

# BREEDING DECISIONS OF KITTLITZ'S MURRELETS *BRACHYRAMPHUS BREVIROSTRIS*, ICY BAY, ALASKA

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## SUMMARY

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The Kittlitz's Murrelet *Brachyramphus brevirostris* is an uncommon, dispersed-nesting seabird endemic to coastal waters of Alaska and eastern Russia. While the range-wide status of this species is unclear, proximate concerns regarding its viability are driven by low breeding propensity and nesting success. We studied individual and environmental factors associated with the decision to breed and timing of nest initiation of Kittlitz's Murrelets in Icy Bay, Alaska, over a 6-year period between 2007 and 2012. We radio-tagged 191 of 569 individuals captured during the spring pre-breeding period. At the time of capture, nearly all murrelets were exhibiting signs of breeding; most were in alternate plumage, paired, in apparently good body condition, and developing a brood patch. Yet an average of only 20% (range 5%–45%) of the radio-tagged murrelets nested annually. More individuals chose to breed during years with an intense Aleutian low-pressure system (i.e. low North Pacific Index) and low average wind speeds in the spring, with such conditions apparently leading to an earlier and stronger phytoplankton bloom. Our results also indicated a weak, positive association between the peak magnitude of chlorophyll-*a* and delayed nest initiation. While we infer that the decision to breed and timing of nest initiation are related in part to factors that reflect spring bloom dynamics, we encourage more directed studies on the relationship between environmental conditions during the spring pre-breeding period and the chronically low reproductive output exhibited by this species.

**Key words:** Alaska, *Brachyramphus*, breeding decision, pre-breeding, murrelet, nest initiation

## INTRODUCTION

Most long-lived seabirds inhabiting high latitudes breed on an annual cycle (Hamer *et al.* 2002) and follow the same general pattern: after spending the winter in distant, often offshore wintering areas, individuals begin to convene in nearshore breeding areas with the onset of spring. At that time, reproductively mature individuals must decide whether to breed and, if so, when to initiate breeding. These two fundamental decisions are influenced by intrinsic factors, such as body condition, breeding experience, individual quality and breeding history (Chastel *et al.* 1995, Cam *et al.* 1998, Bradley *et al.* 2000, Le Bohec *et al.* 2007, Giudici *et al.* 2010); extrinsic factors, such as breeding site conditions and food availability (Peery *et al.* 2004, Janssen *et al.* 2009, Shultz *et al.* 2009); or a combination of both (Sydeman *et al.* 1991, Oro *et al.* 2010, Cubaynes *et al.* 2011). Identifying which factors influence these decisions is key to understanding annual breeding effort in seabirds and thus fundamental to facilitating more effective conservation and management actions, especially for species thought to be undergoing or vulnerable to population declines.

The Kittlitz's Murrelet *Brachyramphus brevirostris* (KIMU) is a small seabird endemic to coastal Alaska and eastern Russia. During the summer breeding period between May and September, KIMUs are found in nearshore marine waters, especially those with glacial influence such as glacial fjords, or near the outflows of glacial

streams and rivers. Unlike most seabirds, the KIMU does not nest in colonies but instead is a dispersed and secretive nester that lays only one egg on cliff ledges or on the ground. Breeding is assumed to be energetically costly (Hatch 2011) because nests can be located far inland (up to 74 km; Day *et al.* 1999) and at high elevations (up to 2500 m; Kissling, unpubl. data), requiring long commutes for parents foraging in the ocean. Nesting adults feeding a single chick typically make several trips to the nest each day for 3–4 weeks before the chick fledges (Kaler *et al.* 2009, Lawonn 2012). At the end of the breeding period, KIMUs migrate to the Bering and Chukchi seas, where at least some overwinter in offshore waters presumably before returning to nearshore waters close to breeding areas in the spring. Most aspects of winter ecology and movements of the KIMU remain unknown.

During the 1990s, at-sea surveys during the summer breeding period demonstrated precipitous declines of KIMU in some parts of the species' range (Kuletz *et al.* 2011a,b; Piatt *et al.* 2011), although the magnitude and certainty of the declines have been debated (Day 2011, Hodges & Kirchhoff 2012, Kuletz *et al.* 2013, Kirchhoff *et al.* 2014). Nonetheless, since 2000, most populations seem to have stabilized (US Fish and Wildlife Service [USFWS] 2013), yet studies of breeding success and productivity indicate that reproduction during the same time period was poor. For example, ground-based searches to locate and monitor nests on Kodiak, Agattu and Adak islands, Alaska,

between 2006 and 2012, demonstrated overall nesting success to be ~16%–50% (Kaler *et al.* 2009, Lawonn 2012; summarized in USFWS 2013). Likewise, using radio telemetry, Kissling *et al.* (2015) found similar results for nests located in glaciated areas of Icy Bay in southeastern Alaska between 2007 and 2012; for nests that were initiated, only 45% were inferred to have fledged a chick successfully.

To a certain extent, low nesting success does not necessarily lead to declining populations if a sufficient number of individuals attempt to breed each year to maintain the population. Yet it appears that breeding propensity of KIMUs also is low. The only direct measure of breeding propensity for this species was estimated in Icy Bay, where only 20% of radio-tagged KIMUs initiated nesting (Kissling *et al.* 2015). Although it was assumed that KIMUs, like other seabirds, probably did not breed every year (Day *et al.* 1999), these data demonstrating markedly low rates of breeding propensity in Icy Bay, coupled with reports of low nesting success at multiple sites across the species range, emphasized concern about the trajectory of the range-wide population.

Here, we sought insight into factors that may influence breeding decisions of KIMUs, including potential reasons that so few radio-tagged murrelets attempted to nest in a given year during our 6-year study (2007–2012) in Icy Bay (see Kissling *et al.* 2015). Specifically, in our retrospective analysis, we hypothesized that (1) breeding of radio-tagged murrelets was associated positively with individual body condition and ocean productivity in the pre-breeding period (March–May); and (2) timing of nest initiation corresponded with peaks in ocean productivity and first availability of nest sites during the pre-breeding period. To the best of our ability, our analysis also tested for possible effects of capture and handling on the decision to breed.

## METHODS

### Study area

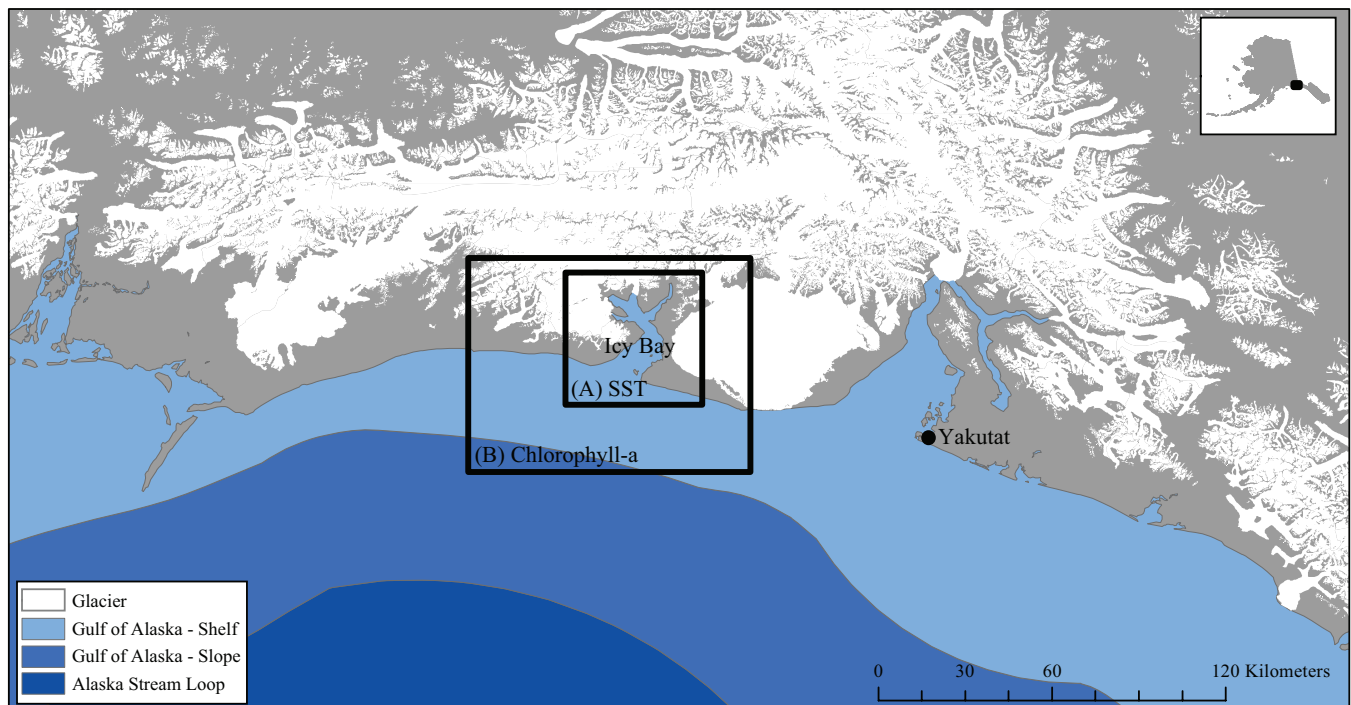
We conducted field work in Icy Bay, Alaska, located in the northeastern Gulf of Alaska, ~110 km northwest of Yakutat (Fig. 1). Icy Bay is a highly dynamic glacial fjord system that has experienced multiple rapid ice advances and subsequent retreats over the past few thousand years (~3 800 years before present), with the most recent being over 40 km of tidewater glacier retreat during the 20th century (Barclay *et al.* 2006).

Currently, Icy Bay is composed of 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 with each terminating at an active tidewater glacier. The Guyot, Yahtse and Tsaa glaciers are considered one glacial system, while the Tyndall Glacier in Taan Fjord is an independent system (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 ~263 km<sup>2</sup>, 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 ~120 km<sup>2</sup> with substantial variability across seasons and years, depending on calving activity.

### Field methods

#### *Capture, radio-tagging and radio-tracking*

We captured KIMUs on the water in and near Icy Bay using the night-lighting method (Whitworth *et al.* 1997) between 8 May



**Fig. 1.** Location of Icy Bay in the northern Gulf of Alaska. Boxes show extent of marine area used to estimate (A) sea surface temperature (SST) and (B) chlorophyll-*a* as variables to explain breeding decisions of the Kittlitz's Murrelet captured and radio-tagged in Icy Bay, 2007–2012.

and 3 June 2007–2012. For each bird captured, we recorded the capture location, time, group size and number of capture attempts. After three attempts, we abandoned the effort in order to minimize disturbance to the bird. If one bird of a pair was captured, we attempted to capture the second bird. We placed each captured bird into a mesh bag (Sea to Summit, Inc., Boulder, Colorado), which was placed into a water-resistant pet carrier (PetSmart Carriers, Inc.) lined with a towel; if both birds of a pair were captured, they often were placed in the same carrier, but in different mesh bags. The bird(s) was then transported to a larger vessel for processing.

We processed each bird individually, generally in the order of arrival at the processing vessel. We weighed each bird, measured wing chord (unflattened) and tail length and attached a uniquely numbered leg band. We noted overall plumage characteristics, including body or wing molt, and any deformities and injuries, and examined the underwing plumage to distinguish second-year birds from after-second-year birds (Pyle 2008). We categorized plumage of each murrelet as basic, alternate or transitional (during the pre-alternate molt; Day *et al.* 1999, Pyle 2008). We scored brood patch development (BP) following Sealy (1974; BP 0–6) with BP 0 indicating no development during the pre-breeding period, BP 3 full development, and BP 6 no development during the post-breeding period.

In all years of our study, we collected blood samples from each captured KIMU for sex identification, determination of hematocrit values and other related studies not reported here (e.g. Hatch 2011, Schaefer 2014). After preparing the injection site with an isopropyl alcohol swab, we drew <2 mL of blood from the ulnar vein, filling three heparinized hematocrit tubes (75 mm) before dabbing the injection site with three pieces of filter paper that then were air-dried. We centrifuged two of the hematocrit tubes in a Clay Adams Autocrit Centrifuge (Becton Dickinson, Franklin Lakes, New Jersey) for 5 min to estimate hematocrit values, which were assumed to be a measure of oxygen-carrying capacity or “health” of the oxygen carrying system (2007, 2010–2012 only; Dawson & Bortolotti 1997); we retained one hematocrit tube with whole blood. All blood samples were frozen immediately following centrifuging. Sex identification was determined using DNA from sex chromosomes (Zoogen, Inc., Davis, California).

We deployed VHF radio transmitters on a subset of after-second-year murrelets captured each year. Age of first breeding of KIMUs is unknown, but is thought to be 2–4 years (Day *et al.* 1999). 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 KIMU, their dispersed nesting habits and battery-life limitations of radio transmitters, we were unable to track individual murrelets beyond a single breeding season. Therefore, we assumed that the radio-tagged murrelets were representative of the local population of murrelets in a given year and across years.

We attached the transmitters (Advanced Telemetry Systems, Inc., Isanti, Minnesota [ATS]; model number A4360, <3.2 g, ~1.5% of bird's mass, 55 pulses min<sup>-1</sup>) using a subcutaneous anchor on the bird's back between the scapulars (Newman *et al.* 1999). During the course of our study, the attachment technique and procedure evolved to minimize perceived pain to the bird and to maximize transmitter retention. In 2007 and 2008, following Lougheed *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, Saint Paul, Minnesota). In 2009–2012, we infused 2 mg kg<sup>-1</sup> of a local anesthetic (1% solution of lidocaine) with a sterile syringe 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 one Ethicon 3-0 monofilament, non-absorbable suture (Ethicon Endo-Surgery, Inc., Blue Ash, Ohio) following Newman *et al.* (1999). In 2010, as part of a separate study to compare transmitter attachment techniques, we affixed transmitters to 14 KIMUs with three 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 (Kissling, unpubl. data). Therefore, we included these 14 individuals in our analysis. Birds were released immediately, and the time of release was recorded. If both birds of a pair were captured, we arbitrarily selected one bird to radio-tag to ensure independence and to minimize disturbance to nesting pairs, and we released the pair together. 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.

#### *Nest locating and monitoring*

We attempted to locate radio-tagged murrelets 2–5 times per week for at least 8 weeks after tagging 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 and radio-tagging. We first 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, weather) to locate incubating birds. For each bird located during an aerial survey, we recorded a GPS location, time of location, and, for birds on the water only, whether the bird was diving based on the VHF signal pattern. 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, Barbaree *et al.* 2014). Because we radio-tagged only one bird of a pair and both parents share incubation duties by switching every 24–48 hours, we were able to adjust flight schedules and routes and to prioritize radio-tagged birds to locate during specific flights to maximize our ability to locate nesting birds. We attempted to investigate all terrestrial locations of radio-tagged murrelets on foot to determine whether the murrelet was incubating or dead or whether the transmitter had become detached from the bird. However, the majority (88%) of assumed nests located during our study were not accessible by foot, even with the assistance of fixed-wing aircraft and helicopter. Therefore, we monitored nearly all nesting activity using a combination of remote dataloggers and aerial telemetry (see Kissling *et al.* 2015 for details).

#### **Data analyses**

We analyzed data for two subsamples of KIMUs: radio-tagged murrelets and murrelets that were captured, but not radio-tagged, hereafter referred to as non-radio-tagged murrelets. While we used only radio-tagged KIMUs to draw inferences regarding breeding decisions (see below), we found it insightful to consider

the characteristics of both subsamples of murrelets. In most years, larger sample sizes of non-radio-tagged murrelets better reflected attributes of the population using the area. Also, by comparing the two subsamples, we were able to evaluate whether the radio-tagged subsample was representative of the local population. Thus, we described proportions of radio-tagged and non-radio-tagged murrelets by sex, mean body mass (g), plumage (basic, alternate and transitional), group size at the time of capture (i.e. paired status), mean hematocrit value (%) and brood patch development score (BP 0–3). When appropriate, we compared the two subsamples (radio-tagged and non-radio-tagged murrelets) using a two-sample *t*-test or  $\chi^2$  test. We set the statistical significance level as  $P < 0.05$  for all tests. Means are reported  $\pm$  one standard deviation (SD). We conducted all analyses in R version 3.0.2 (R Core Team 2013).

#### Breeding propensity and timing

Throughout this paper, we use the terms “breeding” and “nesting” synonymously; we are not aware of a reliable method for distinguishing the two activities for KIMUs and we aimed to be consistent with the terminology used in Kissling *et al.* (2015). We defined breeding propensity as the probability that an after-second-year murrelet will breed in a given year and measured it as the proportion of radio-tagged KIMUs that were detected inland at least one time during the breeding season and were then located on the water within 72 h of the inland location (i.e. the bird was not dead). We then classified each radio-tagged murrelet as a “breeder” or “non-nester” (see Kissling *et al.* 2015 for details). We removed a bird from further analysis if it did not initiate nesting and either died or was not located regularly on the water (<50% of the flights completed), presumably because it had left the study area permanently or because the radio-tag had failed or detached from the bird by 23 June when 90% of the nests had been found (following Peery *et al.* 2004). We made three key assumptions: (1) murrelets detected inland were attempting to nest (i.e. not prospecting for nest sites or engaging in social behavior), (2) murrelets attempting to nest were detected inland at least one time (i.e. failed nests were located), and (3) capture, handling and radio-tagging did not affect initiation of breeding.

We also sought to understand factors that may have influenced nest initiation. We estimated the timing of nest initiation at known and inferred nests using a combination of information collected during capture (e.g. group size, brood patch score), aerial radio-telemetry locations (i.e. on water, on nest) and nest attendance patterns from the dataloggers. The incubation period for a KIMU is 30 d, during which both parents share incubation duties, switching typically every 24–48 h (Kissling, unpubl. data). Following hatching, the chick is brooded typically by one of the parents for the first 24–48 h, and then both parents spend most of their time at sea, only occasionally visiting the nest to deliver food to the chick. If a murrelet re-nested (i.e. met the criteria of a “breeder” in more than one location), we removed the second nesting attempt from these analyses.

#### Explanatory factors

We considered four individual and 12 environmental factors as possible covariates associated with breeding decisions of KIMUs. We measured individual characteristics at the time of capture, and we chose environmental factors that were representative of conditions in or near Icy Bay during the pre-breeding period (March–May). Therefore, in this analysis, we assumed that individual murrelets made the decision to breed or not to breed in a given year when they arrived at Icy Bay in that year.

For individual characteristics, we assessed sex, body mass, plumage category and mean hematocrit value. Following Labocha & Hayes (2012), we assumed that body mass was a reliable indicator of overall body condition. We found only a weak correlation between sex (female) and body mass (Pearson correlation  $r = 0.32$ ,  $P < 0.001$ ). We did not include plumage and hematocrit values as possible covariates in the modeling effort because there was too little variation in plumage of radio-tagged murrelets and because we did not measure hematocrit values for all birds in all years. To test for possible capture and handling effects, we considered total number of minutes between capture and release in our analyses (hereafter handling time).

For environmental factors, we initially considered three monthly indices of ocean, climate or atmospheric conditions in the North

**TABLE 1**  
Sample sizes of male and female Kittlitz's Murrelets captured and radio-tagged in Icy Bay, Alaska, 2007–2012

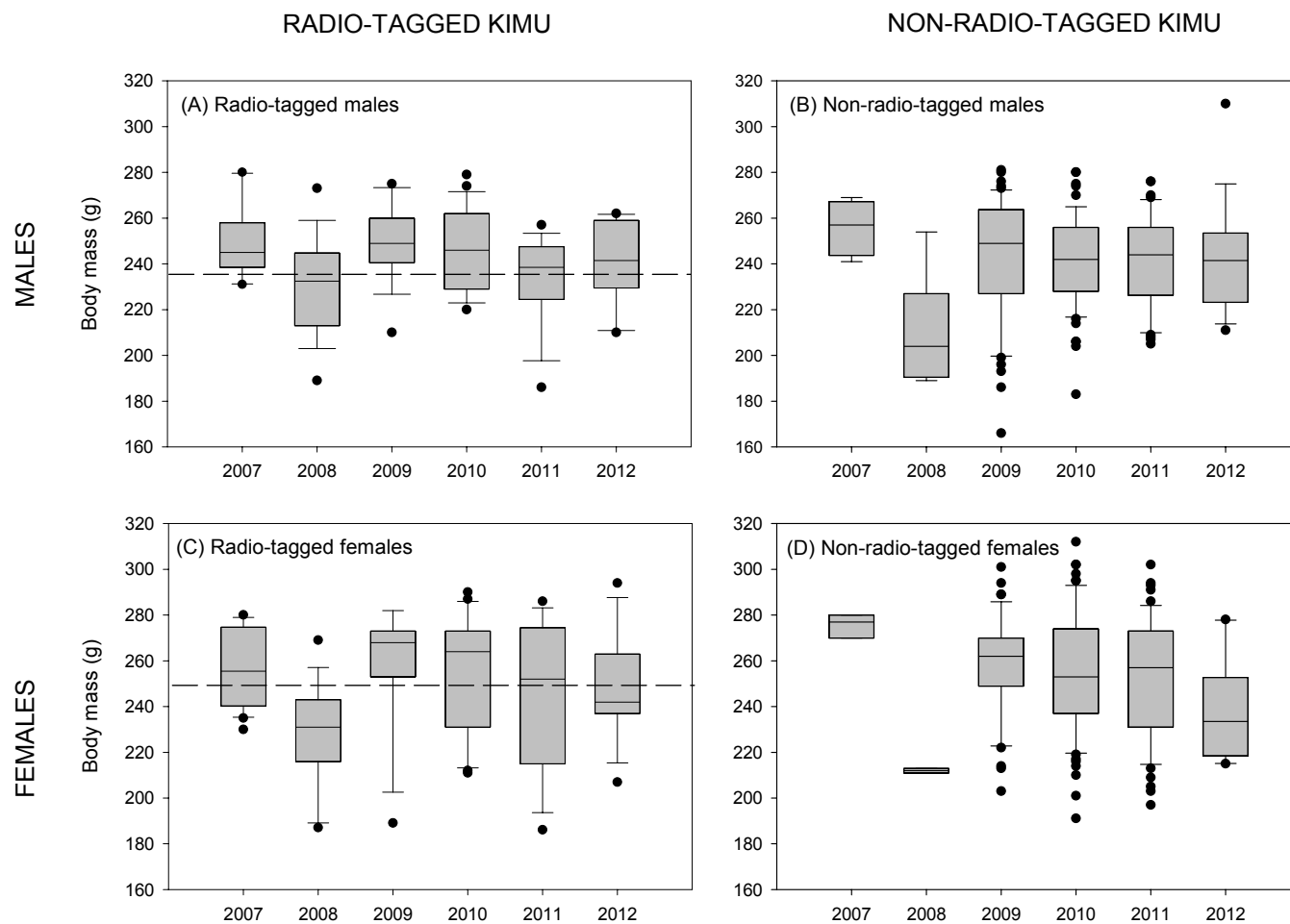
Year	Total number radio-tagged		Number of telemetry flights completed by 23 June	Proportion removed from analysis by reason <sup>a</sup>		Number of radio-tagged murrelets used in analysis		Proportion of breeders	Proportion of non-nesters
	Females	Males		Mortality	Insufficient number of locations	Females	Males		
2007	20	10	14	0.07	0.03	17	10	0.15	0.85
2008	16	16	18	0.06	0.31	8	12	0.05	0.95
2009	13	17	21	0.10	0.20	11	13	0.08	0.92
2010	21	23	25	0.07	0.16	15	19	0.12	0.88
2011	13	18	14	0.00	0.06	11	18	0.45	0.55
2012	12	12	11	0.04	0.04	11	11	0.36	0.64
All	95	96	103	0.06	0.18	73	83	0.20	0.80

<sup>a</sup> Radio-tagged murrelets that died or were not regularly located on the water between capture and 23 June were not include in the annual proportions of breeders and non-nesters.

Pacific Ocean (or broader) averaged across the 3-month pre-breeding period by year: Pacific Decadal Oscillation (PDO), North Pacific Index (NPI) and Oceanic Niño Index (ONI). The PDO and ONI are based primarily on sea-surface temperature (Mantua *et al.* 1997, L'Heureux *et al.* 2013), whereas the NPI is based on sea-level pressure, specifically the strength and position of the Aleutian low-pressure system (Trenberth & Hurrell 1994). All of these indices have been correlated to some type of biological response (e.g. salmon production, spring phytoplankton bloom dynamics; Mantua *et al.* 1997, Henson 2007), although their use in this type of analysis has known pitfalls (see Oro 2014).

We also selected environmental variables expected to indicate or influence ocean productivity at a finer spatial scale compared with PDO, NPI and ONI. We acquired weather station data from nearby Yakutat to estimate average air temperature (°C) and wind speed (km/h; variable WIND) during the pre-breeding period. Our intent was to reflect the prevalence of spring storms and therefore mixing of the water column each year, which is negatively associated with the onset of the spring phytoplankton bloom (Henson 2007). We also recorded total snowfall (cm; variable SNOW) between October and April as an indicator of nest-site access in the spring (Alaska

Climate Database, National Weather Service; [www.arh.noaa.gov/cliMap/akClimate.php](http://www.arh.noaa.gov/cliMap/akClimate.php)). We averaged sea-surface temperature (°C; variable SST) in and near Icy Bay (i.e. both the outer and inner bays; Fig. 1) during the pre-breeding period annually using Reynolds's Optimal Interpolation dataset ([nomad3.ncep.noaa.gov/ncep\\_data/index.html](http://nomad3.ncep.noaa.gov/ncep_data/index.html)). We also assessed several aspects of the spring peak timing and magnitude of chlorophyll-*a* (mg/m<sup>3</sup>) using satellite-derived data processed and described by Waite & Mueter (2013) as an index of primary productivity in our study area (Fig. 1). We hypothesized that murrelets were more likely to nest in years of early and strong heightened chlorophyll-*a*. Specifically, we considered the peak magnitude of chlorophyll-*a* during the spring bloom (variable PeakChloroMag), the midpoint of the 8-d period in which the spring bloom began (defined as when chlorophyll-*a* levels first exceeded 10% of the annual median, or ~1.5 mg m<sup>-3</sup>; variable StartChloroDate), the duration in weeks of the increasing spring bloom calculated as difference between the midpoints of the 8-d periods in which the spring bloom began and peaked (variable Duration), and the mean chlorophyll-*a* level between 12 and 28 May when murrelets arrive in Icy Bay and were radio-tagged (variable MeanChloroMay). There was high correlation (Pearson correlation  $r > 0.6$ ) among some of these

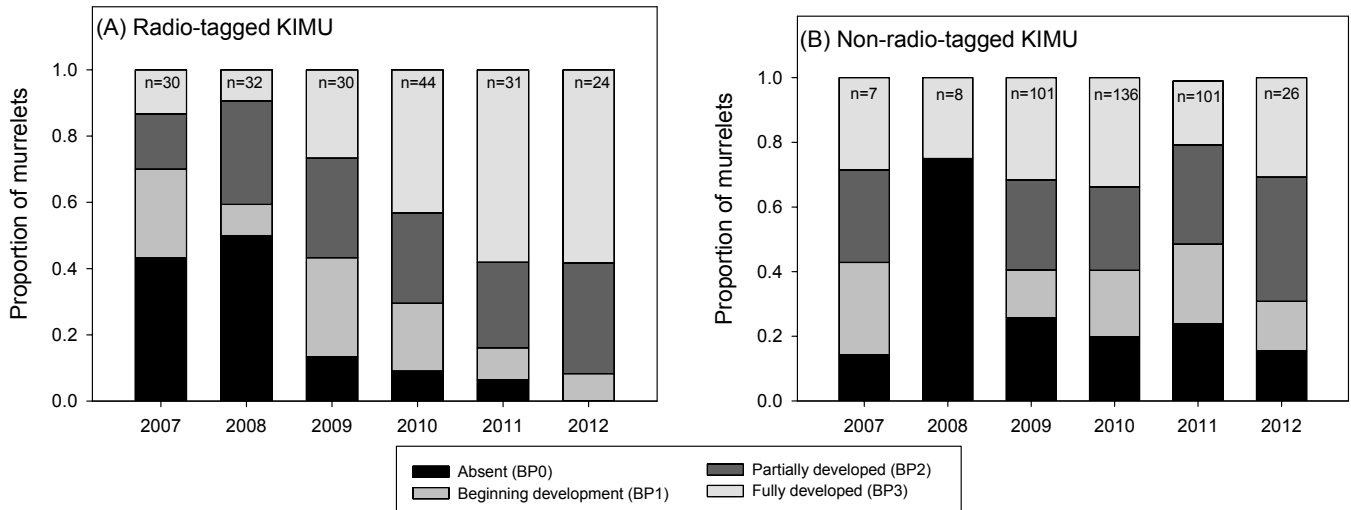


**Fig. 2.** Variation in body mass (g) by sex of radio-tagged and non-radio-tagged Kittlitz's Murrelets (KIMU), Icy Bay, 2007–2012. Across all years and subsamples (radio-tagged, non-radio-tagged) combined, females had a significantly higher body mass compared with males. Within sex, mean body mass was similar between subsamples in all years. The boxes indicate the 25th and 75th percentiles with the median depicted as a horizontal line; the whiskers describe the 10th and 90th percentiles. The horizontal dashed lines are the mean body mass of radio-tagged male (A) and female (B) breeders across all years.

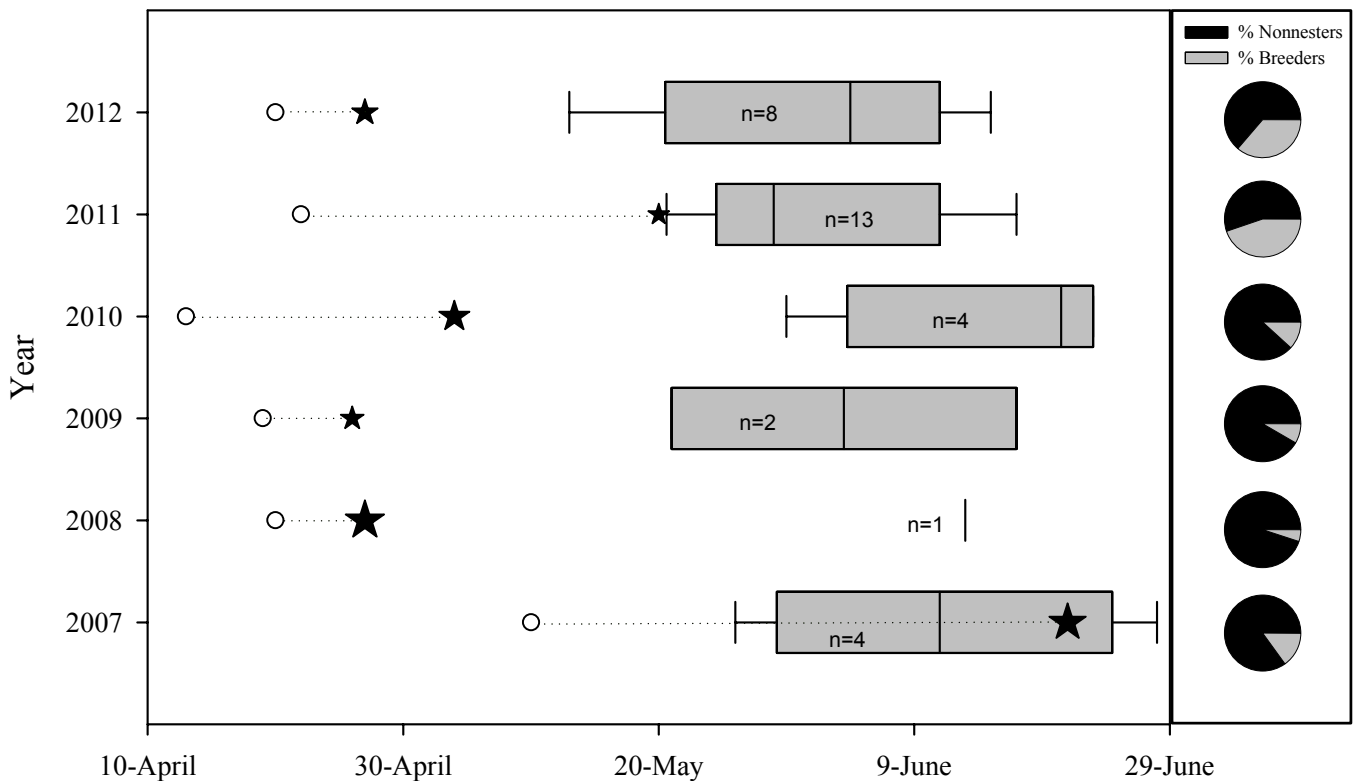
environmental characteristics and, therefore, we reduced them to a subset that included NPI, SNOW, WIND, SST, PeakChloroMag, StartChloroDate and MeanChloroMay.

We fit two generalized linear models to assess the effects of individual and environmental factors on breeding decisions of KIMUs. First, we fit a logistic regression model with breeding status (breeder, non-nester) as the binomial dependent variable and

sex, body mass, handling time, NPI, SST, WIND, PeakChloroMag, StartChloroDate and MeanChloroMay as potential covariates. Second, we fit a model with timing of nest initiation (Julian date; variable NestInitiateDate) as the dependent variable and sex, handling time, SNOW, PeakChloroMag and StartChloroDate as potential covariates. We included sex in all candidate models and log-transformed covariates when appropriate. We developed a set of candidate models and selected the most parsimonious model



**Fig. 3.** Annual proportions of (A) radio-tagged and (B) non-radio-tagged Kittlitz's Murrelets (KIMU) captured by brood patch development score at the time of capture, Icy Bay, Alaska, 2007–2012. Sample sizes (n) included at the top of each bar.



**Fig. 4.** Nest initiation dates (box plots) and breeding propensity (pie charts) of radio-tagged Kittlitz's Murrelets with timing and magnitude of chlorophyll-*a* (circles and stars) near Icy Bay, Alaska, 2007–2012. Open circles indicate the onset of the spring bloom (when chlorophyll-*a* levels first exceeded 1.5 mg/m<sup>3</sup>), and the stars are proportional to the peak magnitude; the dotted lines connecting the two describe the duration of the bloom build-up. Sample sizes of nests each year are given inside boxes. The boxes indicate the 25th and 75th percentiles, with the median depicted as a horizontal line; the whiskers describe the 10th and 90th percentiles. Renesting attempts are not included.

using Akaike information criterion (AIC); in both cases, we ran the global model, the null model (included sex only), and 10 candidate models. To evaluate model fit, we examined probability plots of the models. Parameter estimates are reported  $\pm$  standard error (SE).

## RESULTS

We captured and processed 569 KIMUs, radio-tagging 191 during six spring capture efforts, 2007–2012 (Table 1). All characteristics of radio-tagged individuals, including plumage, paired status, body condition (Fig. 2), hematocrit value and brood patch development (Fig. 3) generally reflected those of the larger subsample of non-radio-tagged individuals.

Nearly all non-radio-tagged and radio-tagged murrelets were in alternate plumage at the time of capture (non-radio-tagged: 92%; radio-tagged: 97%). Although some were undergoing the pre-alternate molt at the time of capture (non-radio-tagged: 6%; radio-tagged: 2%), the remainder were in basic plumage (non-radio-

tagged: 2%; radio-tagged: <1%). Similarly, most murrelets were paired at the time of capture (non-radio-tagged: 86%; radio-tagged: 84%), although we did capture some single murrelets (non-radio-tagged: 7%; radio-tagged: 12%) and some in groups of three or more (non-radio-tagged: 7%; radio-tagged: 4%).

Across all years and both subsamples combined, mean body mass differed significantly between male and female KIMUs ( $t = -5.78$ ,  $P < 0.01$ ; Fig. 2). Mean body mass of non-radio-tagged males was  $241 \pm 23$  g and of radio-tagged males was  $241 \pm 19$  g; non-radio-tagged and radio-tagged females averaged  $254 \pm 26$  g and  $249 \pm 26$  g, respectively (Fig. 2). We did not find any significant differences in mean body mass of non-radio-tagged and radio-tagged KIMUs of either sex (Fig. 2).

Similar to body mass results, across all years with available data (2010–2012) and both subsamples, mean hematocrit values differed between male and female murrelets ( $t = -3.857$ ,  $P < 0.001$ ). We did not find a significant difference in mean hematocrit value of females

**TABLE 2**  
Candidate models used to identify factors associated with the decision to breed and timing of nest initiation in a given year for radio-tagged Kittlitz's Murrelets, Icy Bay, Alaska, 2007–2012

Dependent variable	Model <sup>a</sup>	$\Delta$ AIC	$w_i$
	Sex + NPI + WIND	0.00	0.55
	Sex + NPI + SST + WIND + StartChlorDate + PeakChloroMag	1.91	0.21
	Sex + Body mass + NPI + SST * WIND	2.74	0.14
	Sex + Body mass + Handling time + NPI + SST + WIND + StartChloroDate + MeanChloroMay (Global)	5.45	0.04
ReproStatus <sup>b</sup> (0 = non-nester, 1 = breeder)	Sex + Body mass + Handling time + NPI + SST + WIND + StartChloroDate + PeakChloroMag (Global)	5.45	0.04
	Sex + Handling time + StartChloroDate * PeakChloroMag	6.72	0.02
	Sex + Body mass + WIND + MeanChloroMay	10.15	0.00
	Sex (Null)	12.80	0.00
	Sex + SST + MeanChloroMay	14.38	0.00
	Sex + Handling time	14.80	0.00
	Sex + Body mass + Handling time	15.31	0.00
		Sex + Handling time + PeakChloroMag	0.00
	Sex + SNOW + WIND	1.43	0.14
	Sex + Handling time + NPI + SST + WIND	1.86	0.12
	Sex + Handling time + SNOW + StartChlorDate + PeakChloroMag (Global)	2.07	0.10
	Sex + StartChlorDate * PeakChloroMag	2.22	0.10
NestInitiateDate <sup>b</sup> (Julian date)	Sex + SST * PeakChloroMag	2.52	0.08
	Sex (Null)	2.53	0.08
	Sex + Handling time + StartChloroDate	4.19	0.04
	Sex + NPI + SST	5.90	0.02
	Sex + Handling time + SNOW + NPI	5.95	0.01
	Sex + SNOW + StartChloroDate	6.28	0.01

<sup>a</sup> Models are arranged by increasing differences in Akaike's information criterion ( $\Delta$ AIC) values and relative model weights ( $w_i$ ); selected models are highlighted in gray.

<sup>b</sup> ReproStatus = decision to breed; NestInitiateDate = timing of nest initiation.

(non-radio-tagged: 41.4%  $\pm$  4.0; radio-tagged: 41.3%  $\pm$  4.7) or of males (non-radio-tagged: 45.1%  $\pm$  4.3; radio-tagged: 45.7%  $\pm$  3.2) by subsample.

The proportions of radio-tagged KIMUs assessed by brood patch development score were similar to the corresponding proportions of non-radio-tagged murrelets in most years (2007–2010, 2012; Fig. 3). In 2011 only, the proportions differed significantly between groups ( $\chi^2 = 18.31$ ,  $P < 0.001$ ); we radio-tagged a higher proportion of KIMUs with BP 3 and correspondingly lower proportions of murrelets with BP 0–1 compared with proportions of non-radio-tagged murrelets.

We removed 35 of 191 KIMUs from the sample used to estimate breeding effort and subsequent analyses. The majority (71%) was removed due to an insufficient number of aerial telemetry locations, which did not allow for classification as breeders or non-breeders; the remaining 29% were removed due to death before 23 June (Table 1).

### Breeding propensity and timing

Over the 6-year period, 32 of 156 (20%) radio-tagged KIMUs initiated nests. The annual proportions of radio-tagged KIMUs that were classified as breeders or non-breeders varied significantly among years ( $\chi^2 = 21.17$ ,  $P < 0.01$ ). The highest proportion of breeders was 0.45 in 2011 and the lowest was 0.05 in 2008 (Table 1), representing a nine-fold difference in annual breeding propensity.

Combining all years, 32 KIMUs initiated nests between 12 May and 28 June (Fig. 4). Among years, the median date of nest initiation spanned a 23-d period, although in some years our sample size was very small (e.g. only one nest found in 2008; Fig. 4). Generally, in 2011 and 2012, when the highest proportions of radio-tagged murrelets were classified as breeders (Table 1), median nest initiation dates were earlier (Fig. 4). The only other year with comparatively early nest initiation was 2009, but we located only two nests that year, one with an earlier initiation date (22 May) and one with a later initiation date (18 June).

### Explanatory factors

All of the KIMUs of both sexes that were classified as breeders were in alternate plumage at the time of capture ( $n = 32$  of 32; 100%). Most of the non-breeders ( $n = 121$ ; 78%) were also in alternate plumage ( $n = 121$  of 124; 98%), regardless of sex; one female and one male non-breeder were in transitional plumage ( $n = 2$  of 124; 2%), and one male non-breeder was in basic plumage ( $n = 1$  of 124; <1%). Mean body mass of breeders and non-breeders was nearly equal for males (breeders: 237  $\pm$  19%,  $n = 24$ ; non-breeders: 244  $\pm$  19%,  $n = 59$ ) and for females (breeders: 249  $\pm$  23,  $n = 8$ ; non-breeders: 249  $\pm$  26,  $n = 65$ ). Handling time was highly variable, averaging 77 min ( $\pm$  62) for breeders and 80 min ( $\pm$  50) for non-breeders. Hematocrit values were similar for male non-breeders (45.5  $\pm$  3.5%,  $n = 25$ ) and breeders (46.1  $\pm$  3.1%,  $n = 18$ ), as were values for female non-breeders (41.6  $\pm$  4.6%,  $n = 31$ ) and breeders (43.8  $\pm$  5.2%,  $n = 6$ ).

The best-fit model to explain variation in breeding status of KIMU included sex, NPI and WIND (Table 2). The decision to breed was associated negatively with NPI ( $\beta_{NPI} = -0.51 \pm 0.18$ ) and WIND ( $\beta_{WIND} = -2.26 \pm 0.66$ ), and radio-tagged males ( $\beta_{MALE} = 1.23 \pm 0.47$ ) were more likely to be breeders than radio-tagged females (Table 3). Although the next best-fit model had a  $\Delta AIC$  of only 1.91, it included all of the environmental variables, including NPI and WIND (Table 2) and, therefore, we selected the most parsimonious model. The null model, which included only sex as a covariate, had a  $\Delta AIC$  of 12.8 (Table 2), indicating that the covariates helped explain the observed variation in breeding status.

Timing of nest initiation was best explained by sex, handling time and PeakChloroMag (Table 2). Radio-tagged males ( $\beta_{MALE} = -9.40 \pm 4.36$ ) initiated nesting earlier than radio-tagged females, and timing of nest initiation as measured by Julian date was positively associated with PeakChloroMag ( $\beta_{PCM} = 24.70 \pm 12.48$ ; Table 3), indicating that murrelets nested later in years with a high peak magnitude of chlorophyll-*a* (Fig. 4). Handling time was positively related to nest initiation timing, although the parameter estimate was small and highly imprecise (0.04  $\pm$  0.03; Table 3).

TABLE 3

Parameter estimates from most parsimonious models used to identify factors associated with the decision to breed and the timing of nest initiation in a given year for radio-tagged Kittlitz's Murrelets, Icy Bay, Alaska, 2007–2012

Dependent variable	Covariate	Estimate	Standard error	Test statistic <sup>a</sup>
ReproStatus <sup>b</sup> (0 = non-nester, 1 = breeder)	Intercept	529.09	185.86	2.84
	Sex (male)	1.23	0.47	2.60
	NPI	-0.51	0.18	-2.81
	WIND	-2.26	0.66	-3.42
NestInitiateDate <sup>b</sup> (Julian date)	Intercept	132.77	8.96	14.82
	Sex (male)	-9.40	4.36	2.15
	Handling time	0.04	0.03	1.29
	PeakChloroMag	24.70	12.48	1.98

<sup>a</sup> For the model explaining decision to breed (ReproStatus), we report the  $z$ -value (degrees of freedom = 152); for the model explaining timing of nest initiation (NestInitiateDate), we report the  $t$ -value (degrees of freedom = 29).

<sup>b</sup> ReproStatus = decision to breed; NestInitiateDate = timing of nest initiation.



Most models, including the null model (sex only), had  $\Delta AIC$  values  $< 3.00$  over the best-fit model, and all models had AIC differences  $< 7.00$ , suggesting high uncertainty in model selection (Table 2). For the purpose of reporting, we selected the best-fit and most parsimonious model.

## DISCUSSION

We observed considerable intra- and interannual variation in the decision to breed and timing of nest initiation of KIMUs across the 6-year period of our study. We found a nine-fold difference in breeding propensity and a 23-d span in the median date of nest initiation among years, suggesting that individuals breed both intermittently and asynchronously, as has been found with the congeneric Marbled Murrelet *B. marmoratus* (McFarlane-Tranquilla *et al.* 2003b, Bradley *et al.* 2004, Barbaree *et al.* 2014). Our results generally indicate that the variation associated with breeding decisions of KIMUs in Icy Bay is influenced primarily by local environmental conditions and, to a lesser extent, by individual condition in the pre-breeding period.

Most KIMUs that arrived in Icy Bay in the spring were paired, in alternate plumage and with a brood patch at the time of capture, suggesting that the decision of whether to breed probably was made upon or shortly after arrival. Further, murrelets of both sexes were in seemingly good health and body condition, as indicated by hematocrit levels and body mass; murrelets were not emaciated or lethargic, and they showed no other signs of compromised fitness. The exception to this finding was 2008, when both males and females had lower mean body mass compared with all other years (Fig. 2) and fewer of them had brood patches (Fig. 3). Correspondingly, only 5% of radio-tagged murrelets initiated breeding in that year, and 31% were removed from analyses due to an insufficient number of locations, probably due to movement out of the study area or undetected mortality (Table 1). Overall, however, individual variables considered in our analyses did not explain much of the variation in breeding decisions of the KIMU, nor did they explain why so few murrelets attempted to breed during our 6-year study with perhaps the exception of 2008.

We found that “good” years for breeding were characterized by an intense Aleutian low-pressure system (i.e. low NPI) and low average wind speeds in the spring. These environmental attributes can lead to an earlier onset of water column stratification and, subsequently, an earlier and stronger spring phytoplankton bloom (Brickley & Thomas 2004, Henson 2007). Because phytoplankton provides food for zooplankton (Verity *et al.* 2002) and in turn for small fishes (Platt *et al.* 2003), both of which are consumed by KIMUs (Hatch 2011), we presumed that an enhanced bloom would benefit murrelet reproduction, as has been documented for other seabird species (e.g. Scott *et al.* 2006). Therefore, we were surprised that none of the variables describing the timing or magnitude of chlorophyll-*a* levels were included in the selected model to explain the decision to breed. We considered several explanations for this finding.

First, we may have estimated chlorophyll-*a* at a scale too large to capture the fine-scale foraging dynamics of the KIMU. We derived the estimates from satellite imagery, a method that is not necessarily effective in turbid glacial waters (Waite & Mueter 2013) such as those of Icy Bay. Therefore, we considered a broader area (Fig. 1) surrounding Icy Bay and assumed that those estimates were correlated with the general pattern of bloom dynamics within the bay as well. However, this may not be the case; it is certainly

possible that radio-tagged KIMUs in our study experienced different bloom timing and magnitude at the local scale compared with those estimates used in our model. Second, satellite-derived estimates of chlorophyll-*a* can be difficult to interpret because we cannot account for grazing by zooplankton or the distribution of phytoplankton within the water column (Waite & Mueter 2013). Third, our estimates of chlorophyll-*a* may not be indicative of the food web to which KIMUs belong; in other words, KIMUs may feed on prey that are uncoupled from the spring bloom, as has been found with Adélie Penguins *Pygoscelis adeliae* in the Ross Sea (Ainley *et al.* 2015). Although the underlying mechanism is unclear, our results demonstrate that low NPI and low WIND, both factors that affect spring bloom dynamics, were better predictors of bottom-up processes that influence the decision to breed for KIMU in our study area compared with satellite-derived values of chlorophyll-*a*. We recommend that future research efforts address some of the shortcomings associated with our estimates of chlorophyll-*a*, perhaps by directly measuring factors at the local scale or by classifying types of phytoplankton that compose the spring bloom (e.g. Brewin *et al.* 2011), to identify thresholds associated with breeding and to better understand underlying mechanisms.

Our results indicated a weak, positive association between the peak magnitude of chlorophyll-*a* and delayed nest initiation of KIMUs. While this result suggests that, in fact, the chlorophyll-*a* estimates were accurate and informative, at least in explaining variation in timing of nest initiation, there was substantial uncertainty in model selection as well as a limited sample size of nests. In addition, in years when nesting was initiated earlier, breeding propensity was higher (e.g. 2011 and 2012; Fig. 4), signifying that there may be benefits to nesting earlier, as has been found with other seabird species (e.g. Sorensen *et al.* 2009), but that those benefits may not be associated with the timing or magnitude of the spring bloom. It is logical to expect that KIMUs, like many other seabirds (e.g. Scott *et al.* 2006, Hipfner 2008, Shultz *et al.* 2009, Sorensen *et al.* 2009), would initiate nesting based on a biological cue, to avoid a mismatch in the timing of available prey resources and the need to feed their chicks. Several authors have speculated that *Brachyramphus* murrelet nesting phenology in Alaska was associated with the timing of the spring phytoplankton bloom, i.e. earlier nest initiation in years with earlier blooms (Speckman *et al.* 2000, Arimitsu *et al.* 2011). Our results, however, suggest that the magnitude of the bloom, not the timing of it, was a better predictor of timing of nest initiation. Further, the relationship was the opposite of that expected; birds initiated nesting later in years with a more intense bloom (Fig. 4). Given the high level of model uncertainty and the conflicting patterns observed, we are reluctant to overstate our results. Instead, we emphasize the extreme variation in timing of nest initiation within and among years, which may or may not have been related directly to spring bloom dynamics, and the apparently high degree of behavioral plasticity of KIMUs.

We acknowledge that the results of our study hinge on several key assumptions. First, we assumed that the radio-tagged murrelets were representative of the local murrelet population and we believe that we met this assumption for the most part. The subsample of radio-tagged murrelets was proportionally similar in plumage, group size and body condition to the subsample of non-radio-tagged murrelets. The only potential deviation from this assumption occurred in 2011, when we radio-tagged a higher proportion of murrelets with fully developed brood patches. However, we do not feel that this biased our results because brood patches are known to

be unreliable predictors of reproductive status in *Brachyramphus* murrelets (McFarlane-Tranquilla *et al.* 2003a, Kissling *et al.* 2015), although we recognize the potential significance of this deviation. Second, we made several assumptions in order to distinguish breeders from non-nesters: that murrelets detected inland were attempting to nest; that murrelets attempting to nest were detected inland at least once; and that radio-tagging did not affect initiation of breeding. While we recognize the possibility that we may have violated some of these assumptions on occasion, we do not believe that those infrequent violations greatly influenced or biased our findings (see Kissling *et al.* 2015 for detailed evaluation of these assumptions). Further, handling time had little explanatory power in our models.

We posit that the uncertainties associated with our results were due to our inability to identify or measure the appropriate explanatory variable(s) at the temporal or spatial scale that may be associated with breeding decisions. For example, owing to KIMU biology and natural history, we were not able to consider some key individual characteristics such as breeding experience, breeding activity in the previous year, and age in the models aiming to investigate breeding decisions. These factors are known to influence the decision to breed of other species (Cam *et al.* 1998, Bradley *et al.* 2000, Le Bohec *et al.* 2007, Cubaynes *et al.* 2011), as well as the timing of nest initiation (Sydeman *et al.* 1991, Arnold *et al.* 2004), and they probably have some effect on decisions of individual murrelets. Schaefer (2014) found that higher levels of stress hormones in feathers sampled from KIMUs captured in Icy Bay were associated with lower breeding propensity in the subsequent breeding season, suggesting that some carryover effects exist across seasons and years. Certainly, our ability to track individual murrelets for only a single season was a limiting factor in our study. As field methods and technology improve, our understanding of factors influencing breeding decisions, or why murrelets forego breeding in a given year, should advance greatly.

In conclusion, although we were unable to explain much of the variation in individual breeding decisions of KIMUs during our 6-year study, we felt it was informative to present these results, for two reasons. First, several studies have demonstrated that this species may be experiencing reproductive problems (Day & Nigro 2004, Kaler *et al.* 2009, Lawonn 2012, Kissling *et al.* 2015), yet our study is the only one that has assessed factors affecting individual breeding decisions. Second, there is virtually no information available on this species during the pre-breeding period, including basic demographic data such as body mass. Thus, we urge researchers to view our results as a stepping stone, not an end product. We recommend the following future work to advance our understanding of possible drivers of breeding decisions in KIMU: (1) develop non-lethal field or laboratory methods to age murrelets or to assess previous breeding experience, including approaches to tracking individual breeding effort beyond a single season; (2) design nest-searching studies that can measure breeding propensity and examine hypotheses related to factors affecting breeding decisions; (3) quantify hormone levels of KIMUs captured during the pre-breeding period to evaluate stress response (e.g. corticosterone) and/or parental investment (e.g. prolactin) (Angelier & Chastel 2009, Kitaysky *et al.* 2010, Schaefer 2014) and compare with those of Marbled Murrelets from the same sampling locations to explain interspecific differences in observed breeding propensity (Kissling *et al.* 2015); and (4) measure primary productivity and, if possible, secondary productivity directly throughout the

pre-breeding and breeding seasons to evaluate whether murrelets base breeding decisions on spring conditions or can forecast prey availability during chick-rearing.

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