% and 95% kernel density estimators for murrelets with at least 12 at-sea telemetry locations. We performed the calculations in Geospatial Modeling Environment (Beyer 2012; functions *kde* and *isopleth*), allowing the program to calculate bandwidth (PLUGIN estimator) and using a cell size of 100 m. We then converted each raster file into a polygon shapefile, removed the terrestrial portions, and calculated the area of individual home range and core use areas. Not surprisingly, the 95% and 50% utilization distributions (UDs) were highly correlated ($r = 0.95$); therefore, we chose to use the 50% UD because they were less variable and they captured availability of prey resources better than the 95% UD. Hereafter, we refer to the 50% UD as 'core use areas.' We assumed that the size of marine core use areas was negatively related to prey availability.

We then examined the percent overlap of individual core use areas by year and species, as an indirect measure of prey distribution and predictability (i.e., consistency of foraging hotspots). To calculate overlap, we transformed each individual core use area shapefile to a raster file (100-m cell size), reclassified it to a common scale across all individuals, and layered them together (Cell Statistics, Spatial Analyst, ArcGIS 10.1). We considered the cells with > 50% overlap of individual core use areas to be the population-level core use areas (i.e., the core of the core areas) and calculated percent overlap by year and species. We hypothesized that the percent overlap was positively related to prey availability. When overlap of core use areas was high, prey was concentrated and spatially predictable for murrelets, which would facilitate foraging efficiency.

Nest depredation risk

We assumed that reproduction was negatively impacted by the risk of nest depredation, considered here as depredation of eggs, nestlings, and adults transiting to/from nests, which could lead to nest failure. We are not aware of any events in which an adult Kittlitz's Murrelet was depredated while at a nest. Because we were not able to monitor most murrelet nests directly, we used the percent of vegetation surrounding a nest and raptor productivity as proxies of nest depredation risk.

In areas with mammalian predators, Kittlitz's Murrelets prefer to nest in poorly vegetated terrain, where densities of predators and their prey are presumed to be low (Lawonn *et al.* 2018b). Therefore, we used percent nest vegetation to represent the risk of egg and nestling depredation of Kittlitz's Murrelets, primarily by mammalian predators. Using the 2011 National Land Cover Database (Homer *et al.* 2015), we calculated the percent vegetation (i.e., not barren

land, snow or perennial ice, water) within 500 m of each nest site, following the nest accuracy classification of Felis *et al.* (2016). We hypothesized that nest depredation risk increases with more vegetation around Kittlitz's Murrelet nests. This relationship would obviously not apply to tree-nesting Marbled Murrelets, which may benefit from increased vegetation for cover (Nelson 2020).

Predatory birds will also take Kittlitz's Murrelet eggs, chicks, and transiting adults (Kissling *et al.* 2015b), especially in areas where mammals do not occur (e.g., Aleutian Islands; Kaler *et al.* 2009). Therefore, we used data from a related study on raptor ecology in Icy Bay to estimate annual raptor productivity, which we defined as the mean number of chicks per nest, as a proxy for nest depredation risk. From 2007 to 2012, Peregrine Falcon and Bald Eagle nests and movements of satellite-tagged adults were monitored annually (Fig. 1; SBL, U.S. Fish and Wildlife Service, Juneau, Alaska). With this effort, we learned that Bald Eagles rarely searched for food away from the water, whereas Peregrine Falcons were regularly located in the uplands. Correspondingly, during our study, at least two radio-tagged adult Kittlitz's Murrelets were depredated by Peregrine Falcons enroute to or from their nests and at least 10 km from the ocean (Kissling *et al.* 2015b). While Glaucous-winged Gulls and Common Ravens occur in our study area, we did not observe them in mountainous terrain, especially the former species, which was mostly confined to the colony on Gull Island (Fig. 1). Therefore, we restricted our estimates of raptor productivity to Peregrine Falcons and assumed this proxy was positively related to nest depredation risk.

Energetic costs of nesting

We assumed that reproduction was negatively affected by high energetic costs of nesting. As proxies, we considered commuting distance, elevation, incubation shift length, and precipitation.

We calculated commuting distance (km) as the straight-line distance along the most probable flight corridor, which was determined by watershed topography to shoreline, following Barbaree *et al.* (2015). Because we were unable to reach most nests on foot, we retrieved elevation (m) from a digital elevation model for our study area. These two factors were moderately correlated ($r = 0.61$), so we removed elevation, as Hatch (2011) found commuting distance to be a sensitive parameter in a reproductive energetics model for Kittlitz's Murrelets. We predicted that longer commuting distances would increase energetic costs and have a negative impact on reproduction.

Next, we considered incubation shift length of nesting murrelets. Previous research on other seabird species has shown that incubation shifts tend to be longer when foraging ranges increase or during years of poor food availability (Gaston & Noble 1986, Gaston 2004, but see Blight *et al.* 2010). We estimated mean incubation shift length as one-, two-, or three-day intervals using nest video, datalogger, and/or telemetry data. If we were missing data (~18%), which occurred between nest discovery and deployment of cameras or dataloggers, we imputed it using the mean shift length for individual nests. Because murrelet parents share incubation duties, which require fasting while incubating and foraging while not incubating, we posited that longer rather than shorter incubation shifts would be more energetically demanding, leading to lower nesting success (negative relationship).

Finally, we used precipitation as a measure of inclement weather, which Kaler *et al.* (2009) reported as a primary cause of Kittlitz's

Murrelet nest failure during chick rearing on Agattu Island. We tallied total precipitation (cm) in Yakutat for July and August, the months that generally encompassed chick-rearing for murrelets in our study area (Climate Data Online, National Oceanic and Atmospheric Administration; <http://ncdc.noaa.gov/cdo-web>). We predicted that murrelet parents would need to brood chicks more with increased precipitation, resulting in higher energetic costs of nesting and reduced nesting success.

Data analysis

Reproductive metrics

We estimated annual breeding propensity, nesting success, and fecundity of Kittlitz's Murrelets from 2007 to 2012 and Marbled Murrelets for 2011 and 2012 only. Following Kissling *et al.* (2015a), we defined breeding propensity as the probability that an ASY murrelet attempted to nest, nesting success as the proportion of nests that survived through the fledging stage, and fecundity as the annual production of females per ASY female in the population. If a murrelet renested, we removed the original nest from further analysis. Across the six-year period, two Kittlitz's Murrelets renested, both in 2011, and two Marbled Murrelets renested, one in 2011 and one in 2012.

For estimation, we classified each radio-tagged murrelet as a non-nester or nester for breeding propensity and each nest as failed or successful for nesting success, following the same criteria outlined in Kissling *et al.* (2015a). We used generalized linear mixed models (binomial error, logit link) in a Bayesian framework. For Kittlitz's Murrelets, we included year as a random effect in the models of breeding propensity (Appendix Fig. A1, available online) and nesting success (Appendix Fig. A2). In contrast, for Marbled Murrelets, we treated year as a fixed effect in the models because data were limited to just two years. Given that *Brachyramphus* murrelets have a clutch of one egg and the sex ratio in our study was equal (Kissling *et al.* 2015a), we then calculated the product of breeding propensity and nesting success and divided it in half to estimate mean fecundity and its associated standard error (SE) and 95% credible interval (CrI). Although we report similar values in Kissling *et al.* (2015a), the Bayesian approach used here generated better estimates of variance.

Explanatory factors

Some explanatory factors were recorded at the individual murrelet level and, therefore, were used to explain variation in reproductive status and nest fate, while others were measured at the population level and were used to assess effects on annual fecundity (Table 1). We limited our analyses of explanatory factors to Kittlitz's Murrelets. We radio-tagged a small number of Marbled Murrelets in only two years, and this species was not the motivation of our study. Nonetheless, we present summary statistics of explanatory factors for both murrelet species in the overlapping years of data (i.e., 2011 and 2012) for comparison, with the aim of gaining insight into ecological drivers of Kittlitz's Murrelet reproduction. More is known about the nesting ecology of Marbled Murrelets (summarized in Nelson 2020).

We developed a set of hypotheses for each reproductive metric for Kittlitz's Murrelets and the factors for which we had data (Table 1). At the individual level, we predicted that successful nesters would

remain longer in the study area, have smaller core use areas, and spend less time diving. We also posited that nest success would be negatively associated with the amount of vegetation surrounding the nest site, commuting distance, and incubation shift length. At the population level, we hypothesized that annual fecundity would be positively associated with percent overlap of marine core use areas and proportion of capelin biomass in the diet of Rhinoceros Auklet chicks, and that it would be negatively associated with raptor productivity and total precipitation.

To test our hypotheses, we used marine and terrestrial factors as predictors in generalized linear models that we used for estimating annual breeding propensity, nesting success, and fecundity (see JAGS code provided in Appendix). We scaled covariates to have a mean of 0 and standard deviation of 1. We then multiplied each regression parameter with a binary indicator (z), which was assigned a Bernoulli ($p = 0.5$) prior, to assess the evidence of an effect of each covariate in the model (Kuo & Mallick 1998, Royle & Dorazio 2008, Kery 2010).

We explored the effect of sample size on the precision of coefficients of explanatory factors in our models of breeding propensity, nesting success, and fecundity. We replicated each dataset by two, five, and 10 times, to represent roughly two, four, and five times the generation length of Kittlitz's Murrelet (12.1 years; Day *et al.* 2020). For breeding propensity and nesting success, we increased the number of years to facilitate the use of year as a random effect in the models. We quantified the change in precision as change in credible interval widths. With this *post hoc* analysis, we asked how much data we would have needed to detect an effect of the exploratory factors given their variability and that of the reproductive metrics.

We fit all models using JAGS (Plummer 2003) with R 4.2.1 (R Core Team 2019) using the package "R2jags" as an interface. We used weakly informative priors on all parameters (see JAGS code provided in Appendix) and three Monte Carlo Markov Chain (MCMC) chains of 50 000 iterations, discarding the first 15 000 per chain as burn-in. We assessed model convergence through visual inspection of trace plots and the Gelman-Rubin diagnostic (Brooks & Gelman 1998). We assumed convergence had occurred when chains overlapped substantially, and the Gelman-Rubin diagnostic was < 1.1 for all parameters.

Various relationships are shown in supplementary figures in the Appendix (Figs. A1–A7).

RESULTS

Reproductive metrics

Across the six-year period of our study, the posterior mean breeding propensity of Kittlitz's Murrelets was 0.21 (CrI = 0.15–0.27; Fig. 4A), though annually, breeding propensity ranged from 0.09 in 2008 (CrI = 0.01–0.22) to 0.41 in 2011 (CrI = 0.24–0.59; Appendix Fig. A1). In 2011 and 2012, when both species were telemetered, Marbled Murrelets had higher breeding propensity than Kittlitz's Murrelets (Fig. 5A).

We found 34 Kittlitz's Murrelet nests and 13 Marbled Murrelet nests in the uplands adjacent to Icy Bay by tracking telemetered ASY birds throughout the breeding season (Fig. 1). For both species, two

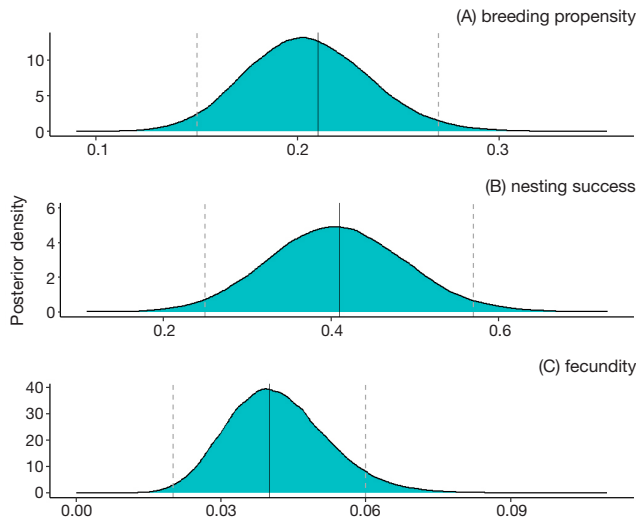


Fig. 4. Posterior distributions for reproductive metrics of Kittlitz's Murrelets *Brachyramphus brevirostris*, Icy Bay, Alaska, 2007–2012. The posterior means are indicated with a solid black line and the 95% credible intervals are indicated with gray dashed lines.

of these nests were re-nest attempts. Between 2007 and 2012, the posterior mean of nesting success of Kittlitz's Murrelets was 0.41 (CrI = 0.25–0.57; Fig. 4B). Annual estimates were highly variable and imprecise, ranging from 0.22 in 2010 (CrI = 0.00–0.56) to 0.56 in 2008 (CrI = 0.13–0.99; Appendix Fig. A2). In 2011 and 2012, the posterior mean nesting success for Marbled Murrelets was nearly double that of Kittlitz's Murrelets (Fig. 5B).

Across all years, fecundity for Kittlitz's Murrelets was 0.04 (CrI = 0.02–0.06; Fig. 4C), with annual fecundity ranging from 0.01 in 2010 (CrI = 0.00–0.05) to 0.10 in 2011 (CrI = 0.04–0.18; SM Fig. 3). Fecundity was notably higher in Marbled Murrelets than in Kittlitz's Murrelets in overlapping years (Fig. 5C).

Explanatory factors

Prey availability

Proxies of prey availability for individual Kittlitz's Murrelets varied by reproductive status and nest fate but did not always support our hypotheses. Compared to non-nesters, nesting murrelets remained longer in the study area (nester mean departure date = 201 [July 20; range = 150–218] versus non-nester = 192 [July 11; range = 140–218]), which was consistent with our hypothesis. Conversely, nesting murrelets had larger marine core use areas (nester mean core size = 122.5 km² [range = 36.4–336.5] versus non-nester = 84.1 km² [range = 7.6–222.7]) and spent more time diving (nester mean proportion = 0.25 [range = 0–0.53] versus non-nester = 0.19 [range = 0–0.45]; Fig. 6A). We found the same pattern for murrelets that nested successfully versus those that failed: successful nesters departed later (successful mean departure date = 206 [July 25; range = 196–218] versus failed = 197 [July 16; range = 150–215]). Successful nesters also had larger core use areas (successful mean core size = 130.4 km² [range = 36.4–336.5] versus failed = 116.1 km² [range = 60.4–203.8]) and spent more time diving (successful mean proportion = 0.28 [range = 0.15–0.53] versus failed = 0.24 [range = 0–0.39]; Fig. 6B).

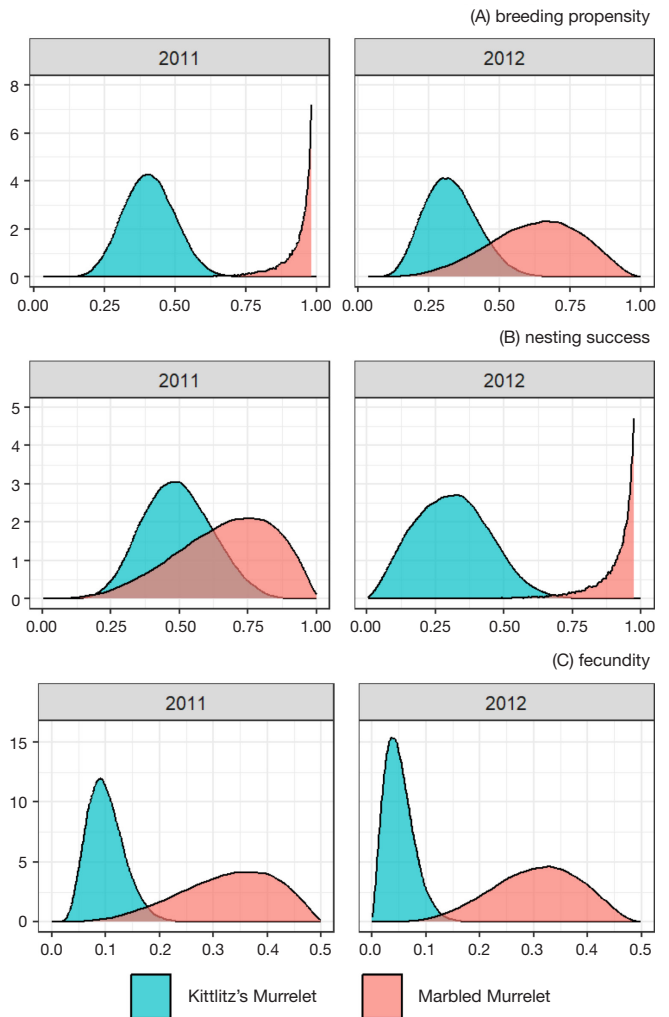


Fig. 5. Posterior distributions for reproductive metrics (A) breeding propensity, (B) nesting success, and (C) fecundity of Kittlitz's *Brachyramphus brevirostris* and Marbled *B. marmoratus* murrelets, Icy Bay, Alaska, USA, 2011 and 2012.

In 2011 and 2012, study findings for Marbled Murrelets were consistent with our hypotheses about prey availability, whereas the findings for Kittlitz's Murrelets were not (Fig. 6C). Marbled Murrelets had much higher breeding propensity and nesting success, and they departed later (Marbled mean departure date = 209 [July 28; range = 181–229] versus Kittlitz's = 194 [July 13; range = 140–218]), had smaller core use areas (Marbled mean core size = 65.0 km² [range = 9.0–206.1] versus Kittlitz's = 124.3 [range = 41.2–336.5]), and spent less time diving (Marbled mean proportion = 0.16 [range = 0–0.35] versus Kittlitz's = 0.20 [range = 0–0.38]).

At the population level, our proxies for prey availability varied annually. As we predicted, the degree in overlap of marine core use areas of Kittlitz's Murrelets was highest in years with the highest fecundity (2011 and 2012), though the pattern was weak (Fig. 7A, Appendix Figs. A3, A4). We also observed a high degree of overlap in marine core use areas for Marbled Murrelets relative to Kittlitz's Murrelets in 2011 and 2012 (Appendix Fig. A5). Lastly, the proportion of capelin biomass in the chick diet of Rhinoceros Auklets at Middleton Island, which ranged from 0.09 in 2007 to 0.55 in 2012 and averaged 0.37 across all years (Hatch *et al.* 2023),

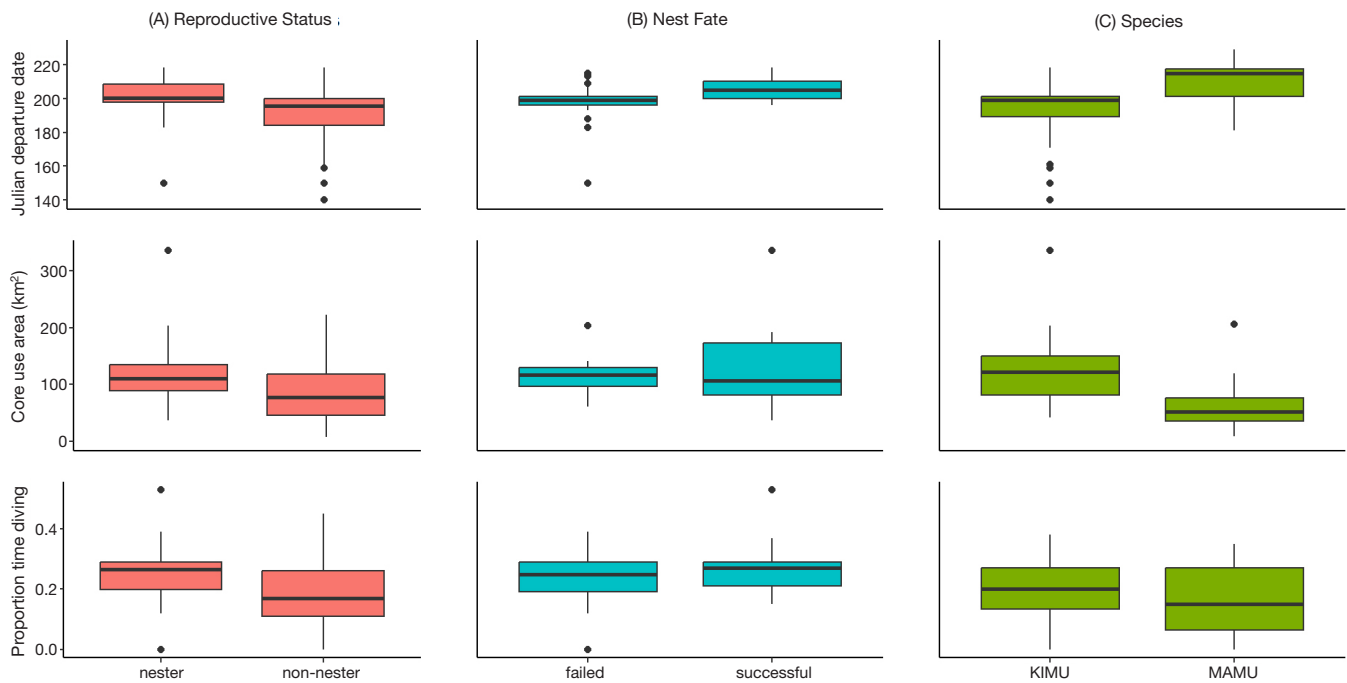


Fig. 6. Boxplots describing data distribution of proxies to prey availability for Kittlitz's Murrelets *Brachyramphus brevirostris* by (A) reproductive status and (B) nest fate from 2007 to 2012; and for (C) *Brachyramphus* species in 2011 and 2012, Icy Bay, Alaska, USA. Proxies included maximum Julian date that telemetered murrelets were in the study area (top panel); marine core use area measured as the 50% utilization distribution of radio-tagged murrelets (middle panel); and proportion of time diving, as recorded during telemetry flights (bottom panel). For (C) species, Kittlitz's Murrelets are denoted KIMU and Marbled Murrelets are denoted MAMU.

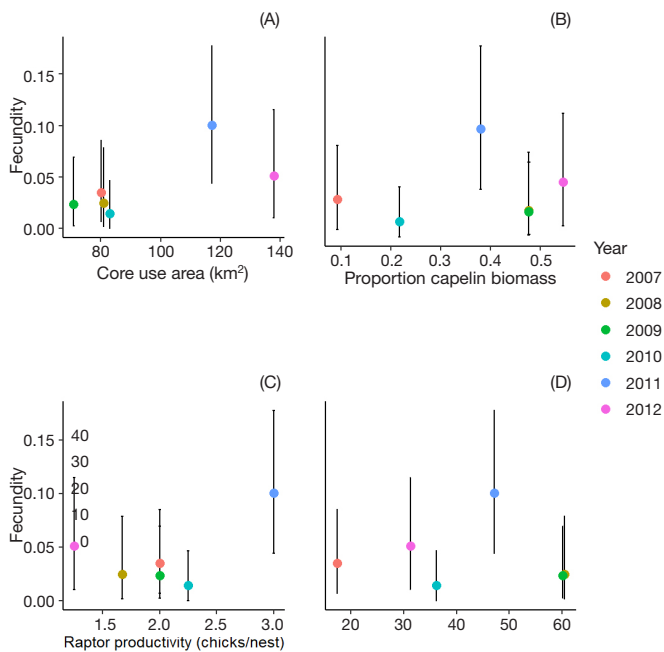


Fig. 7. Scatterplots showing the relationship between fecundity and (A) size (km^2) of > 50% overlap of marine core use area of individual Kittlitz's Murrelets *Brachyramphus brevirostris*, (B) proportion of Pacific Capelin *Mallotus catervarius* biomass in chick diet of Rhinoceros Auklets *Cerorhinca monocerata* at Middleton Island, (C) productivity measured as mean number of chicks per nest at Peregrine Falcon *Falco peregrinus* eyries, and (D) total precipitation (cm) in July and August, Icy Bay, Alaska, USA, 2007–2012. The error bars denote the 95% credible intervals for fecundity.

did not have a consistent relationship with reproduction of Kittlitz's Murrelets in our study area (Fig. 7B).

Nest depredation risk

Only four (13%) Kittlitz's Murrelet nests were on the ground in scree (Fig. 2B), and 26 nests (81%) appeared to be on cliff ledges of nunataks (Fig. 2A) and glacial cirques (Fig. 2C); we were not able to discern nest platform for two (6%) of the nests. Likewise, only four (36%) Marbled Murrelets nests were in trees (Fig. 2D). The other nests ($n = 7$; 64%) were located on cliff ledges with about half on cliffs intermixed with shrubs and conifers (Fig. 2F) and the other half surrounded by snow and ice (Fig. 2E).

The proportion of vegetation surrounding nests of Kittlitz's Murrelets was extremely low and lacked variation (Fig. 8A), as most nests were in areas dominated by barren land and perennial snow and ice (Appendix Fig. A6). Contrary to our prediction, successful nests had a mean proportion of vegetation of 0.06 (range = 0–0.53) and failed nests averaged 0.02 (range = 0–0.16). Only 28% of nest areas contained vegetated land cover classes and half of these included < 3% vegetation. In contrast, the proportion of vegetation surrounding Marbled Murrelet nests was highly variable (Fig. 8B; mean = 0.65, range = 0–1.00), with 31% of nests located in habitat more typical of Kittlitz's Murrelets (Appendix Fig. A6). Two Marbled Murrelet nest areas (15%) included only vegetated land cover classes.

Across all years, five Peregrine Falcon eyries were located, and estimated mean productivity was 2.03 chicks per year (SE = 0.54; Fig. 7C). Annual productivity ranged from 1.25 chicks in 2012 to 3.00 chicks in 2011. In any given year, three to five eyries were

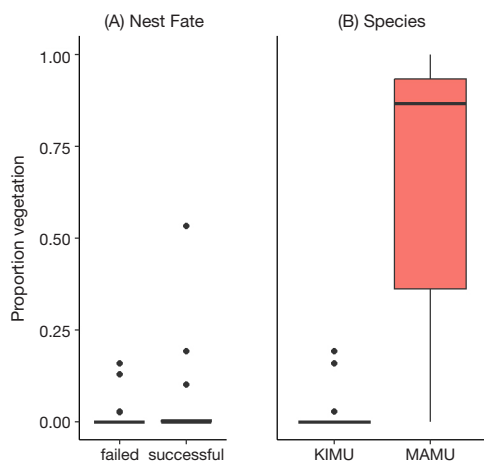


Fig. 8. Boxplots describing data distribution of the proportion of vegetation surrounding nests of (A) Kittlitz's Murrelets *Brachyramphus brevirostris* by nest fate from 2007 to 2012, and (B) *Brachyramphus* murrelets in 2011 and 2012, Icy Bay, Alaska, USA. We used the proportion of vegetation within 500 m of nests as a proxy to nest depredation risk. For (B) species, Kittlitz's Murrelets are denoted KIMU and Marbled Murrelets are denoted MAMU.

monitored, and they produced zero to four chicks, as some eyries were occupied by at least one non-nesting adult, and others were not occupied at all in some years. Unexpectedly, in 2011 when fecundity was highest (Fig. 7C), raptor productivity also was highest, which was not consistent with our hypothesis.

Energetic costs of nesting

Proxies to energetic costs of nesting for individual Kittlitz's Murrelets were variable. As predicted, successful nesters had shorter commuting distances (mean = 14.7 km, range = 0.8–40.4) than failed nesters (mean = 22.7 km, range = 0.4–54.2), but incubation shifts were similar (successful mean = 1.6 days [range = 1.0–2.1] versus failed mean = 1.5 days [range = 1.1–2.1]; Fig. 9A). During our study, we often observed incubation shifts of Kittlitz's Murrelets that lasted two days and, infrequently, three days. In 2011 and 2012, mean commuting distance for Kittlitz's Murrelets (21.9 km, range = 0.4–54.2) was more than thrice that of Marbled Murrelets (6.4 km, range = 0.1–21.2; Fig. 9B), even though they were nesting in similar habitats (see results for Depredation risk). Similarly, mean incubation shift length for Kittlitz's Murrelets (1.4 days, range = 1.0–1.9) was greater than for Marbled Murrelets who only displayed a 1.0-day shift length.

Total annual precipitation during the breeding season was highly variable, ranging from 17.4 cm in 2007 to 60.5 cm in 2008. Opposite of our prediction, when fecundity was highest in 2011, total precipitation was moderately high, and when fecundity was lowest in 2010, precipitation was moderately low (Fig. 7D).

Model outcomes

Few of the explanatory factors were useful for explaining variation in reproductive metrics of the Kittlitz's Murrelet (Table 2). The only factor that was included in more than 50% of the iterations of all three models was departure date. It was included in 83% of the model iterations for breeding propensity and 52% for nesting

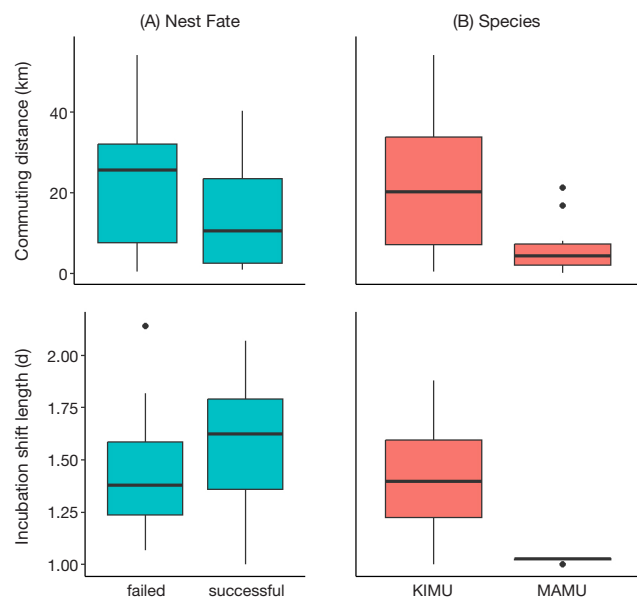


Fig. 9. Boxplots describing data distribution of proxies to energetic costs of nesting for (A) Kittlitz's Murrelets *Brachyramphus brevirostris* by nest fate from 2007 to 2012 and (B) *Brachyramphus* species in 2011 and 2012, Icy Bay, Alaska, USA. Proxies included one-way commuting distance (km) between the nest and ocean (top panel) and mean incubation shift length (days; bottom panel). For (B) species, Kittlitz's Murrelets are denoted KIMU and Marbled Murrelets are denoted MAMU.

success. Further, only departure date and proportion of time diving (for breeding propensity only) had 95% CrIs of the logit-scale posterior medians that did not contain 0, though marine core use area size was close to having a directional effect (i.e., the 95% CrIs barely included 0). However, proportion of time diving and core use area size had opposite relationships with breeding propensity and nesting success compared to what we expected, as did incubation shift length. We found no relationship between any of the proxies and annual fecundity, which was expected given that we only had six years of data. While none of the explanatory factors were useful, proxies of prey availability had the strongest relationships with reproduction of Kittlitz's Murrelets.

For all reproductive metrics, precision of explanatory factor coefficients increased with sample size (Fig. 10). The most rapid increase occurred for breeding propensity, followed by nesting success, and then fecundity. These results underscore the relationship between departure date and both breeding propensity and nesting success. Interestingly, some explanatory factors proved uninformative regardless of sample size, including proportion time diving, percent nest vegetated, and incubation length for nesting success, and proportion of capelin biomass in chick diet and precipitation for fecundity.

DISCUSSION

In this study, we aimed to assess three hypotheses about factors that could limit Kittlitz's Murrelet reproduction: prey availability, nest depredation risk, and energetic costs to nesting. Although none of our hypotheses were strongly supported with the proxies used for these three factors, we built on previous investigations

TABLE 2

Logit-scale posterior median and 95% credible intervals (CrI) and the proportion of time explanatory factors were included in each model to explain variation in reproduction of Kittlitz's Murrelets *Brachyramphus brevirostris* in Icy Bay, Alaska, USA, 2007–2012

Reproductive metric	Explanatory factor	Proportion times included in model ^a	Logit-scale posterior median (95% CrI) ^b
Breeding propensity	Departure date	0.83	0.80 (0.17–1.56)
	Marine core use area size	0.20	0.50 (-0.01–1.05)
	Proportion time diving	0.47	0.66 (0.14–1.23)
Nesting success	Departure date	0.52	2.26 (0.10–5.16)
	Marine core use area size	0.19	1.15 (-0.02–2.85)
	Proportion time diving	0.10	0.38 (-0.98–1.92)
	Percent nest vegetated	0.11	-0.04 (-1.73– 1.81)
	Commuting distance	0.15	-1.06 (-2.73–0.23)
	Incubation shift length	0.07	0.13 (-1.12–1.44)
Fecundity	Marine core use area overlap	0.01	0.02 (-4.31–4.41)
	Proportion of capelin in diet	0.00	0.00 (-6.65–6.63)
	Raptor productivity	0.01	0.02 (-3.18–3.18)
	Precipitation	0.01	0.00 (-5.90–5.91)

^a Variable inclusion in the model was determined using a binary indicator.

^b The posterior median and CrI was generated only from Monte Carlo Markov Chain iterations when the binary indicator was 1.

into this species' breeding ecology by linking marine and terrestrial habitats of individual murrelets for the first time, as opposed to only monitoring nests (Kaler *et al.* 2009, Lawonn *et al.* 2018a, Kissling & Lewis 2016) or populations at sea with age ratio surveys (Day & Nigro 2004, Kuletz *et al.* 2008). Moreover, we offer the first comparison of factors influencing reproduction of individual Kittlitz's and Marbled murrelets in the same study area. As such, we gained new insights into the species' ecology and life history that could guide future studies with similar goals.

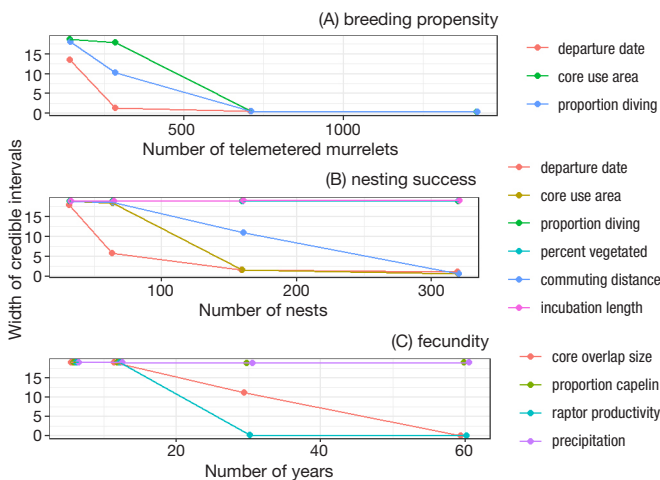


Fig. 10. The effect of sample size on precision of explanatory factor coefficients for (A) breeding propensity, (B) nesting success, and (C) fecundity. Precision was calculated as the difference in the 95% credible intervals. The points denote the number of replicates (1, 2, 5, and 10) of each dataset, including the number of years modeled as a random effect for breeding propensity and nesting success. Both points and lines are slightly offset for visibility.

We found the most overall support for the prey availability hypothesis. The proxies representing prey availability had the most concordance and consistency in their relationships with reproduction, especially departure date. While departure date does not cause poor reproduction, it had the strongest effect on model results of all explanatory factors considered; it seemed to be a reliable indicator of something meaningful in the system, which we assumed was prey availability. Successful nesters stayed longer in the study area, had larger core use areas, and spent slightly more time diving. Some of these findings were counter to our predictions, but collectively they indicated that successful nesters expended greater effort to acquire sufficient prey than failed nesters and non-nesters, both of which left the study area sooner, presumably in search of food. We also found that the size of marine core use overlap was greatest in years when fecundity was highest, suggesting that Kittlitz's Murrelets were more likely to be successful nesters when prey resources were concentrated and spatially predictable, as reported by Pastran *et al.* (2022) for Marbled Murrelets. Otherwise, murrelets spread out across the study area (i.e., with low overlap), perhaps to avoid intraspecific competition when prey resources were limited and less predictable, as is common for colonial-nesting seabirds (Gaston *et al.* 2007). These relationships held for the more successful Marbled Murrelets, which remained longer in the study area, had smaller core use areas, and spent less time diving than Kittlitz's Murrelets in overlapping years (further discussed below).

For the energetic costs of nesting hypothesis, the only moderately informative proxy was commuting distance. Nests further from the ocean were more likely to fail, though the effect of this explanatory factor on nest fate was weak, at least until we increased the sample size of nests. Tagging studies similar to ours found that breeding Marbled Murrelets were not constrained by commuting distance (Hull *et al.* 2001, Barbaree *et al.* 2015, Lorenz *et al.* 2017, Pastran *et al.* 2022, and others), though sample sizes may have been too small to detect an effect. With a bioenergetics model, Hatch (2011)

determined that a 20% change in commuting distance resulted in an 8% change in field metabolic rate for nesting Kittlitz's Murrelets. The additional energetic cost could be compensated for by increasing incubation shift length and/or increasing foraging effort away from the nest during incubation, both of which we observed in our study (Fig. 9). This offset could also be achieved by increasing energy content of prey delivered during chick rearing. However, if commuting distance exceeds 35 km, Kittlitz's Murrelets may not be able to compensate for the added costs (Hatch 2011), at least in south-coastal Alaska where elevation rapidly increases with distance from the ocean. Only 20% of our nests were located more than 35 km from the water, and 67% of those failed, loosely supporting this threshold for commuting distance.

The results of this study for the nest depredation risk hypothesis were inconclusive. Nearly all Kittlitz's Murrelet nests were surrounded by negligible vegetation, so lack of variation in this explanatory factor likely limited its usefulness. However, it may be a more informative proxy at a larger scale more comparable in size to the home range of potential predators, in other study areas (e.g., non-glacially-dominated habitats such as the Aleutian Islands or northern Alaska), and/or for Marbled Murrelets, which may benefit from increased vegetation as cover where tree nesting is more common. In our study, Marbled Murrelets regularly nested in habitat that was more typical of Kittlitz's Murrelets (Appendix Fig. A4), suggesting that the glacially-influenced systems of south-coastal Alaska were likely where the species diverged ecologically; outside of these systems, Marbled Murrelets usually nest in trees where the depredation risk is different (Nelson 2020). As with all proxies used to explain variation in Kittlitz's Murrelet fecundity, raptor productivity was uninformative. However, as the number of years in the dataset increased, it appeared to become a more useful proxy. Confusingly, raptor productivity had a positive effect on fecundity, which may reflect bottom-up benefits for raptors (i.e., food) when murrelets are concentrated (i.e., high core use overlap). Alternatively, this result suggests raptor productivity was not a reliable proxy for nest depredation risk but instead represents something else in the system.

Admittedly, the lack of compelling results in our study could be because we used poor proxies to represent our three hypotheses. Some of our proxies were derived from the birds themselves and, therefore, were not independent of the response variable (i.e., reproductive status and nest fate). Perhaps not coincidentally, these proxies were the most informative in our models (i.e., departure date, time spent diving, and to a lesser extent, marine core use area size). Also, forage fish tend to be patchily distributed and highly dynamic (McGowan *et al.* 2019), and it is unlikely that any of our proxies for prey availability sufficiently captured their spatial and temporal variability. Further, our proxies only considered conditions during the breeding season in Icy Bay, not those faced by murrelets during the non-breeding season or previous breeding attempts, both of which can result in carryover effects that impact future reproduction (Fayet *et al.* 2016). Finally, the relationships between several of our proxies and reproduction could be interpreted in more than one way. For example, murrelets could spend more time diving when prey availability is high to exploit discovered patches of forage fish, as has been found with Steller Sea Lions *Eumetopias jubatus* (Goundie *et al.* 2015) and Adelie Penguins *Pygoscelis adeliae* (Lescroel *et al.* 2021), not when prey availability is low as we inferred from our results. Nevertheless, the value of our study lies with the contrasting results for Kittlitz's and Marbled murrelets, not with the quality of our proxies. Clearly, *in situ* measurements

of prey availability, nest depredation risk, and energetic costs of nesting would have been useful but also somewhat limiting without data on the full annual cycle of Kittlitz's Murrelets.

Despite our data limitations and inability to identify strong drivers of reproductive variability of Kittlitz's Murrelets, we did gain several new insights. The most revealing information was gained by comparing reproductive metrics and explanatory factors between *Brachyramphus* murrelets. As noted by Kissling *et al.* (2015a), Marbled Murrelets outperformed Kittlitz's Murrelets in all aspects of reproduction in Icy Bay. With our analysis in this study, we identified possible explanations for the disparity. Marbled Murrelets had smaller core use areas, spent less time diving, used greater diversity of nesting habitat, commuted shorter distances to nests, and had shorter incubation shifts. Contrary to our expectations, Icy Bay was more favorable to Marbled Murrelets and less optimal for Kittlitz's Murrelets, at least during the years of our study. Kittlitz's Murrelets had to work much harder than Marbled Murrelets, and in accord Kittlitz's Murrelets were less productive. This finding was similar to the findings of other studies that showed that Marbled Murrelets in the threatened portion of their range (i.e., California to British Columbia) had larger marine ranges than those in the non-threatened portion (i.e., Alaska), suggesting that home range size may be indicative of the overall habitat quality of an area (Lorenz *et al.* 2017, Pastran *et al.* 2022). If so, despite its extensive glacial influence, Icy Bay may serve as sink habitat for Kittlitz's Murrelets, given that Kittlitz's Murrelets have much larger home ranges than Marbled Murrelets and yet far outnumber them.

As congeners, Kittlitz's and Marbled murrelets have similar life histories and ecology, except for a few key differences. Note, however, that extending these factors beyond the local area of our study should be viewed with caution. First, during the pre-breeding period, Kittlitz's Murrelets forage primarily on zooplankton (Day *et al.* 2020), whereas Marbled Murrelets feed on both zooplankton and forage fish (Nelson 2020). Because zooplankton tend to have lower caloric value compared to forage fish (Davis *et al.* 1998, Anthony *et al.* 2000), Kittlitz's Murrelets may enter the breeding period with insufficient energy reserves. Second, as demonstrated in this study and others where these two species coexist, Marbled and Kittlitz's murrelets occupy different marine spaces, with Marbled Murrelets typically occupying warmer and less turbid waters compared to Kittlitz's Murrelets (Day *et al.* 2003, Stephensen *et al.* 2016). This niche separation has been attributed to optical specialization, as Kittlitz's Murrelets have larger eyes that may increase foraging efficiency in turbid waters with low light (Day *et al.* 2003). We believe this explanation has merit, but we suspect that if waters are too turbid, foraging efficiency of Kittlitz's Murrelets rapidly decreases, which may have been a factor in our study. Third, in Alaska, Marbled Murrelets nest on tree limbs, cliff ledges, or on the ground (Figs. 2D–F; Barbaree *et al.* 2014), while Kittlitz's Murrelets nest solely on the ground or cliff ledges (Fig. 2A–C; Kaler *et al.* 2009, Lawonn *et al.* 2018b). The fact that Marbled Murrelets use a greater diversity of nest platforms than Kittlitz's Murrelets allows them to minimize commuting distance, especially in years when prey may be limited. Fourth, Kittlitz's and Marbled murrelets have different non-breeding season distributions (Day *et al.* 2020, Nelson 2020), though some overlap occurs (Day 2006), which may contribute to disproportionate carryover effects. Lastly, Kittlitz's Murrelets are slightly larger than Marbled Murrelets (mean = 236 g and 205 g, respectively; Day *et al.* 2020, Nelson 2020) and, as noted above, they tend to use cooler waters and nest

in cooler habitats, consistent with Bergmann's rule. These attributes may result in higher energetic demands and increased sensitivity to variability in prey for Kittlitz's Murrelets compared to Marbled Murrelets (Hatch 2011).

While these differences in life history and ecology of Kittlitz's and Marbled murrelets are not new information, our study is the first to link them directly to reproduction through the study of individual murrelets. Lawonn *et al.* (2018a) speculated that Marbled and Kittlitz's murrelets likely experience similar energetic constraints during breeding, noting that populations of both species appear to have declined in the Gulf of Alaska, coinciding with changes in forage fish. Our findings do not support this theory, as Marbled Murrelets clearly outperformed Kittlitz's Murrelets reproductively in our study area. Based on our results, we posit that the limitation on Kittlitz's Murrelets' reproduction may not be prey abundance or quality, but rather access to prey. Marbled Murrelets in our study area seemed to use both marine and terrestrial resources more efficiently than Kittlitz's Murrelets, resulting in reproductive output that was three to four times higher. With the continued loss of glaciers in Alaska (Arendt *et al.* 2009), marine waters will eventually become less turbid and vegetation succession will occur (Arimitsu *et al.* 2012, Lydersen *et al.* 2014, Arimitsu *et al.* 2016), reducing foraging habitat and increasing commuting distance to nesting habitat of Kittlitz's Murrelets. Although this level of system-wide change will take decades if not hundreds of years, ultimately, Kittlitz's Murrelets will either need to adapt in a way that allows them to coexist with Marbled Murrelets, or they will need to relocate further north (Kissling 2023), or perhaps inland to freshwater lakes (Ruden 2016), to nest. Otherwise, recruitment will suffer and eventually the population will decline.

Another key insight from our study was the effect of sample size on our results. While our approach was simple, it demonstrated that our study was too small in scope and too short in length to definitively identify ecological drivers of reproduction for Kittlitz's Murrelets. With the original sample sizes, the explanatory factors did not contribute much information to our models, resulting in binary indicators dominated by 0 and strong influence of the priors on parameter estimates. However, as we increased sample sizes, the MCMC iterations were no longer driven by the binary indicators. Consequently, some explanatory factors rapidly gained importance, while others remained insignificant (Fig. 10). These results are somewhat encouraging, indicating that a total of 750 murrelets should be tagged over a 30-year period, which amounts to an average of about 25 murrelets/year. This target is not an unreasonable goal if research resources are sufficient. Advances in tag technology that allow tracking of individuals across years would also greatly facilitate our ability to diagnosis carry-over effects and poor reproduction of this species and would likely reduce sample size requirements.

An important limitation of this *post hoc* analysis was that it assumes stationary relationships and the same degree of variability in reproduction and explanatory factors as the original dataset. Although this assumption may not be realistic in a dynamic system like Icy Bay, it was fortuitous that our study observed a 10-fold difference in fecundity, as this difference may bound most of the variability, even though it is not sustainable longer term (Kissling 2023). To relax this critical assumption, we performed a similar analysis while keeping the number of study years the same (i.e., six years) and only increasing the number of tagged murrelets and nests

monitored. This exercise yielded comparable results (Appendix Fig. A7), suggesting that our approach is consistent and useful for planning future studies with similar goals. Additionally, using actual measures of nesting success and causes of nest failure, along with more accurate proxies (or direct metrics) of prey availability, nest depredation risk, and energetic costs, would likely lead to stronger conclusions more quickly and with smaller sample sizes.

Lastly, as hypothesized, our results highlight a positive correlation between departure date and both the breeding propensity and nesting success of Kittlitz's Murrelets. Although this relationship is somewhat intuitive—since murrelets must be present in the study area to attempt nesting and to nest successfully—it has potentially significant implications for at-sea population surveys that aim to estimate abundance and trends. Annual abundance estimated at sea may be correlated with reproductive effort, at best reducing precision and at worst introducing bias. Kissling *et al.* (2024) showed that temporary emigration from Icy Bay did not bias abundance and trend estimates, but their analysis did not account for departure date or permanent annual emigration. Lorenz *et al.* (2017) reported similar findings for Marbled Murrelets in Washington; in years of low breeding propensity, murrelets ranged further with longer-distance movements than in years of high breeding propensity. Thus, for murrelet population monitoring efforts that rely solely on at-sea surveys, we suggest including an additional data source to account for the relationship between breeding and departure data and avoid spurious conclusions (e.g., Lorenz & Raphael 2018).

Investigating the breeding ecology of Kittlitz's Murrelets is difficult, largely owing to their dispersed and cryptic nesting habits and affinity to nest in some of the most remote and inaccessible regions of Alaska. To date, our six-year field effort in Icy Bay represents the most intensive investigation into the factors potentially limiting population growth of this ice-associated species. Yet, like other Kittlitz's Murrelet studies, we struggled here to identify ecological correlates of variability in reproduction. Given the prevalence of non-breeding in this species, investigating environmental and demographic drivers of non-breeding—either alongside or instead of breeding—would provide valuable insights. Compared to other seabirds, the Kittlitz's Murrelet has one of the highest ratios of egg weight to adult female body mass, highest chick growth rates, lowest fractions of adult mass at fledging, and shortest periods between hatching and fledging (Lawonn *et al.* 2018a, Day *et al.* 2020). Therefore, the evidence suggests that non-breeding is the norm. By focusing less on non-nesters compared to nesters, we may be compromising our ability to fully understand drivers of Kittlitz's Murrelet natural-history patterns. For example, Cubaynes *et al.* (2011) found that young-aged Red-footed Boobies *Sula sula* attempted to nest for the first time in El-Niño years, presumably because of reduced competition from older-aged boobies that were skipping breeding. For *Brachyramphus* murrelets, these kinds of demographic data are elusive and probably always will be. This highlights the need to look beyond nesting birds if we want to advance our knowledge about factors that affect the natural history patterns and populations of murrelets.

In conclusion, our study emphasizes the value of using a comparative approach and multiple metrics to diagnose poor reproduction in species with low population levels for reasons that are not clear, such as the Kittlitz's Murrelet. However, for such species, data collected during one-time studies like ours are likely to always

be too sparse to rigorously test hypotheses. To facilitate more efficient learning, we offer two related recommendations. First, we encourage the use of integrated population models (IPM) to estimate population dynamics and test hypotheses about ecological drivers (e.g., Kissling 2023). IPMs combine multiple datasets, including those of different data types, into a single modeling framework, often reducing uncertainty and improving inference (Schaub *et al.* 2007). They are a particularly powerful tool when data are sparse, disparate, and conflicting, as is often the case with many vulnerable species (Zipkin & Saunders 2018). Second, we recommend a monitoring framework that is designed to accumulate evidence iteratively across a sequence of studies (Nichols *et al.* 2019). The foundation of such a framework is an overarching research question and set of hypotheses, for which hypothesis-specific models (e.g., IPMs) are developed and used to make predictions that are then compared with observations as new data become available. We think that combining these two approaches holds great promise for advancing our knowledge about bet-hedging species with complex life histories that are known or suspected to be declining. Only by doing so can we address the conservation conundrum, identify what is limiting their population growth and, if possible, implement conservation actions to stabilize and reverse the decline.

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