



Research Article

Multi-State Mark–Recapture Model to Estimate Survival of a Dispersed-Nesting Seabird, the Kittlitz’s Murrelet

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ABSTRACT The Kittlitz’s murrelet (*Brachyramphus brevirostris*) is a small, dispersed-nesting seabird that often occurs in glacially influenced marine waters of Alaska and eastern Russia during the breeding season. Owing to its association with glacial habitats and apparent population declines in some parts of its range, the Kittlitz’s murrelet has been the subject of considerable conservation concern in recent years. We present the first-ever estimates of breeding season and annual survival of the Kittlitz’s murrelet. We estimated survival by capturing 914 murrelets and radiotagging 191 of them in Icy Bay, Alaska, 2007–2012. We used a multi-state mark–recapture framework to estimate breeding season survival. Daily survival probabilities were similar in the 3 spatial states (Icy Bay, Gulf of Alaska, nest; range = 0.996–0.999), resulting in an overall 60-day breeding season survival probability of 0.89 (SE = 0.04). The only apparent source of fatality of Kittlitz’s murrelets during the breeding season was avian predators, specifically bald eagle (*Haliaeetus leucocephalus*) and peregrine falcon (*Falco peregrinus*). We estimated mean apparent annual survival across all years as 0.80 (SE = 0.33) with a recapture probability of 0.079 (SE = 0.032), resulting in a 305-day non-breeding season survival probability of 0.90 (SE = 0.37). We found that survival was lower than expected based on life-history theory and allometry, and that fatality risk was greater in the breeding season compared to other parts of the year. Our results indicating low survival rates of Kittlitz’s murrelets are consistent with the observed decline of 10% per annum in the local population of this species in Icy Bay. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS Alaska, *Brachyramphus*, demography, Kittlitz’s murrelet, mark–recapture, multi-state, seabird, survival.

The Kittlitz’s murrelet (*Brachyramphus brevirostris*) is a small, dispersed-nesting seabird (family Alcidae) endemic to coastal Alaska and eastern Russia. During the summer breeding season, this species is distributed irregularly in coastal, near shore waters with most individuals concentrating in highly dynamic glacial fjords and bays, and near the outflows of glacial-fed rivers (summarized in U.S. Fish and Wildlife Service [USFWS] 2013). As the end of the breeding season nears, individuals migrate asynchronously along the coast and northward toward the Bering, Chukchi, and Beaufort seas where they presumably molt before following the ice edge southward with the onset of winter (Madison et al. 2012). Owing to issues with tag retention, individuals have not been tracked for more than a few months after tagging during the summer and never beyond late October; regardless, these preliminary data suggest a post-breeding

migration distance of roughly 1,000–3,500 km (Madison et al. 2012; M. L. Kissling, U.S. Fish and Wildlife Service, unpublished data). Although less is known about the distribution of Kittlitz’s murrelets in the winter months, small numbers are observed regularly in open leads of water within the sea ice of the Bering and Chukchi seas (K. J. Kuletz, U.S. Fish and Wildlife Service, unpublished data), as well as in the ice-free waters of south-coastal Alaska (Stenhouse et al. 2008). In early spring, murrelets begin to arrive in breeding areas once again. Thus, areas with glacial ice or sea ice, both attributes that are rapidly changing within this species’ range (Markon et al. 2012), are thought to be the preferred habitats of Kittlitz’s murrelets during most of their annual cycle (Kuletz et al. 2003), although the reason(s) for this association is unclear (USFWS 2013).

The range-wide status of the Kittlitz’s murrelet also has been difficult to assess (Kissling 2011). A few local populations appeared to have declined substantially in the 1980s–1990s (Kuletz et al. 2011a,b; Piatt et al. 2011; but see Kirchhoff et al. 2014) but have since stabilized (USFWS 2013). Although a candidate for listing under the United

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States Endangered Species Act since 2004, the USFWS decided in 2013 that listing this species as threatened or endangered was not warranted (USFWS 2013). The reasons for not listing were generally attributed to the recent stabilization of most populations and the lack of an identified threat or threats affecting Kittlitz's murrelets at the population or species level. Additionally, little information was available on key demographic parameters such as reproduction, survival, and breeding success, and how these parameters may vary with changes to glacial dynamics and ice.

As is true for most seabirds, the population growth rate of the Kittlitz's murrelet should be most sensitive to changes in adult survival (Caswell 2001, Gaston 2004, Mills 2012). Life-history theory suggests that the Kittlitz's murrelet should exhibit high adult survival probabilities (Stearns 1992) because individuals delay maturation, lay a clutch of only 1 egg, and may not breed every year (Day et al. 1999). In addition, both field studies and allometric predictions of the closely related but better studied marbled murrelet (*B. marmoratus*) demonstrate moderate to high annual adult survival (Beissinger 1995, Cam et al. 2003, Peery et al. 2006). Nevertheless, no estimates of adult survival exist for Kittlitz's murrelet. This is partially due to their solitary nesting habits and apparent preference for nesting in remote, inaccessible, mountainous areas (summarized in USFWS 2013). Consequently, methods typically applied to other seabird species, such as re-sighting banded individuals at colonies (e.g., Jones et al. 2007, Morrison et al. 2011), are not feasible for Kittlitz's murrelets.

We present the first-ever estimates of breeding season and annual survival for this species, and identify apparent causes of Kittlitz's murrelet fatality during the breeding season. We conducted our study over a 6-year period

(2007–2012) in Icy Bay, Alaska. We generated breeding season survival estimates within a multi-state mark-recapture framework to account for spatial variation in detection probabilities and movement probabilities among spatial states (Lebreton and Pradel 2002, Devineau et al. 2014). This framework also allowed us to examine the influence of spatial variation on demographic processes, specifically survival and emigration.

STUDY AREA

Our study was centered in Icy Bay, Alaska, USA, located in the northeastern Gulf of Alaska and approximately 110 km northwest of the town of Yakutat (Fig. 1). Icy Bay supports 3% of the global population of Kittlitz's murrelets (USFWS 2013) and is one of the densest populations of this species during the breeding season (Kissling et al. 2011). In addition, the glacially influenced marine and terrestrial habitats of Icy Bay are similar to other core population areas in south-coastal Alaska such as Prince William Sound and Glacier Bay where the majority of the global population occurs during the breeding season (USFWS 2013).

Icy Bay is a highly dynamic glacial fjord system that has experienced multiple, rapid ice advances and subsequent retreats over the past few thousand years (approx. 3,800 years before present) with the most recent retreat of approximately 40 km during the 20th century (Barclay et al. 2006). Currently, Icy Bay comprises 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 4 distinct fjords with each terminating at an active tidewater glacier. The Guyot, Yahtse, and Tsaa Glaciers are considered to be 1 glacial system, and the Tyndall Glacier in Taan Fjord is an independent system

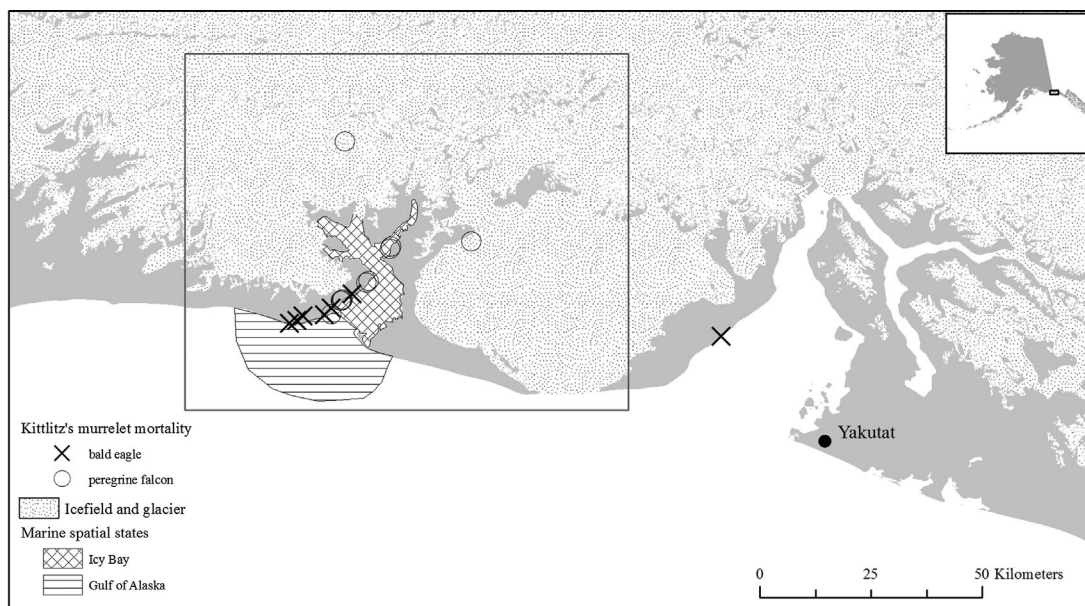


Figure 1. Study area and spatial state boundaries for estimating survival of the Kittlitz's murrelet, Icy Bay, Alaska, 2007–2012. Locations and probable causes of fatalities of radio-tagged murrelets indicated with symbols. The box surrounding the study area describes upland area regularly searched to locate radio-tagged murrelet nests and fatalities.

(Viens 1994). The Malaspina Glacier, the largest piedmont glacier in North America (Molnia 2008), is situated immediately 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 the open water surface area to be approximately 120 km² with substantial variability across seasons and years depending on glacial calving activity.

The uplands adjacent to the inner bay are dominated by the high peaks of the Saint Elias and Robinson Mountains, most of which are 1,000 m–2,000 m in elevation. Within this mountain range, Mount Saint Elias reaches 5,489 m in elevation only 20 km from tidewater, and permanent snow and ice of the 4 tidewater glaciers, the Malaspina Glacier, and other glaciers extend from the Bagley Icefield (approx. 30 km from tidewater).

METHODS

Sampling

We captured Kittlitz's murrelets on the water from 5-m inflatable boats using the night-lighting method (Whitworth et al. 1997) and processed them on a 22-m support vessel in and near Icy Bay during 2 capture sessions each year for 6 years, 2007–2012 (Table 1). The first capture session occurred between 8 May and 3 June (all years; hereafter referred to as the spring session) and generally corresponded to the period when Kittlitz's murrelets arrived in the nearshore waters of Icy Bay prior to nesting (Day 1996). The second capture session took place between 16 July and 5 August (2008–2011 only; hereafter referred to as the summer session) and largely overlapped with a period of active nesting, predominantly when chicks were being fed (Day 1996). Capturing murrelets during the intervening period (early June–mid-July) proved unproductive because there was insufficient darkness surrounding the summer solstice for the night-lighting method to be a viable capture technique. Because we designed our study to be a mark–

recapture study, we hoped to recapture individual murrelets in subsequent capture sessions or years. We attempted to capture murrelets throughout the bay, moving the larger processing vessel nightly depending on weather and ice conditions. Generally, we anchored the processing vessel in or near the center of the bay, which allowed the capture boats to search for murrelets throughout the bay and outside of the mouth provided that we maintained radio contact with the processing vessel. The upper reaches of the bay often were inaccessible or dangerous because of ice floes, especially during the first capture session prior to spring ice breakup.

For each bird captured, we recorded the capture location, time, group size, and number of capture attempts. If, after 3 attempts, an individual could not be netted, we abandoned the effort to minimize disturbance to the bird. If 1 bird of a pair was captured, we attempted to capture the second bird. If a captured bird was banded already, we relayed the band number to the processing vessel using very high frequency (VHF) radios to determine whether or not the bird was banded during a different capture session or year; if so, we considered it to be a recaptured bird and transported it to the processing vessel. If the bird was captured earlier in the same night or session, we recorded capture information as described above and released the bird on site. During our study, we did not recapture a bird that was banded initially in a different study area or by different investigators. For transport, we placed each bird into a mesh bag (Sea to Summit, Inc., Boulder, CO) that we placed into a water-resistant, cardboard pet carrier (PetSmart, Inc., Phoenix, AZ) lined with a towel; if we captured both birds of a pair, we often placed them in the same carrier but in different mesh bags. We then transported the bird(s) to the processing vessel.

We processed each bird individually, generally in the order of arrival at the processing vessel. We weighed each bird, measured natural wing chord and tail length, and attached a unique-numbered band to the right leg. We noted overall plumage characteristics, including body or wing molt, presence of an egg tooth, and any deformities and injuries, and examined the underwing plumage to distinguish second-year birds from after-second-year birds (Pyle 2008). We scored brood patch (BP) development following Sealy (1974;

Table 1. Capture and radiotagging effort for estimating breeding season and annual survival of adult Kittlitz's murrelet (KIMU) in Icy Bay, Alaska, 2007–2012.

Capture session	Year	Capture effort				No. radio-tagged	No. telemetry flights
		No. capture nights	Range of capture dates	No. individual ad KIMU captured	No. KIMU recaptured in different years		
Spring	2007	8	15–22 May	37		30	25
	2008	17	12 May–3 Jun	40	0	32	41
	2009	15	12–7 May	132	5	30	35
	2010	15	10–25 May	181	3	44	35
	2011	18	8–29 May	131	10	31	27
	2012	9	14–29 May	48	7	24	20
	All	82		569	25	191	183
Summer	2008	11	23 Jul–2 Aug	40	0		
	2009	18	18 Jul–3 Aug	70	1		
	2010	19	16 Jul–5 Aug	80	2		
	2011	20	16 Jul–5 Aug	155	6		
	All	68		345	9		

BP 0–6). We drew <2 cc of blood from the ulnar vein of the left wing (typically); we determined sex using DNA from sex chromosomes (Zoogen, Inc., Davis, CA).

We deployed VHF radio transmitters on a subset of after-second-year murrelets captured each year. To the best of our ability, given that we often experienced challenging field conditions (e.g., rough seas), we chose individuals to radio-tag at random provided that they did not have any obvious injuries, deformities, or other physical limitations. Because of the small size of the Kittlitz's murrelet, their dispersed-nesting habits, and battery-life limitations of radio transmitters, we were unable to track individual murrelets beyond a single breeding season. We attached the transmitters (Advanced Telemetry Systems, Inc., Isanti, MN [ATS]; model number A4360, <3.2 g in weight, approx. 1.5% of bird's mass) using a subcutaneous anchor on the bird's back between the scapulars (Newman et al. 1999). During the course of our study, the attachment procedure evolved to minimize perceived pain to the bird while maximizing transmitter retention. In 2007 and 2008, following Loughheed et al. (2002); we did not use a local anesthetic at the attachment site and we glued the posterior part of the transmitter to the back feathers of the bird with a cyanoacrylate adhesive (VetBond™ Tissue Adhesive, 3M™, St. Paul, MN). In 2009–2012, we infused 2 mg/kg of a local anesthetic (1% solution of Lidocaine) under the skin on the back of the neck where the transmitter was to be attached and we secured the posterior part of the transmitter to the bird with 1 3–0 monofilament, non-absorbable suture (Ethicon™, Cincinnati, OH) following Newman et al. (1999). In 2010 as part of a related study to compare transmitter attachment techniques, we affixed transmitters to 14 Kittlitz's murrelets with 3 sutures only (i.e., no subcutaneous anchor); we did not find any difference in transmitter retention or bird behavior compared to those birds equipped with transmitters with subcutaneous anchors (M. L. Kissling, unpublished data); therefore, we included these 14 individuals in our assessment of survival. Following processing, we released birds immediately from the processing vessel. If we captured both birds of a pair, we selected 1 bird to radio tag to ensure independence and to minimize disturbance to nesting pairs, and we released the pair together.

Across all years, we averaged 14 minutes (SD = 8) to transport birds to the processing vessel, 33 minutes (SD = 47) on the vessel but prior to processing, and 13 minutes (SD = 10) to process birds. Therefore, overall we retained birds for approximately 1 hour (mean = 61 min; SD = 48). All capture and handling procedures were reviewed and approved by the Alaska Department of Fish and Game (2007–2009) and USFWS (2010–2012) Institutional Animal Care and Use Committee.

Following capture, we attempted to locate radio-tagged murrelets 2–5 times per week for at least 8 weeks using fixed-wing aircraft equipped with H-style antennas mounted on the struts. Generally, we began flying to locate radio-tagged murrelets immediately following capture. We first attempted to locate all radio-tagged murrelets on the water in or near Icy Bay. Depending on weather conditions, we began searching for signals by flying at 457 m (1,500 ft) above ground level (AGL); at this altitude we could detect a signal

approximately 10 km away based on test transmitter trials (provided there were no mountainous barriers). We generally flew the mouth of the bay first extending as far offshore as the pilot deemed safe before flying into the upper reaches of the fjords. We then increased altitude to 914 m (3,000 ft) AGL, where we were able to detect a signal up to 30 km away, which included most of the marine portion of the study area (Fig. 1). If we did not detect birds at sea, we flew over all assumed potential nesting habitat within reason (e.g., fuel constraints) to locate incubating birds. In southeastern Alaska, Kittlitz's murrelets are known to nest up to 54 km from ocean and up to 2,555 m (8,383 ft) in elevation in mountainous areas often above or near hanging glaciers on the walls of glacial valleys and cirques (M. L. Kissling, unpublished data). Access to these areas was weather dependent and therefore, we were not able to follow a standard flight pattern but instead aimed to cover as much ground as possible by adjusting AGL, following cloud-, fog-, and wind-free valleys, and searching areas as systematically as possible given safety and logistical constraints. By locating radio-tagged murrelets on the water first, we reduced the number of frequencies that needed to be scanned while searching terrestrial habitat for murrelets on a nest. During each flight, our goal was to locate all radio-tagged murrelets in our study area.

For each bird located during an aerial survey, we recorded a global positioning system (GPS) location, time of location, and, for birds on the water only, whether or not the bird was diving as determined by the regularly varying occlusion of the radio signal. We attempted to access by foot all locations where we found signals on land to determine whether or not the bird was incubating or dead, or the transmitter became detached from the bird. For fatalities, we collected the carcass, feathers, and transmitter, and noted the apparent cause of death based on proximity to raptor eyrie or nest and condition of murrelet remains. Given the mountainous terrain, remote location, and often-inclement weather of our study site, we were not able to locate radio-tagged murrelets daily, as has been done with other murrelet telemetry studies (e.g., Bradley et al. 2004, Peery et al. 2004). Because we radio-tagged only 1 bird of a pair and both parents share incubation duties by switching usually every 24–48 hours (Lawonn 2012), we adjusted flight schedules and routes to prioritize radio-tagged birds during specific flights to maximize our ability to locate nesting birds.

Data Analysis

We estimated breeding season survival from radio-tagged murrelets using a multi-state mark-recapture approach (Lebreton and Pradel 2002, Devineau et al. 2014). The multi-state framework allowed us to estimate different detection probabilities for each spatial state, ensuring accurate state-specific survival probabilities, along with movement (or transition) rates among states. Using this approach, we assumed a geographically closed population, but compared to more traditional mark-recapture analyses, this assumption was relaxed because we could allow for movement within a large spatial area. We identified 5 states: 3 spatial states (Icy Bay,

Gulf of Alaska, nest), 1 state for known fatalities, and 1 unobservable state. We assigned each individual radio-tagged murrelet to 1 of these 5 states at the conclusion of every aerial telemetry flight. We defined the boundaries of 2 marine spatial states, Icy Bay and Gulf of Alaska, using our at-sea survey area of inference (Kissling et al. 2007) and the extent offshore (approx. 20 km) that we were able to fly safely and regularly, which was also approximate to the extent of the northern Gulf of Alaska shelf (Piatt and Springer 2007). The nest state simply included the surrounding uplands of Icy Bay and we used it only for murrelets located at a nest. More than 98% of all aerial detections fell within 1 of these 3 spatial states (Icy Bay, Gulf of Alaska, nest). The state reserved for known fatalities included only murrelets that we confirmed to be dead. The unobservable state (hereafter referred to unknown state) included murrelets that we were no longer able to track because of radio-tag failure, permanent emigration, or fatality with transmitter loss and therefore was an absorbing state.

We limited estimates of breeding season survival of an individual murrelet to 60 days after tagging to reduce the likelihood of battery failure during the analytical timeframe while still encompassing the expected breeding period (15 May–14 July; Day 1996). We calculated 60-day survival as the product of 60 daily survival probabilities averaged over each spatial state weighted by the probability of being in each state each day. We considered 5 models of breeding season survival and detection probability (Table 2). We expected most of the variation in state transition and detection probability to be explained by murrelet nesting behavior. In our study area, Kittlitz's murrelets often nest on the ground, or on ledges of glacial cirques or mountains in remote, inaccessible areas (M. L. Kissling, unpublished data). Both male and female parents take turns incubating the egg at the nest every 24–72 hours for roughly 30 days total; immediately following hatching, 1 parent broods the chick for another 24–48 hours, but thereafter, parents visit the chick only to deliver food (1–12 times per day for both adults) for 21–40 days until fledging (Kaler et al. 2009, Lawonn 2012, USFWS 2013). For these reasons, locating nests of Kittlitz's murrelets in a glacial landscape can be challenging especially given logistical and weather constraints. Therefore, in our set of candidate models, we included a variable that described whether or not a murrelet was nesting (nest) to account for a change in behavior from nest initiation to fledging, and another variable that indicated whether or not a murrelet was incubating (incubation) to account for a change in behavior during incubation only. We modeled these variables as

individual covariates observed by tracking radio-tagged murrelets to nests. All models allowed daily survival probability to vary across the 3 spatial states because we modeled survival as a state transition in the multi-state model and all transition probabilities for a given state must sum to 1. Modeling survival across states would have placed a formidable constraint on the entire model structure.

In addition to breeding season survival, we also estimated apparent annual survival by fitting a Cormack–Jolly–Seber model to the data from annual captures and recaptures of banded birds (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992). We considered 3 candidate models with apparent survival constant, varying by sex, and varying across years. We used a constant recapture probability except for 2007 when recapture probability was fixed to 0. We lacked a sufficient number of recaptures to fit more complicated models (Table 1). We defined the annual period as 1 July–30 June of the following year and, as required by Cormack–Jolly–Seber models, assumed a geographically closed population across years. Our analysis was limited to murrelets captured and banded for the first time between 2007 and 2011 because those initially banded in 2012 contributed no information toward annual survival.

We fit both the multi-state mark–recapture and Cormack–Jolly–Seber models in Program MARK (White and Burnham 1999) and selected the best model based on Akaike's Information Criterion with a small sample correction (AIC_c; Burnham and Anderson 2002).

We calculated non-breeding season survival by dividing mean apparent annual survival by the estimates of 60-day breeding season survival. Because survival is a multiplicative process, we used the following equation: $p(\text{mean annual survival}) = p(\text{breeding season survival}) \times p(\text{non-breeding season survival})$. Therefore, the non-breeding season survival probability refers to the 305-day period outside of the 60-day breeding season survival period.

RESULTS

We captured and banded 914 individual adult Kittlitz's murrelets and radio-tagged 191 of them during 150 capture nights, 2007–2012. We recaptured 73 banded Kittlitz's murrelets, but most murrelets were recaptured within the same session of their capture ($n = 38$); only 1 murrelet was initially banded in the spring and recaptured in the summer session of the same year. We recaptured 34 murrelets at least 1 spring after the bird's initial capture with the majority recaptured in the subsequent year ($n = 26$), but we did

Table 2. Candidate models and model selection results for a multi-state mark–recapture analysis of radio-tagged Kittlitz's murrelets, Icy Bay, Alaska, 2007–2012. Model names are denoted by state transition parameters (Ψ) and detection probability (p). We present Akaike's Information Criterion with a small sample correction (AIC_c), model weight (w_i), and the number of parameters (K) for each model.

Model	AIC _c	Δ AIC _c	w_i	K
Ψ (state, nest) p (state, nest)	6,638.2	0.0	1.00	18
Ψ (state, nest) p (state)	6,671.0	32.8	0.00	17
Ψ (state, incubation) p (state)	6,742.9	104.7	0.00	17
Ψ (state, incubation) p (state, incubation)	6,744.2	106.0	0.00	18
Ψ (state) p (state)	6,754.1	115.9	0.00	15

recapture a few murrelets 2 years later ($n=5$), 3 years later ($n=2$), and 4 years after initial capture ($n=1$).

Across the 6-year period, we completed 183 aerial telemetry flights, resulting in 3,320 locations of radio-tagged murrelets (mean = 17.4 locations per bird) and 34 apparent nests. Between 15 May and 14 July, the approximate 60-day breeding season period for murrelets in our study area, we located 81% (SD = 13%, range = 46–100%) of the radio-tagged murrelets available for location during telemetry flights ($n=142$).

We observed or inferred 19 of 191 radio-tagged Kittlitz's murrelets to have died within 60 days of initial capture (range = 2–4 fatalities annually). The median number of days between capture and inferred fatality was 27 days (range = 4–60). We recovered 16 carcasses and transmitters to confirm fate; the remaining 3 were inaccessible because of unsafe terrain. We located 10 fatalities at or near occupied peregrine falcon (*Falco peregrinus*) eyries or commonly used plucking posts and 6 in or near occupied bald eagle (*Haliaeetus leucocephalus*) nests (Fig. 1). Two fatalities were located in the glaciated uplands in suitable Kittlitz's murrelet nesting habitat; we attributed these fatalities to peregrine falcon predation because of their proximity to occupied eyries and movements of peregrine falcons recorded by satellite transmitters as part of a complimentary study (S. B. Lewis, U.S. Fish and Wildlife Service, unpublished data). One fatality was located approximately 80 km to the east of our study area on the northern shores of Yakutat Bay; we speculate that this murrelet was killed by a bald eagle. We attributed 12 Kittlitz's murrelet fatalities to peregrine falcons and 7 to bald eagles.

The best model in the multi-state mark–recapture analysis included covariates state and nest to estimate both state transition parameters and detection probabilities of Kittlitz's

murrelets during the breeding season (Table 2). The null model and models that included incubation as a covariate had a difference of at least 100 AIC_c units compared to the best model, suggesting that the covariate nest explained much of the variation in transition rates among states and detection probabilities.

Daily survival probabilities were similar in the 3 spatial states (Icy Bay, Gulf of Alaska, nest; range = 0.996–0.999; Table 3), resulting in an overall 60-day breeding season survival probability of 0.89 (SE = 0.04). As expected, detection probabilities varied considerably among the 3 spatial states (Table 3). The probability of detecting a murrelet in either marine spatial state was high (Icy Bay: 0.999, Gulf of Alaska: 0.972), but the probability of detection at a nest for the first time was low (0.296) increasing to moderate for subsequent detections at the nest (0.700).

The daily probability of a Kittlitz's murrelet transitioning among states was low (i.e., most murrelets remained in the same state as found the previous day). Not surprisingly, non-nesting murrelets were more likely to remain in a state (range of probability = 0.677–0.808) compared to nesting murrelets (range = 0.571–0.668). Of the murrelets that transitioned among states, the majority moved into Icy Bay either from the Gulf of Alaska (0.279) or from a nest (0.249; Table 3). The daily probability of a murrelet initiating a nest (i.e., moving to a nest for the first time) was 0.058 from both marine states. Few murrelets moved to the unknown state from Icy Bay (0.008) or Gulf of Alaska (0.016) and none moved from a nest to the unknown state.

The best model for estimation of apparent annual survival of Kittlitz's murrelets allowed survival to vary across years; the next best model assumed constant apparent survival

Table 3. Parameter estimates and associated variance from a multi-state mark–recapture model of Kittlitz's murrelet breeding season daily survival, movement (transition), and detection probabilities (p), Icy Bay, Alaska, 2007–2012.

Initial state	Transition state	Estimate	SE	95% CI	
				Lower	Upper
Icy Bay	Icy Bay (nester)	0.668	0.034	0.601	0.735
	Icy Bay (non-nester)	0.808	0.009	0.790	0.826
	Gulf of Alaska	0.153	0.009	0.137	0.171
	Nest, after 1st detection	0.169	0.033	0.113	0.244
	Nest, up to 1st detection	0.029	0.006	0.020	0.043
	Survival (1-mortality)	0.998	0.001	0.996	0.999
	Unknown	0.008	0.002	0.006	0.013
	p	0.999	0.006	0.014	1.000
Gulf of Alaska	Gulf of Alaska (nester)	0.571	0.039	0.495	0.647
	Gulf of Alaska (non-nester)	0.677	0.018	0.642	0.712
	Icy Bay	0.279	0.015	0.250	0.309
	Nest, after 1st detection	0.135	0.035	0.080	0.219
	Nest, up to 1st detection	0.029	0.008	0.016	0.050
	Survival (1-mortality)	0.999	0.001	0.994	1.000
	Unknown	0.014	0.003	0.009	0.022
	p	0.972	0.011	0.939	0.987
Nest	Nest (no transition)	0.602	0.047	0.510	0.694
	Icy Bay	0.249	0.035	0.187	0.323
	Gulf of Alaska	0.145	0.026	0.102	0.203
	Survival (1-mortality)	0.996	0.003	0.985	0.999
	Unknown	0.000	0.000	0.000	0.000
	p , up to 1st detection	0.296	0.037	0.228	0.373
	p , after 1st detection	0.700	0.057	0.578	0.799

($\Delta AIC_c = 6.4$) followed by the model that included sex as a covariate ($\Delta AIC_c = 8.2$). We estimated mean apparent annual survival across all years as 0.80 (SE = 0.33) with the Cormack–Jolly–Seber model to account for differences in sample sizes among years and for sampling covariance among year-specific estimates. We estimated recapture probability as 0.079 (SE = 0.032). The overall 305-day non-breeding season survival probability was 0.90 (SE = 0.37), which translates to a daily survival probability of 0.999.

DISCUSSION

We found that both breeding season and annual apparent survival of Kittlitz's murrelets in Icy Bay were low, especially during the breeding season. The 60-day breeding season survival of radio-tagged murrelets ($\hat{S} = 0.89$) was not much greater than the estimated, but highly imprecise, annual apparent survival of 0.80 based on recaptures of banded murrelets. In fact, the daily mortality probability of Kittlitz's murrelets during the breeding season (0.002) was higher than that outside of the breeding season (0.001), suggesting that individuals experience higher fatality risk in the near shore waters of Icy Bay compared to the offshore overwintering areas such as the Bering and Chukchi seas.

Although lower than those predicted by life-history theory and allometry, we feel confident in our breeding season survival estimates for several reasons. First, we relocated radio-tagged murrelets regularly throughout the summer resulting in high detection probabilities (>0.97; Table 3). Thus, we rarely failed to detect a murrelet present in the study area, and lost few murrelets to the unknown state, which can also be viewed as an apparent emigration rate. Moreover, the estimate of known mortality probability (presented in Table 3 as survival probability) was biased slightly low, if biased at all, compared to true mortality because some of the murrelets permanently in the unknown state may have died. Although radio failure possibly occurred, we believe this happened infrequently, if at all. We know from a few opportunistic relocations using aerial telemetry that at least some of the murrelets in the unknown state were equipped with functioning radios and were alive outside of our study area (e.g., Yakutat Bay, approx. 80 km to the east), but we did not survey those areas regularly because of logistical and funding constraints. Thus, we consider our estimate of breeding season survival to be a maximum estimate that may be biased slightly high because of fatalities in the unknown state.

The only source of breeding season fatality of Kittlitz's murrelets observed in our study area was apparent predation by peregrine falcons (63%) and, to a lesser extent, bald eagles (37%). Peregrine falcons and bald eagles have different food habits and foraging strategies. Generally, both species hunt the terrestrial and marine habitats close to shore then bring captured prey to plucking posts or nests before consuming them. However, peregrine falcons mostly prey on birds and take only live prey (White et al. 2002), whereas bald eagles have a more varied diet, preying on live birds and fish, as well as carrion (Buehler 2000). Thus, we believe that fatalities attributed to peregrine falcons likely were a result of active

predation on murrelets. In fact, we witnessed delivery of a live murrelet by a falcon to its eyrie. Although bald eagles are capable of capturing live murrelets, we cannot rule out that bald eagles scavenged carcasses of murrelets that died because of other cause(s). An alternative explanation of the apparent bald eagle predation on Kittlitz's murrelets is kleptoparasitism from peregrine falcons. On 2 occasions during our study, we observed a peregrine falcon to capture live prey, then drop it when a bald eagle gave chase, at which point the bald eagle recovered it. Other researchers have reported this behavior by bald eagles (Watson 2002, Dekker et al. 2012) and acknowledged it as having a potential effect on seabird populations (see Hipfner et al. 2012 for overview). Regardless, it remains to be tested whether the low survival probability was a function of avian predators themselves or another factor placing murrelets at elevated risk of predation. We also note that 2 of the 19 fatalities documented during our study occurred inland (Fig. 1), probably while the murrelet was transiting to or from a nest, indicating that risk of predation on adult Kittlitz's murrelets was not limited to the water.

As with all field studies that involve capture, handling, and marking of wild animals, we assumed that banding and radio-tagging Kittlitz's murrelets did not bias our results. Peery et al. (2006) found that radio-tagged marbled murrelets had a lower probability of surviving the year after they were marked compared to murrelets that were banded only, suggesting a radio-tagging effect (see also Barron et al. 2010 for overview). We did not have a sufficient number of recaptures to conduct the same analysis, but we have several other lines of evidence to suggest that radio-tagging did not bias our estimates of breeding season or annual apparent survival. First, we tested for potential acute effects of radio-tagging on survival of Kittlitz's murrelets by comparing differences in survival for the first 5 days and the remaining 55 days following capture and tagging. The best model did not contain an effect on survival (Appendix A); moreover, the estimated logit-scale effect size for a 5-day effect was positive (0.24, SE = 0.41) with a 95% confidence interval that incorporated 0. Second, our estimates of breeding season survival included only a 60-day period after tagging; thus, radio-tagged murrelets in our study were not subject to potential longer-term chronic effects that have been reported in tagging of other avian species (e.g., Steenhof et al. 2006, Saraux et al. 2011). Third, as part of a complimentary study on raptor diet in our study area, we found the proportion of Kittlitz's murrelets that had radio-tags and were delivered to raptor nests (15.3%; S. B. Lewis, unpublished data) was nearly equal to the proportion of the estimated number of Kittlitz's murrelets in Icy Bay that were radio-tagged (16.0%), suggesting that all murrelets were at risk of depredation, not just those fitted with radio-tags. Finally, we captured radio-tagged murrelets in years following tagging, indicating that radio-tagged Kittlitz's murrelets were capable of surviving across years and, in some cases, breeding in subsequent years. Thus, although we recognize the potential impacts and risks to capture and radio-tagging murrelets, we did not find evidence to indicate

a measurable effect (using our methods) or that any such effect biased our estimates of survival.

In contrast to our breeding season survival estimates based on radio telemetry, our estimate of annual apparent survival based on recaptures of banded individuals likely was biased low relative to true annual survival probability. Apparent survival probabilities confound permanent emigration and mortality into a single parameter. Given our observations of radio-tagged murrelets moving to other bays within a season, it seems logical that murrelets move to other bays or areas across years as well, as evidenced by the lack of genetic structure in Kittlitz's murrelets in the Gulf of Alaska (Friesen and Birt 2012), thereby violating the assumption of a geographically closed population. If banded murrelets permanently did not return to Icy Bay across the years of our study, which was likely considering the low recapture probability (0.079), then those murrelets contributed to reducing the annual apparent survival estimate. If banded murrelets temporarily emigrated to other areas and returned in future years of the study, that would only reduce our estimated recapture probability. We expected to recapture more banded murrelets because on any given year, we captured 4–26% of the estimated annual population size using Icy Bay, and cumulatively across all years, we banded 65% of the mean population size (approx. 1,400 Kittlitz's murrelets; M. L. Kissling, unpublished data). Thus, we concluded that annual fidelity to Icy Bay was low. Taken together, our over-estimated breeding season survival and under-estimated annual survival suggest that the vast majority of Kittlitz's murrelet fatality was occurring during the breeding season.

Our estimates of survival of Kittlitz's murrelet are somewhat comparable, albeit on the lower end, to those of the congeneric marbled murrelet and other small alcids in the northern Pacific Ocean. The predicted annual survival probability for marbled murrelets from allometric and comparative methods was 0.835–0.845 (Beissinger 1995, Beissinger and Peery 2007). These predictions were confirmed with field studies in California ($\hat{S}' = 0.868$ – 0.896 ; Peery et al. 2006) and British Columbia ($\hat{S}' = 0.829$ – 0.929 ; Cam et al. 2003) using similar mark–recapture methods as used in our study. For further comparison, at Triangle Island off the coast of British Columbia, apparent annual survival of rhinoceros auklets (*Cerorhinca monocerata*) was similar ($\hat{S}' = 0.86$), whereas that of tufted puffins (*Fratercula cirrhata*) was markedly higher ($\hat{S}' = 0.91$ – 0.96); in contrast, annual survival of Cassin's auklets (*Ptychoramphus aleuticus*) was lower ($\hat{S}' = 0.75$ – 0.84), especially in years with extreme climate events ($\hat{S}' = 0.44$ for females; Morrison et al. 2011). Further, researchers reported mean survival rates of least auklets (*Aethia pusilla*) as roughly 0.75 on Saint Paul Island (Jones 1992) and of whiskered auklets (*A. pygmaea*) as 0.708–0.835 on Buldir Island, Alaska, (Jones et al. 2007). Although these are just examples, it does demonstrate that even though Kittlitz's murrelet adult survival appears to be low, it is not necessarily unprecedentedly so. In fact, larger seabirds tend to have higher survival rates than smaller ones (Gaston 2004) and for offshore feeders to exhibit higher survival rates than inshore feeders (Lack 1968); both of

which suggest that it is not wildly unusual that the Kittlitz's murrelet, a small seabird that feeds near shore, would experience comparatively low survival rates.

Survival of seabirds has been correlated most often with bottom-up processes such as climate or environmental variability that is assumed or known to affect prey availability (e.g., Bertram et al. 2005, Peery et al. 2006, Jones et al. 2007, Kitasky et al. 2010, Morrison et al. 2011, Sandvik et al. 2012). However, several recent studies have found that the mechanistic drivers of seabird survival probably are more complex, involving a combination of bottom-up and top-down (e.g., predation) processes and individual traits (e.g., body mass; Harding et al. 2011, Horswill et al. 2014). We were not able to estimate survival annually with reliability and precision for 2 reasons: 1) We were not able to track individuals with radio-telemetry beyond 1 breeding season because of battery life limitations of transmitters, and 2) we had a low mean recapture probability of banded birds. Consequently, we could not explore possible correlations between annual survival rates of Kittlitz's murrelets and environmental conditions to understand better factors that may be influencing survival, as has been done for many colonial-nesting seabird species that can be resighted or recaptured at the colony. However, we can infer from our results that top-down processes appear to be affecting the population of Kittlitz's murrelets that we studied, probably more so than bottom-up processes given that fatality risk of individual murrelets was greater during the breeding season compared to other times of the year.

Although underlying, but unknown factors may have contributed to murrelet fatality during the breeding period, the ultimate cause was predation by peregrine falcons and bald eagles. Both of these species appear to have increased significantly in our study area since the early 1990s (Kozie 1993; S. B. Lewis, unpublished data) and both have been implicated in the declines of other bird species (Ydenberg et al. 2004, Anthony et al. 2008, Hipfner et al. 2012). Likewise, we estimated a population decline in Kittlitz's murrelets of 10% per annum between 2002 and 2012 in Icy Bay (M. L. Kissling, unpublished data). We recognize that this decline could be attributed to annual differences in emigration, but at this time, it is not reasonable to estimate movements of individual murrelets at a broader scale or at multiple study areas simultaneously. Until tracking individuals within and across seasons and study areas is possible, we emphasize the need to understand proximate demographic causes of suspected declines for this species; annual abundance estimates provide little insight into mechanistic drivers of population change, and thus certainty in population declines necessitate complimentary demographic data (e.g., Matthiopoulos et al. 2014).

MANAGEMENT IMPLICATIONS

Our estimates of breeding season and apparent annual survival are valuable for management and conservation of Kittlitz's murrelet in Icy Bay and across its range for several reasons. First, our estimates are consistent with the observed decline of 10% per annum between 2002 and 2012 in the Icy Bay

population (M. L. Kissling, unpublished data), validating the current survey design and protocol used to monitor this population (Kissling et al. 2007). Second, the comparatively low breeding season survival suggests managers should consider adult survival explicitly in future management actions, especially those implemented during the summer months, rather than rely on the assumption that the species' life history suggests high survival. Several potential sources of murrelet fatality such as gill net entanglement or oil spills may further reduce breeding season survival in other core population areas if risk of these events is not minimized. Third, our survival estimates can be used to assess population dynamics of Kittlitz's murrelets by developing population projection models, including those that provide estimates of extinction probabilities, to help inform management and legal decisions under the United States Endangered Species Act. Ultimately, our results provide a better basis from which to evaluate the current and future status of the Kittlitz's murrelet and to identify bottlenecks that may be limiting population growth.

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APPENDIX A. TESTING FOR POTENTIAL ACUTE EFFECTS OF RADIO-TRANSMITTER ATTACHMENT ON APPARENT SURVIVAL OF KITTLITZ'S MURRELETS

Candidate models and model selection results for Cormack–Jolly–Seber models of Kittlitz’s murrelet mark–recapture data to evaluate the potential acute effects of radio-transmitter attachment on apparent survival (Ψ), Icy Bay, Alaska, 2007–2012. We tested for differences in survival for the first 5 days after radio-tagging versus survival for the remaining 55 days after radio-tagging. We considered models with 1-, 3-, and 5-day effects as well as an acute effect

Model	AIC_c	ΔAIC_c	w_i	K
Ψ (no effect) p (.)	2,153.29	0.00	0.36	2
Ψ (1-day effect) p (.)	2,154.26	0.97	0.22	3
Ψ (5-day effect) p (.)	2,154.93	1.64	0.16	3
Ψ (3-day effect) p (.)	2,155.28	1.99	0.13	3
Ψ (5-day linear effect) p (.)	2,155.29	2.00	0.13	3

with logit-linear decline in magnitude over 5 days. We assumed constant detection probability (p) in all models evaluated. We present Akaike’s Information Criterion with a small sample correction (AIC_c), model weight (w_i), and the number of parameters (K) for each model.