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ADDRESSING THE CHALLENGES OF MONITORING A RARE AND
ELUSIVE SEABIRD

By

ANNE LOUISE SCHAEFER

B.S., South Dakota State University, Brookings, SD, 2011

Thesis

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Approved by:

Dr. Sandy Ross, Dean of the Graduate School
Graduate School

Dr. Paul M. Lukacs, Chair
Wildlife Biology Program, Department of Ecosystem and Conservation Sciences

Dr. Creagh Breuner, Committee Member
Organismal Biology and Evolution, Division of Biological Sciences

Dr. Mark Hebblewhite, Committee Member
Wildlife Biology Program, Department of Ecosystem and Conservation Sciences

Michelle Kissling, Ex Officio Committee Member
U.S. Fish and Wildlife Service
Addressing the challenges of monitoring a rare and elusive seabird

Chairperson: Dr. Paul Lukacs

ABSTRACT

The Kittlitz’s murrelet (Brachyramphus brevirostris) is a small alcid endemic to Alaska and eastern Russia. Due to its pelagic lifestyle, researchers lack information regarding environmental conditions experienced by Kittlitz’s murrelets throughout the year and how these conditions impact their physiology and vital rates. Further, unlike most seabirds, the Kittlitz’s murrelet is a dispersed nester; therefore, data are limited for this species even within the breeding season. The goal of this research was to evaluate and improve the monitoring methods for the Kittlitz’s murrelet throughout the year. I approached this goal from 2 different perspectives. First, I worked to clarify abundance and trend estimates that have been questioned due to uncertainty in species identification. Second, I used physiological measures to examine the relationships between stress, parental investment, breeding propensity, and environmental conditions experienced by Kittlitz’s murrelets throughout the year. To address uncertainties in species identification, I conducted a field experiment to quantify misidentification and non-identification rates of Brachyramphus murrelets during abundance surveys and evaluate the impacts of covariates on each. I found that misidentification of species was rare and did not bias abundance estimates. Additionally, non-identification was common beyond observation distances of 140 m, though this depended on observer experience, murrelet behavior, and sea conditions. To understand the environmental conditions experienced by Kittlitz’s murrelets throughout the year, I measured corticosterone (avian stress hormone) and prolactin (parental expression hormone) and evaluated their relationships with breeding propensity and ocean productivity metrics. Higher levels of stress during the pre- and post-breeding seasons reflected lower rates of breeding propensity in the following season. Additionally, higher stress was associated with lower sea surface temperatures during the pre-breeding season, and earlier capture dates, longer time-spans between capture and processing, and lower body mass during the late-breeding season. Prolactin positively reflected CORT during the early breeding season and sex during the late breeding season. These results emphasize the need for continued research to understand the mechanisms linking the stress physiology, foraging ecology, and breeding ecology of the Kittlitz’s murrelet and other species that depend on similar resources.
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CHAPTER 1: ADDRESSING THE CHALLENGES OF MONITORING A RARE AND ELUSIVE SEABIRD

INTRODUCTION

In order to properly manage any wildlife population, understanding of the species’ status, trends, and biology must first be acquired. However, threatened, endangered, and elusive species pose a unique challenge for monitoring and management. The nature of rarity inherently constrains quick or easy collection of data. Thus, researchers often lack information regarding the life history strategies, population abundances, and population structures of the very species we are most interested in conserving. Moreover, fewer data result in greater statistical and biological uncertainty. Therefore, in order to implement effective and informed conservation actions, it is important for researchers to test and validate current monitoring methodologies and also explore new tools for monitoring small or elusive populations reliably throughout the year.

The overall aim of this thesis was to evaluate and improve monitoring methods for rare and elusive species throughout the year. I approached this goal from 2 very different angles. First, I worked to facilitate the interpretation of abundance and trend estimates when species identification is not certain (Chapter 2). Second, I explored the use of physiological measurements as a tool for understanding the environmental conditions experienced by individuals throughout the year, and how these conditions impact physiology and population vital rates (Chapter 3).

CHAPTER 2

An assumption of most abundance estimation methods is that all sampled individuals are identified correctly (e.g., Buckland et al. 2001). However, this may not be a suitable
assumption, especially when morphologically similar species overlap in range.

Accounting for errors in identification is particularly important for species that co-occur in unequal proportions but are equally likely to be misidentified. In this circumstance, misidentification will disproportionately affect the less abundant species by artificially inflating abundance estimates (Kirchhoff 2011, Conn et al. 2013). One method that has been used to minimize misidentification risk is to identify individuals to the lowest taxonomic unit for which positive identification is certain (“non-identification”; Buckland et al. 2001). However, the resulting variable proportion of “unidentified” individuals results in less precise estimates of species abundance, hindering clear interpretation of species-specific abundance estimates and complicating the comparison of results across space and time. Therefore, quantification of both the misidentification and non-identification rates is important for clear and accurate interpretation of abundance and trend estimates, especially for rare species. Further, understanding the observational and environmental factors driving each rate can inform the development of monitoring protocols that minimize both misidentification and non-identification.

To address this issue, I conducted a field experiment to measure misidentification and non-identification rates of two similar seabird species and to identify the environmental and observational factors influencing each rate during distance-sampling abundance surveys carried out at sea. The system in which I examined this question was with Brachyramphus murrelets along coastal Alaska. Over the past 20 years, Kittlitz’s murrelet (B. brevirostris) populations declined in parts of their Alaskan range (Kuletz et al. 2011a, b, Piatt et al. 2011), although populations now appear to have stabilized (USFWS 2013). Along southern, coastal Alaska, the range of the Kittlitz’s murrelet
overlaps completely with that of the more common and morphologically similar, marbled murrelet (*B. marmoratus*). The 2 species are difficult to distinguish in the field, leading some to question the reliability of abundance and trend estimates for the Kittlitz’s murrelet (Hodges and Kirchhoff 2012). The results from the field experiment indicated that misidentification was low in this system and had no effect on the interpretation of abundance estimates. Even so, observer experience was the main driver of variation in misidentification rates, with more experienced observers making fewer errors. Moreover, I found that non-identification of individuals was common beyond observation distances of 140 m, though this depended on observer experience, murrelet behavior, and sea conditions.

The techniques used in the field experiment were specific to the *Brachyramphus* murrelet study system, but could be generalized for use in any system, aquatic or terrestrial, to measure identification rates and identify the factors influencing those rates. Results may reveal important patterns or relationships that can provide guidelines for modification of survey protocols to increase confidence in species identification and thereby increase the precision of abundance estimates. For example, in this system I suggest reducing the scanning width to ~150 m when observers are inexperienced or when sea conditions are rough. Further, observer experience was an important driver of both misidentification and non-identification; thus, these results emphasize the need for consistent rigorous observer training before and during surveys. Methods similar to those used in the field experiment could be modified to evaluate observer training and determine whether observers are qualified to perform surveys. These modifications to the
current survey protocol would increase confidence in species identification and facilitate comparison of results across surveys areas.

CHAPTER 3

The second goal of my thesis was to explore the use of physiological measurements as a tool for understanding the environmental conditions experienced by individuals throughout the year and how these conditions impact physiology and population demographics. Understanding the drivers of variation in population vital rates requires long-term, consistent collection of data, which is often financially and logistically unfeasible. Further, due to life-history strategies, many species are not available for direct monitoring efforts during all parts of the year (e.g., seasonal migrants). Physiological measurements, such as hormones measured in blood plasma, feces, feathers, or fur, can be used to make indirect observations regarding the conditions experienced by individuals throughout the year, from which population demographics may be predicted or inferred (Satterthwaite et al. 2012).

I examined the relationship between stress physiology, parental investment, and breeding propensity in a rare, elusive, and seasonally migratory seabird species. I also sought to identify the environmental factors (i.e. food availability) influencing variation in parental investment and stress throughout the year. I examined these questions within the Kittlitz’s murrelet system in Alaska. The Kittlitz’s murrelet spends ~80% of the year at sea; thus, researchers lack information regarding the environmental conditions encountered by individuals for most of the year. Further, the Kittlitz’s murrelet is a cryptic and dispersed nester (Day et al. 1999), so researchers lack data on this species even within the breeding season. I found evidence that higher stress levels outside of the
breeding season correlated with lower breeding propensity during the upcoming season. In contrast, within the breeding season, higher levels of stress were associated with greater parental investment. My results also suggest correlations between stress and environmental conditions, such as sea surface temperature, and individual-level characteristics, such as sex and body mass.

These results provide new insight regarding when Kittlitz’s murrelets may make breeding decisions and how stress levels and food availability might influence those decisions. Kittlitz’s murrelets, like other seabirds, are highly visible top predators in the marine environment. Therefore, the response of Kittlitz’s murrelets to environmental conditions may represent not only the responses of other predators that rely on similar resources, but also may represent the condition of the marine environment. These results emphasize the need for continued research to understand the mechanisms linking stress physiology, foraging ecology, and breeding ecology of the Kittlitz’s murrelet, which could be used to inform management and conservation of this and similar species. Moreover, this study also indicates the importance of the development, exploration, and validation of new monitoring methods that allow for new insights into little-studied population processes.

**CONCLUSIONS**

The goal of this thesis was to evaluate, improve upon, and explore new methods for monitoring rare and elusive species throughout the year. When conducting any monitoring program, it is important to test and validate the methods being used and their underlying assumptions. This is especially critical when monitoring small populations, which biases due to assumption violations may disproportionately affect. Moreover,
exploration of new, cost-effective sampling methods will be essential for continued monitoring efforts into the future as budgets shrink while the number of species of conservation concern grows.
**LITERATURE CITED**


CHAPTER 2: TESTING FACTORS INFLUENCING IDENTIFICATION RATES OF TWO SIMILAR SPECIES DURING ABUNDANCE SURVEYS

ABSTRACT

The Kittlitz’s murrelet (Brachyramphus brevirostris) is a small seabird endemic to Alaska and eastern Russia. During the last 2 decades, apparent population declines occurred across parts of the species’ Alaskan range. However, the reliability of these declines has been called into question due in part to uncertainty and variability in species identification. I conducted a field experiment to quantify misidentification and non-identification (i.e. incomplete identification) rates of Kittlitz’s murrelets and the morphologically similar marbled murrelets (B. marmoratus) during abundance surveys and evaluate the relative impacts of environmental and observational factors on each. I applied these results to previously-collected survey data to measure potential bias on abundance estimates induced from varying identification rates. Overall, the average misidentification rate during the field experiment was 0.032 (SE = 0.004) with observer experience explaining most of the observed variation. Abundance estimates adjusted for uncertainty in species identification reflected little bias. The overall non-identification rate was much higher, however, than misidentification (0.21, SE = 0.01). Non-identification rates increased with greater observation distance, in choppy sea states, and when murrelets exhibited diving behavior. Identification rates decreased with increased observer experience and when murrelets exhibited flushing behavior. Because observer experience was an important driver of both misidentification and non-identification rates, I stress the importance of conducting rigorous observer training before and during surveys to increase confidence in species identification.
INTRODUCTION

Detecting changes in population abundance forms the foundation for most wildlife monitoring programs. However, robust estimation of population abundance can be challenging when species are rare, elusive, or inhabit remote areas. A common assumption of most abundance estimation methods is that all observed individuals are correctly identified (e.g., Buckland et al. 2001). However, this may not be a valid assumption, especially for circumstances in which morphologically similar species overlap in range.

Misidentification of species is a pervasive, though often overlooked, issue for wildlife monitoring programs (Bart 1985, Simons et al. 2007, McClintock et al. 2010, Conn et al. 2013). For example, Hull et al. (2010) found that observers misclassified 23% of juvenile Cooper’s hawks (*Accipiter cooperii*) as juvenile sharp-shinned hawks (*A. striatus*) at a raptor migration watch site. Further, expert observers misidentified 5% of anuran call survey observations under simplified field conditions (McClintock et al. 2010). If species identification errors are not properly accounted for, bias may be introduced into abundance and trend estimates (Simons et al. 2007, Conn et al. 2013), limiting managers’ ability to make informed decisions or implement effective conservation actions. Accounting for errors in identification is especially important for species that co-occur in unequal proportions but are equally likely to be misidentified. In this circumstance, misidentification will disproportionately affect the less abundant species by artificially inflating abundance estimates (Kirchhoff 2011, Conn et al. 2013). Just 1% misidentification of each species in a skewed hypothetical population consisting of 2% Species A and 98% Species B could result in a 48% increase in the abundance
estimate of Species A but only a 1% change in the estimate of Species B (Kirchhoff 2011). Because conservationists usually are more interested in the less abundant species, misidentification-induced bias could have potentially large implications on our ability to effectively manage and conserve small populations. 

One method that can minimize potential misidentification is to identify individuals to the lowest taxonomic unit for which positive identification is certain (hereafter, “non-identification”; Buckland et al. 2001). For example, non-identification of individuals is common in fish (e.g., Petitgas et al. 2003), reptile (e.g., Parente et al. 2006), cetacean (e.g., Conn et al. 2013), and avian (e.g., Hoekman et al. 2011) surveys. However, the resulting variable, and sometimes large, proportion of “unidentified” individuals results in less precise estimates of species abundance, hindering clear interpretation of species-specific trends and complicating the comparison of results across space and time.

Although allowing for non-identification of individuals during surveys reduces the risk of misidentification errors, misidentification may not be completely eliminated. Therefore, quantification of both the misidentification rate and then non-identification rate and the environmental and observations factors influencing each is critical for accurate interpretation of abundance and trend estimates, particularly for rare species.

I examined misidentification and non-identification rates of Kittlitz’s (Brachyramphus brevirostris) and marbled (B. marmoratus) murrelets during at-sea abundance surveys along coastal Alaska. Over the last 20 years, apparent population declines occurred throughout a few core areas of the Kittlitz’s murrelet’s Alaskan range (Kuletz et al. 2011a, b, Piatt et al. 2011), although causes of the declines remain unclear.
Recently, both the magnitude and reliability of the declines have been called into question due to issues related to species identification and the quality of historical estimates (Day 2011, Hodges and Kirchhoff 2012, Kirchhoff et al. 2014). Due to its extreme and dispersed nesting strategy (Day et al. 1999), boat-based surveys conducted at sea are the most efficient method for monitoring the population abundance of this species (Drew and Piatt 2008, Day 2011). However, abundance and trend estimation for the Kittlitz’s murrelet have been complicated by the high variation in the number of individuals present in survey areas during the breeding season and changes in survey objectives, designs, and methods across time and survey sites (Day 2011, Kirchhoff 2011, summarized in USFWS 2013). For example, earlier surveys tended to use fixed-width strip transects and focus on recording all marine wildlife (Kirchhoff 2011). Further, less emphasis was given to species-specific identification, thus historical surveys included large proportions of murrelets that were unable to be identified to the species level (Day 2011).

Additional complications for trend and abundance interpretation of Kittlitz’s murrelet have stemmed from the overlap in range along coastal Alaska of the marbled murrelet, a morphologically similar and more abundant congener. These species are comparable in size, shape, coloration, and behavior. Due to their similarities and spatial overlap, marbled murrelets are surveyed concurrently with Kittlitz’s murrelets. A keen observer can discern the Kittlitz’s from the marbled murrelet by noting several key features: the relatively shorter bill and neck lengths of the Kittlitz’s murrelet, the rufous-brown flecking in the plumage of the marbled murrelet, and the white outer-tail feathers of the Kittlitz’s murrelet, which are only visible when taking flight off the water. These
distinguishing characteristics can be difficult to detect at large distances or under variable light and sea conditions. As a result, Kittlitz’s and marbled murrelets are potentially subject to both misidentification and non-identification during surveys.

In nearly all areas where these species overlap, species compositions are highly skewed, with marbled murrelets greatly outnumbering Kittlitz’s. Thus, misidentification-induced bias of abundance estimates would be expected to disproportionately affect the abundance estimates of Kittlitz’s murrelets, the rarer species. Further, varying proportions of murrelets are only identified to the genus level (\textit{Brachyramphus}; “unidentified”) during surveys (Day 2011), adding additional uncertainty to abundance and trend estimates. For example, the proportion of unidentified murrelets recorded during abundance surveys across the Kittlitz’s murrelet’s range has varied from 0.00–0.89 (Kuletza et al. 2011b, Kissling et al. 2011, summarized in Day 2011). During analysis, this proportion of unidentified murrelets typically is either withheld from species-specific abundance and density estimates, which in some cases may bias estimates low, or allocated to the species level (Day 2011). However, because the methodology and the spatial scale at which this allocation occurs (study area: e.g., Hoekman et al. 2014, strata: e.g., Kendall and Agler 1998, or transect: e.g., Aritmsu et al. 2010) vary among study areas, it is difficult to compare results across space and time (Day 2011).

Despite the high potential for misidentification of \textit{Brachyramphus} murrelets during surveys, this issue has mostly been ignored. When combined with non-identification, misidentification could muddle accurate interpretation of trend estimates.
and compromise researchers’ ability to detect changes in Kittlitz’s murrelet population abundance, hindering conservation of the species.

I conducted a field experiment to quantify misidentification and non-identification rates of *Brachyramphus* murrelets during abundance surveys carried out at sea and to identify the environmental and observational factors influencing those rates. I predicted that misidentification and non-identification would increase with greater observation distances (m), lower observer experience levels, rougher seas (Beaufort scale), sunny and rainy weather conditions, larger murrelet group sizes, when murrelets exhibited evasive diving behavior, and in mixed-species groups. I then applied the results of the field experiment to previously collected at-sea survey data to measure potential bias in abundance estimates resulting from varying identification rates and to evaluate different methods of allocating unidentified *Brachyramphus* murrelets to the species level. The overall goal of the latter objective was to determine the appropriate spatial scale at which the allocation should occur to facilitate the interpretation and comparability of abundance estimates that are used to estimate population trend.

**METHODS**

**Field Methods**

I conducted the field experiment in Glacier Bay National Park and Preserve, Alaska (58.5° N, 137° W; Figure 2-1), 13–18 July 2013, when most abundance surveys for this species in Alaska are completed (Day 2011). Glacier Bay is a deep, narrow fjord located in southeastern Alaska with roughly 3,560 km² of marine surface area. Similar to most other areas within the Kittlitz’s murrelet’s range, marbled murrelets greatly outnumber Kittlitz’s in Glacier Bay, with the most recent population estimates being 7,210 (SE =
2,046) Kittlitz’s murrelets and 84,428 (SE = 15,394) marbled murrelets (Hoekman et al. 2014). Within the bay, I confined the field experiment to the Sitakaday Narrows and the Beardlsee Islands where *Brachyramphus* murrelets occur in sufficient numbers to conduct the experiment efficiently (Hoekman et al. 2014).

The field experiment followed the at-sea, distance sampling survey protocol outlined in Kissling et al. (2007) with minor adjustments. Prior to beginning the field experiment, I trained 6 surveyors of varying experience (range 0–5 years) in *Brachyramphus* murrelet identification. I encouraged all surveyors to identify murrelets to the species level, while also providing them the option of recording murrelets to the genus level, or as “unidentified murrelets.” Four people participated in the field experiment at the same time: 2 surveyors, 1 photographer, and the boat pilot. I rotated surveyors throughout the experiment to ensure each surveyor recorded observations under the full range of field conditions. Before each trial (each replicate of the experiment), the surveyors chose a group of murrelets on the water and recorded the estimated distance of the group from the survey vessel (m), Beaufort sea state (3 categories: glossy, rippled, choppy), weather state (3 categories: < 50% cloud cover, > 50% cloud cover, light rain/mist), murrelet group size, and murrelet behavioral response (3 categories: loafing, flushing, diving) of each individual within the group. After noting these initial covariates, surveyors made independent observations of the species of each individual murrelet within the group. The boat pilot then approached the group with the vessel at standard survey speed (< 10 km/hr) while the surveyors independently recorded updated observations at 20–40 m intervals. Throughout the entire process, the photographer took up-close photographs of the selected murrelet group, making an effort
to keep all individuals within each frame. I limited group size to a maximum of 4 individuals to facilitate capturing all birds in each image. After completing the field experiment, I identified the true species membership of each recorded individual using the photographs, which I compared against the recorded observations of the surveyors to determine accuracy. I considered correct identification for each individual within the group separately, thus identification had a binomial outcome (misidentification analysis: 0 = incorrect, 1 = correct; non-identification analysis: 0 = unidentified, 1 = identified).

I applied the results from the field experiment to at-sea survey data collected in nearby Icy Bay, Alaska (60º N, 141.4º W; Figure 2-1), 7–9 July 2012. Icy Bay consists of a shallow outer bay, deep inner bay, and four radiating glacial fjords, each with an active tidewater glacier (Barclay et al. 2006). The marine surface area of Icy Bay is ~263 km², although, as a result of heavy ice floes and ice bergs, only ~120 km² is open water that can be surveyed. In contrast to most other survey areas across their range, Kittlitz’s murrelets in Icy Bay consistently outnumber marbled murrelets (Kissling et al. 2011), thus observer expectancy bias in this area would be more prevalent in favor of Kittlitz’s than marbled murrelets. Initially, I planned to conduct the identification field experiment in Icy Bay, but due to logistical constraints, I completed the field experiment in Glacier Bay. Thus, for the purposes of assessing bias in abundance estimates due to varying identification rates, I assumed identification rates estimated in Glacier Bay were applicable to Icy Bay. I believe this was reasonable because of the similarities between the two study areas and the survey conditions experienced in each area.

I conducted at-sea surveys in Icy Bay following the protocol outlined in Kissling et al. (2007), the same protocol used for the field experiment. Briefly, 2 surveyors
recorded all *Brachyramphus* murrelets within 300 m in front and to an unlimited distance on either side of the boat. Along with each observation, surveyors recorded the perpendicular distance of the murrelet group from the transect line (m), group size, and environmental variables, such as sea and weather state. During surveys, Icy Bay is subdivided into 2 geographic strata, Main Bay and Taan Fjord, each with pelagic transects running perpendicularly to the shoreline. Two observers surveyed 1 stratum each day; therefore, it took 2 days to complete a full survey of the bay. One observer had 5 years of previous survey experience, whereas the other observer had no murrelet survey experience but also participated in the Glacier Bay field experiment. During this survey, the average group size was 1.5 (SD = 0.9) and the maximum group size was 7 (n = 1); therefore, I do not expect limiting the group size to 4 individuals during the field experiment caused bias in identification rates.

**Statistical Methods**

I performed all analyses using R version 3.0.3 (R Core Team 2014) and program Distance version 6.0 (Thomas et al. 2009). I used Akaike’s Information Criterion (AIC, Akaike 1973) to select the best model of the candidate model set and assessed model fit via inspection of residuals.

**Misidentification analysis and application.** I calculated misidentification rates for the entire field experiment, each experience level (0–5 years), and for each species (Kittlitz’s or marbled). I then developed generalized linear mixed models (GLMMs) with a binomial error structure and a random effect for group to evaluate the relative contribution of explanatory variables on species misidentification (Hosmer and Lemeshow 2000). Variables included in the models were sea state, weather state,
observation distance, observer experience, murrelet group size, murrelet behavior, and whether or not the group was composed of mixed species. For this analysis, I only included observations of birds identified to the species level (no unidentified observations).

Using the most supported model from the misidentification analysis in Glacier Bay, I predicted the probability that Brachyramphus murrelets identified during the survey in Icy Bay were correctly identified. I then re-calculated Kittlitz’s and marbled murrelet abundance estimates using the predicted probabilities of correct identification and compared the adjusted estimates to the unadjusted estimates. I calculated the variance using the delta method (Seber 1982) and assigned unidentified birds to the species level based on the overall proportion observed during the survey.

Non-identification analysis and allocation. I calculated non-identification rates for the entire field experiment, each level of experience, and for each species. I then modeled the relative contribution of the recorded covariates on non-identification of murrelets during at-sea surveys using GLMMs with a binomial error structure, including random intercepts for each observer and murrelet group to account for observer and group correlations (Hosmer and Lemeshow 2000). I evaluated the same explanatory variables as in the misidentification analysis; however, I included data from all murrelets recorded during the field trials (even those identified incorrectly). I then used the results from the best-fit model to predict the conditions in which observers were unlikely to identify murrelets to the species level.

Using the survey data from Icy Bay, I developed and compared 4 strategies to allocate unidentified murrelets to the species level. Each allocation method differed in
either the spatial scale at which I estimated abundance or the spatial scale at which I allocated unidentified murrelets to a species. For my first strategy (“Global”), I estimated the total *Brachyramphus* murrelet abundance and encounter rate by geographic stratum (Main Bay and Taan Fjord) and then prorated unidentified murrelets to species based on the total proportion of each species observed during the entire survey. My second strategy (“Strata”) was similar to Global except that unidentified birds were allocated to the species level based on the proportion observed per stratum. For my third method, (“Total Transect”) I estimated abundance and encounter rate by transect and allocated unidentified murrelets based on the overall proportion of each species observed during the entire survey. Lastly, I developed a strategy (“Individual Transect”) similar to the Total Transect scenario, except I apportioned unidentified murrelets based on the proportion of each species observed per transect.

For all 4 strategies, I first fit a global, hazard-rate detection function by pooling together all *Brachyramphus* murrelet observations recorded during the survey. The detection function estimates the probability that an object (in this case a group of murrelets) at a given perpendicular distance from the transect line is detected (Buckland et al. 2001). I estimated the variance using the delta method (Seber 1982). For the Global and Strata methods, I estimated the variance empirically; however, for the Total and Individual Transect strategies I assumed a Poisson variance structure due to the lack of spatial replication (Buckland et al. 2001). I assessed the results based on the calculated variance estimates and their associated assumptions.

Finally, I quantified the number of identified murrelets necessary to have confidence in the species-specific ratio that is used to inform the allocation of
unidentified murrelets to the species level. I calculated the binomial probability variance over a range of species proportions (i.e. probability of success) and identification counts (i.e. number of successes). Lower variance values indicated higher precision and confidence in the species proportion used for unidentified murrelet allocation.

RESULTS

Misidentification Analysis and Application

The misidentification rate for the field experiment was 0.032 (SE = 0.004, n = 81 of 2,228 observations on 183 murrelet groups), with experience-specific misidentification rates ranging from 0.00–0.05 (Figure 2-2). Observers misidentified Brachyramphus murrelets at similar rates (Kittlitz’s = 0.034, SE = 0.004; marbled = 0.037, SE = 0.010; Table 2-1), indicating there were limited species-specific differences in identification. Observer experience best explained the variation in misidentification (Table 2-2A). Results from the most supported model indicated that misidentification decreased as experience increased (β = 0.90, SE = 0.17; AUC = 0.61).

During the Icy Bay survey, the probability of correct identification for each individual murrelet was estimated at essentially 1 for both the inexperienced and experienced observer. Adjusted abundance estimates based on the inexperienced observer resulted in a change of -0.01% for Kittlitz’s murrelets and 0.08% for marbled murrelets from the unadjusted estimates, while adjusted estimates based on the more experienced observer led to a -0.0001% and 0.002% change.
Non-Identification Analysis and Allocation

The overall non-identification rate during the field experiment was 0.21 (SE = 0.01; \( n = 650 \) of 3,082 observations on 191 murrelet groups) with experience-specific non-identification rates ranging from 0.10–0.48 (Figure 2-2). Observers classified marbled murrelets proportionally more than Kittlitz’s murrelets (Kittlitz’s = 0.18, SE = 0.01; marbled = 0.22, SE = 0.02; \( p \)-value = 0.001).

Observer experience, choppy sea state, distance, behavior, and the interaction between sea state and distance best explained the observed variation in non-identification during the field experiment with high predictive power (Table 2-2B; AUC = 0.85). Results from the most supported model indicated that non-identification decreased with increased observer experience and when murrelets exhibited flushing behavior, and increased in choppy sea states and with increased observation distances (Table 2-3). Non-identification also seemed to increase when murrelets demonstrated diving behavior; however, the correlation with this variable was not significantly different from zero (Table 2-3). Using this fitted model, the distance at which individual observers were equally likely to identify a murrelet to the species level or not varied from ~140–280 meters (Figure 2-3).

The 4 unidentified \textit{Brachyramphus} murrelet allocation strategies resulted in similar total \textit{Brachyramphus} and species-specific abundance estimates, but variable estimates of variance. There were minimal differences between the Global and Strata strategies (Table 2-4), because the proportion of \textit{Brachyramphus} murrelets in each stratum of Icy Bay was approximately equal during the survey (Main Bay = 15 Kittlitz’s: 1 marbled, Taan Fjord = 12 Kittlitz’s: 1 marbled). Allocating unidentified murrelets by
the proportion observed per transect resulted in a 4% decrease in Kittlitz’s murrelet abundance and a 65% increase in marbled murrelet abundance (Individual Transect) compared to allocation by the overall proportion (Total Transect; Table 2-4).

The binomial probability variance over a range of species proportions and identification counts displayed a wide range depending on the skew in the species ratio and the number of identified individuals (Figure 2-4). High variation was associated with lower numbers of identified birds and more balanced species ratios. Low variation, thus higher confidence in the observed proportion, was associated with higher numbers of identified individuals and less balanced species ratios. When species ratios were highly skewed, variation was low with as few as 20–30 identified individuals. However, when species ratios were approximately equal, identification of 40–60 individuals resulted in higher confidence in the observed ratio used to inform species-specific allocation of unidentified murrelets.

DISCUSSION

Threatened and endangered species create a unique challenge for monitoring and management. Rarity itself restricts quick and simple collection of data. Therefore, managers must often make policy or management decisions despite large uncertainty. Understanding the variation in misidentification and non-identification rates of individuals during monitoring efforts is critical to accurate interpretation of abundance and trend estimates, particularly for rare species.

In contrast to many recent studies (e.g., Hull et al. 2010, McClintock et al. 2010, Shea et al. 2011), misidentification was low in this system and did not bias abundance estimates. While I only found a relationship between misidentification and observer
experience, this may not necessarily mean relationships with observation distance, sea state, weather state, group size, or murrelet behavioral responses do not exist.

Misidentification was a rare event during the field experiment, and therefore I may not have a large enough sample size to evaluate the significance of these variables fully, despite a large number of observations \((n = 2,228\) observations on 183 murrelet groups). Regardless, the infrequency of misidentification and the resulting lack of statistical power to detect these relationships clarify and support *Brachyramphus* murrelet abundance estimates from recent history that used similar survey methodologies.

However, these estimates of misidentification may be biased low for a number of reasons. First, I lack experimental data for observations made during rainy conditions, which I would expect to increase misidentification rates. Though coastal Alaska is characterized by high precipitation and surveys often are conducted in the rain, the 6-day period during which I conducted the field experiment was unusually sunny with no precipitation (as was the entire summer of 2013), so I was unable to test this hypothesis. Second, observers focused on a single murrelet group at a time during the field experiment. During surveys, depending on the density of murrelets, observers often have to make very rapid identification decisions and then move on or risk missing groups on or close to the survey line. Allowing only quick glimpses at each murrelet group could increase identification errors. Finally, misidentification could be lower due to observer expectancy bias. The observers participating in the field experiment knew they were being evaluated for accuracy. Mills and Knowlton (1989) demonstrated that observers performed better when they knew they were being tested compared to when they were
unaware they were being tested. Given the setup and planning for the current study, I was unable to avoid this issue.

Because these misidentification rates may be low, misidentification could potentially have larger impacts on abundance estimates than I was able to demonstrate in the current study. However, these results do provide insight into the factors contributing to misidentification of *Brachyramphus* murrelets and indicate methods for minimizing the risk of misidentification during surveys. Observer experience best explained variation in misidentification rates. Therefore, these results emphasize the importance of rigorous observer training for increasing consistency and confidence in species identification across survey areas.

The non-identification rate across all observers was well within the range of rates previously reported for murrelet surveys (range: 0.00–0.89; Day 2011). As expected, less experienced observers recorded individuals as unidentified at higher rates compared to more experienced observers, and non-identification rates increased with observation distance. The maximum distance tested during the field experiment was 250 m, so inference beyond that distance is limited. Behavioral response was also important for predicting whether or not an observer recorded an individual murrelet as identified. As murrelets flush off the water and take flight they fan out their tail feathers for just a few seconds. During this time, it is possible for an observer to see the white outer-tail retrices of the Kittlitz’s murrelet (marbled murrelets have only brown retrices). Seeing the flash of white on the tail is the easiest and most definitive way to confirm species identification in the field, which the results of the field experiment reflect.
It is difficult to assess the best approach for allocating unidentified murrelets to the species level because we do not and cannot know truth. My results suggest that murrelets should be allocated to species based on the proportion observed per stratum (Strata) if the survey site is subdivided into geographic strata. If not, I recommend apportioning unidentified murrelets based on the overall species ratio observed during the survey. In this analysis, the Global and Strata results were essentially the same because the proportion of murrelets observed within each stratum was almost equivalent. However, this may not always be the case. Kittlitz’s and marbled murrelets generally are distributed differently within a study area depending on habitat characteristics (Day et al. 1999, 2003). For example, Kittlitz’s murrelets prefer highly turbid glacial- or glacial-stream-affected habitat, whereas marbled murrelets prefer glacial-unaffected habitat without ice cover (Day et al. 2003). Therefore, species proportions across strata potentially could be very different, depending on the habitat characteristics of the survey site.

I do not recommend allocation of unidentified murrelets based on the proportion observed per transect for 2 reasons. First, the variance estimated from this method is likely underestimated because murrelets are not distributed randomly (Buckland et al. 2001), but instead are distributed relative to the habitat characteristics of the study site (Day et al. 1999, 2003). Thus, this method provides a false level of confidence in the estimated abundance. Second, apportioning murrelets based on the proportion observed per transect may use too fine of a spatial scale. For example, this method could not be used if the only observations on a given transect were recorded as unidentified murrelets.
An alternative strategy that may be considered for future work is to assign unidentified murrelets to species based on the species ratio observed within a certain distance from the vessel. Because the probability of identification declines with increasing distance, this method would ensure that only reliable identifications are used to inform species-specific abundance estimates. I did not include this strategy in the current analysis because, during the Icy Bay surveys, only the perpendicular distance of the murrelet group from the transect line were recorded, not the angle and distance of the murrelet group from the survey vessel, which is more reflective of the method used in the field experiment.

I pooled all observations for Kittlitz’s and marbled murrelets for the regression analyses due to small sample sizes; although environmental and observational factors may drive variation in identification rates of Kittlitz’s and marbled murrelets differently. However, because the 2 species are quite behaviorally and morphologically similar, the mechanisms driving misidentification and non-identification are likely the same or at least very similar. Additionally, although Kittlitz’s and marbled murrelets were unidentified at slightly different rates, it is difficult to assess whether these differences are related to species-specific traits or to the skewed sample sizes for each species due to the differences in the population sizes of Kittlitz’s and marbled murrelets in Glacier Bay (7,210 Kittlitz’s murrelets, 84,428 marbled murrelets; Hoekman et al. 2014). If there are indeed species-specific differences in identification, these results would suggest that allocation based on observed proportions may not be appropriate. However, research opportunities exist to further evaluate this issue, ideally within a system in which the species ratios are flipped.
I provide the following suggestions for future Kittlitz’s murrelet survey efforts:
First, modify the scanning width (the distance in front and to either side of the survey vessel out to which observers record murrelets) depending on observer experience level and sea state for a given survey. Results from the non-identification analysis suggest observers are unlikely to identify a murrelet to the species level at distances greater than ~150 m for less experienced observers and distances greater than ~250 m for more experienced observers. With inexperienced observers or rough seas, it would be prudent to focus efforts on distances closer to the vessel to ensure all birds are detected on or close to the survey line, and also to promote higher rates of identification. Second, to have high confidence in the species proportions used to inform species-specific abundance estimates, a sufficient number of individuals must be recorded reliably to the species level (Figure 2-4). In an area with a heavily skewed species composition (e.g., 0.85), identification of ~30 murrelets would result in a robust species proportion, while in an area with a more balanced species composition (e.g., 0.50), identification of ~60 individuals is necessary. Finally, observer experience is an important driver of both misidentification and non-identification of Brachyramphus murrelets. It is also the factor researchers are most able to control and improve. Conducting rigorous and high quality observer training before and during surveys is the best way to increase confidence in species identification. Methods similar to those used in the field experiment could be modified to evaluate observer training and determine whether observers are qualified to perform surveys. Further, development of a standardized training program would provide consistency and quality control across surveys and improve comparability of results across the range of the Kittlitz’s murrelet.
Although the methods used for this field experiment were tailored to the *Brachyramphus* murrelet study system, these techniques could be modified for use in any system, marine or terrestrial, to quantify identification rates and identify the factors influencing those rates. Results may reveal important patterns or relationships that can provide guidelines for adjusting survey protocols to increase confidence in species identification and increase the precision of abundance estimates.

**LITERATURE CITED**


Figure 2-1. Map identifying the location of the *Brachyramphus* murrelet field experiment, Glacier Bay National Park and Preserve, July 2013, and abundance surveys, Icy Bay, Alaska, July 2012.
Figure 2-2. Misidentification and non-identification rates (± SE) of *Brachyramphus* murrelets based on the experience levels (0, 1, 2, and 5 years) of 6 observers, Glacier Bay, Alaska, July 2013.
Figure 2-3. The probability of observers of varying experience levels (0, 2, and 5 years) identifying a *Brachyramphus* murrelet to the species level under 2 sea states (glossy, choppy) and 3 behavioral responses (loafing, flushing, diving) across a range of observation distances (m), Glacier Bay, Alaska, July 2013. Dashed horizontal lines delineate a 50% probability of species identification.
Figure 2-4. The binomial probability variance for a range of species ratios and number of individuals identified to the species level. Cooler colors indicate lower variance and higher confidence in the resulting proportions, while warmer colors indicate higher variance and less confidence in the proportions.
Table 2-1. Contingency table indicating the number of murrelets correctly and incorrectly identified (misidentified) during the *Brachyramphus* murrelet identification field experiment in Glacier Bay, Alaska, July 2013.

<table>
<thead>
<tr>
<th>Actual</th>
<th>Predicted</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Kittlitz’s</td>
<td>Marbled</td>
<td></td>
</tr>
<tr>
<td>Kittlitz’s</td>
<td>340</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Marbled</td>
<td>69</td>
<td>1807</td>
<td></td>
</tr>
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</table>
Table 2-2. Model selection results for the *Brachyramphus* murrelet identification analyses, Glacier Bay, Alaska, July 2013. The most supported covariates for each analysis were: A) observer experience (0–5 yr), and behavior (loafing, flushing, diving); B) observer experience, choppy sea state (Beaufort 2: small chop, waves 0.3–0.6 m), distance of murrelets from the vessel (m) and behavior.

<table>
<thead>
<tr>
<th>A. Models: Misidentification</th>
<th>ΔAIC</th>
<th>K&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observer Experience</td>
<td>0.00</td>
<td>3</td>
<td>370</td>
</tr>
<tr>
<td>Observer Experience + Behavior</td>
<td>1.13</td>
<td>5</td>
<td>367</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>B. Models: Non-Identification</th>
<th>ΔAIC</th>
<th>K&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observer Experience + Choppy Sea State * Distance + Behavior</td>
<td>0.00</td>
<td>9</td>
<td>1759</td>
</tr>
<tr>
<td>Choppy Sea State + Distance * Observer Experience + Behavior</td>
<td>0.63</td>
<td>9</td>
<td>1760</td>
</tr>
<tr>
<td>Observer Experience + Choppy Sea State * Distance + Flushing</td>
<td>1.68</td>
<td>8</td>
<td>1763</td>
</tr>
<tr>
<td>Choppy Sea State + Distance * Observer Experience + Flushing</td>
<td>1.84</td>
<td>8</td>
<td>1763</td>
</tr>
</tbody>
</table>

<sup>a</sup>K = Number of Parameters
Table 2-3. Coefficient estimates for the most supported *Brachyramphus* murrelet non-identification model. All terms in the model were important, except for diving behavior.

Glacier Bay, Alaska, July 2013.

<table>
<thead>
<tr>
<th>Fixed Effects</th>
<th>Estimate</th>
<th>SE</th>
<th>z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>0.81</td>
<td>8.91</td>
</tr>
<tr>
<td>Observer Experience (yr)</td>
<td>0.80</td>
<td>0.29</td>
<td>2.74</td>
</tr>
<tr>
<td>Choppy Sea State</td>
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<td>0.81</td>
<td>-3.46</td>
</tr>
<tr>
<td>Distance (m)</td>
<td>-0.045</td>
<td>0.003</td>
<td>-18.41</td>
</tr>
<tr>
<td>Flushing Behavior</td>
<td>1.84</td>
<td>0.46</td>
<td>4.03</td>
</tr>
<tr>
<td>Diving Behavior</td>
<td>-0.57</td>
<td>0.29</td>
<td>-1.95</td>
</tr>
<tr>
<td>Choppy Sea State * Distance</td>
<td>0.013</td>
<td>0.006</td>
<td>2.19</td>
</tr>
</tbody>
</table>
Table 2-4. I allocated unidentified murrelets to the species level (K = Kittlitz’s, M= marbled) based on the overall proportion observed during the survey (Global and Total Transect), the proportion per stratum (Strata), or the proportion observed per transect (Individual Transect). I estimated abundance (N) and encounter rate by stratum (Global, Strata) or by transect (Total and Individual Transect). All 4 strategies all resulted in similar total abundance estimates, but variable estimates of variance. Icy Bay, Alaska, 2012.

<table>
<thead>
<tr>
<th></th>
<th>( \hat{N} ) (Total)</th>
<th>SE (Total)</th>
<th>( \hat{N} ) (K)</th>
<th>SE</th>
<th>( \hat{N} ) (M)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Global</td>
<td>1144</td>
<td>348</td>
<td>1071</td>
<td>327</td>
<td>73</td>
<td>36</td>
</tr>
<tr>
<td>Strata</td>
<td>1144</td>
<td>347</td>
<td>1071</td>
<td>328</td>
<td>73</td>
<td>36</td>
</tr>
<tr>
<td>Total Transect</td>
<td>1126</td>
<td>135</td>
<td>1054</td>
<td>129</td>
<td>72</td>
<td>30</td>
</tr>
<tr>
<td>Individual Transect</td>
<td>1126</td>
<td>135</td>
<td>1007</td>
<td>127</td>
<td>119</td>
<td>82</td>
</tr>
</tbody>
</table>
CHAPTER 3: THE INFLUENCE OF OCEAN PRODUCTIVITY ON STRESS AND PARENTAL INVESTMENT IN A LONG-LIVED SEABIRD

ABSTRACT

Seabird demographic rates are sensitive to changes in prey resources. Thus, it is important for managers to understand the environmental conditions experienced by seabirds throughout the year. Direct measures of prey abundance and availability are difficult to assess. Instead, physiological measurements can be used to understand environmental conditions experienced by seabirds throughout the year, from which population demographics may be predicted or inferred. I measured corticosterone (CORT, the primary avian stress hormone) in both plasma and feather samples and prolactin (PRL, involved in parental expression) in plasma samples from Kittlitz’s murrelets (Brachyramphus brevirostris) and evaluated their relationships with breeding propensity and ocean productivity metrics (i.e. food availability) during different parts of the year. High feather CORT during the pre- and post-breeding periods reflected lower breeding propensity in the subsequent breeding season. Additionally, higher pre-breeding season CORT levels were associated with lower spring sea surface temperatures, while higher CORT in the late-breeding season reflected earlier capture dates, longer time-spans between capture and processing, and lower body masses (g). Circulating plasma CORT concentrations in May best explained variation in PRL during the early breeding season, while sex of the individual and year were important parameters for explaining PRL during the late breeding season. These results provide new insight regarding when Kittlitz’s murrelets may make breeding decisions and how stress may influence this decision. Further, these results support the use of physiological measure for examining tradeoffs between stress and future reproduction and emphasize the need for continued
research to identify the mechanisms linking the stress physiology, foraging ecology, and breeding ecology of the Kittlitz’s murrelet and other species that depend on similar resources.

**INTRODUCTION**

Most free-living animals inhabit environments with patchily distributed resources (Johnson et al. 1992). This is especially true for seabirds that forage in the marine environment, where prey availability depends on a multitude of ephemeral abiotic and biotic factors (e.g., light and nutrient availability, sea surface and surface air temperature, sea level pressure, surface winds, upwelling strength, species composition, and phenology; Behrenfeld et al. 2006, Brown et al. 2011). Variability in prey has been shown to have large influences on seabird populations (e.g., Becker and Beissinger 2006, Lee et al. 2007), particularly on nesting seabirds that must rely on prey resources and foraging locations that are within commuting distance of their nest. When prey resources are scarce or highly variable, restriction in the foraging range of nesting seabirds can have cascading effects that reduce reproductive success (Suryan et al. 2002). Evidence also suggests that poor environmental conditions experienced outside of the breeding season can carry-over into other parts of the year, negatively influencing survival and subsequent breeding decisions (Marra and Holberton 1998, Sorenson et al. 2009, Dale and Leonard 2011). Thus, understanding the environmental conditions experienced by seabirds within and outside of the breeding season may help clarify seabird demographic rates and population processes.

The glucocorticoid hormone corticosterone (hereafter, CORT) is a principal mediator of allostasis in vertebrates, functioning to activate energy stores and adjust
physiology and behavior so an individual can cope with predictable (e.g., migration, breeding) and unpredictable (e.g., low food availability, inclement weather) stressors successfully (for review, see McEwen and Wingfield 2003, Landys et al. 2006). Stressors (factors that disturb homeostasis, or maintenance of internal equilibrium) activate the hypothalamic-pituitary-adrenal axis, which rapidly synthesizes and secretes CORT from the adrenal gland into the blood stream (Breuner 2010). Baseline circulating plasma CORT levels maintain homeostatic energetic balance (Landys et al. 2006), while stress-induced CORT concentrations trigger physiological and behavioral responses to environmental challenges (Sapolsky et al. 2000). The stress response prompts a number of physiological and behavioral adjustments, such as the breakdown of proteins, generation and mobilization of glucose, suppression of the digestive, immune, and reproductive systems, reduction in parental care, and increases in food searching behaviors (Wingfield et al. 1998, Sapolsky et al. 2000).

In seabirds, CORT can provide a measure of stress resulting from limited forage availability (Kitaysky et al. 1999, 2007, Angelier et al. 2009a), an important regulator of seabird population dynamics (Lack 1966). Baseline circulating plasma CORT levels reflect an individual’s nutritional history for the previous hours or day, while acute stress-induced levels indicate the individual’s nutritional history for the previous weeks (Kitaysky et al. 2007, 2010). For example, current food availability best explained baseline CORT levels of common murres (Uria aalge), while stress-induced CORT levels reflected changes in food abundance during the previous month (Kitaysky et al. 2007). The majority of seabird studies have focused on circulating CORT in the plasma. However, CORT concentrations accumulated in feathers provide an integrative measure
of stress experienced by the individual for the entire period of feather growth (weeks; Bortolotti et al. 2008, Lattin et al. 2011), with higher circulating plasma CORT concentrations during feather growth correlated to increased concentrations of CORT in feathers (Lattin et al. 2011).

If stress exceeds threshold levels during the breeding season, longer-lived species such as seabirds can buffer negative impacts on their own survival by foregoing breeding in a given year or by abandoning the current breeding attempt (Drent and Daan 1980, Cam et al. 1998, Wingfield et al. 1998). In birds, this trade-off is mediated partially by CORT and the pituitary hormone prolactin (hereafter, PRL), which is responsible for the initiation and expression of parental behavior. Circulating PRL concentrations provide a measure of parental investment in the current breeding attempt (for review, see Buntin 1996, Angelier and Chastel 2009). Elevated PRL levels are associated with increased incubation behavior, chick provisioning, and nest defense (Buntin et al. 1991, Wang and Buntin 1999). Both short- and long-term stress reduce PRL concentrations (Angelier et al 2009b, Angelier and Chastel 2009, Schmid et al. 2011). For example, capture and restraint stress increases CORT while decreasing PRL in snow petrels (Pagodroma nivea; Angelier et al. 2009b). Additionally, long-term energetic constraints, such as extended fasting, depress PRL levels (Angelier and Chastel 2009). This finding suggests that analysis of PRL levels may also serve as an indicator for periods of restricted forage availability and provide insight into the impact of environmental conditions on reproductive performance of birds.

The Kittlitz’s murrelet (Brachyramphus brevirostris) is a small, diving seabird endemic to coastal Alaska and eastern Russia. Over the last two decades, apparent
population declines occurred in many areas of the species’ Alaskan range (Kuletz et al. 2001a, b, Piatt et al. 2011), although populations appear to have stabilized recently (USFWS 2013). Unlike most seabirds, the Kittlitz’s murrelet is a cryptic and dispersed nester, usually choosing nest sites on cliff ledges, bare ground, or non- or sparsely-vegetated scree slopes (Day et al. 1999, Kaler et al. 2009, Lawonn 2012). Due to this extreme nesting strategy, knowledge regarding the reproductive performance of the species remains limited; however, data from the study areas containing the majority of monitored nests indicate that breeding propensity and breeding success can be low (19–23%; USFWS 2013).

Though our understanding of the foraging ecology of the species is incomplete, stable isotope analyses ($\delta^{15}$N and $\delta^{13}$C) indicate high inter-seasonal variation in diet, presumably due to changes in prey availability throughout the year (Hatch 2011). During the pre-breeding period, murrelets feed primarily on macrozooplankton (Hatch 2011), whereas during the breeding season murrelets forage on both macrozooplankton and schooling forage fishes, such as Pacific sand lance ($Ammodytes hexapterus$), capelin ($Mallotus villosus$), and juvenile Pacific herring ($Clupea pallasi$; Day et al. 1999, Hatch 2011). Following the breeding season, Kittlitz’s murrelets seem to feed primarily on schooling fishes in offshore waters (Hatch 2011).

Similar to other seabirds, the Kittlitz’s murrelet spends the majority of the year at sea, only coming to land to nest during the breeding season (May–August; Day 1996). Following the breeding season, most North American Kittlitz’s murrelets migrate along the Alaskan coastline towards the Bering and Chukchi seas (Madison et al. 2012) and overwinter presumably along the ice edge or in open water leads in the ice in the Bering
Sea (Day et al. 1999, summarized in USFWS 2013). This pelagic lifestyle leaves Kittlitz’s murrelets largely unavailable for direct monitoring efforts for most of the year; thus, we lack information regarding environmental conditions experienced by murrelets during the non-breeding season and, particularly, how these conditions impact future survival and subsequent breeding decisions (Marra and Holberton 1998, Sorenson et al. 2009, Dale and Leonard 2011).

To address these uncertainties, I examined the relationship between stress physiology, parental investment, and breeding propensity of Kittlitz’s murrelets. I also examined the environmental factors that may influence variation in parental expression and stress throughout the year. I predicted that environmental factors indicative of lower ocean productivity conditions would be associated with higher stress and lower levels of parental investment (Kitaysky et al. 2007, 2010, Angelier and Chastel 2009, Schmid et al. 2011). I evaluated stress based on concentrations of CORT measured in stress-induced plasma and feather samples, and parental investment based on concentrations of PRL measured in plasma.

METHODS

Sample Collection

I collected blood plasma and feather samples from captured, adult Kittlitz’s murrelets during May and late July/early August (2007–2012), in Icy Bay, Alaska (60º N, 141.4º W; Figure 3-2). These are the only times of the year during which murrelets can be captured in this area due to the seasonal movements of Kittlitz’s murrelets and because night-lengths are too short at this high latitude during the intervening period (June–mid July). Murrelets were captured using the night-lighting method (Whitworth et al. 1997).
Once captured, each bird was placed into a mesh bag, which was set inside a cardboard pet-carrier and transported to a larger vessel for processing. Brood patch score (an indicator of breeding condition, 0–6; Sealy 1974) and standard morphometric measurements were recorded, and blood and 2 types of feather samples (secondary feather clips and ~4 black-tipped breast feathers) were collected from each captured murrelet. Blood was collected from the ulnar vein into a heparinized syringe and vacutainer, which was centrifuged for 10 minutes at 5000 rpm. Plasma was then pipetted off the red blood cells and stored in low temperature freezer vials. All plasma samples were frozen immediately after centrifugation. Each spring a subset of birds were fitted with VHF radio transmitters and relocated using fixed-wing aircraft for ~8 weeks during the breeding season to assess the reproductive performance of this population. Refer to Kissling et al. (In review a) for a complete description of field methods.

The Kittlitz’s murrelet molts biannually, with feathers produced over a ~2-week period (Pyle et al. 2009). Murrelets grow secondary feathers in the post-breeding period during the pre-basic molt (August–September) and they grow black-tipped breast feathers in the pre-breeding period during the partial pre-alternate molt (March–April). Therefore, collection of plasma and 2 feather types during capture enabled me to make insights regarding the population’s physiological status for 4 distinct periods of the year (Figure 3-1; Table 3-1). Although I could not compare feather to plasma levels across seasons, I evaluated individual variation within a sampling period and population variation within a sampling period across years.
Laboratory Methods

**Plasma.** I measured total circulating CORT in blood plasma samples using enzyme immunoassay kits (4 assays for all samples; Enzo Life Sciences, Farmingdale, NY, USA). I optimized the procedure following the protocol outlined in Wada et al. (2007) to a 1:20 dilution of raw plasma with 2% steroid displacement buffer. In brief, I added 4 µl 1:10 diluted steroid displacement reagent to 20 µl raw plasma and vortexed the sample. After 5 min, I added 380 µl EIA assay buffer to each sample, resulting in a final dilution of 1:20, and then added 100 µl of each sample to individual wells in triplicate. For purposes of comparison, I set up a 6 point standard curve in triplicate ranging from 15.63–20,000 pg ml⁻¹ CORT. I also included an external CORT standard of 500 pg ml⁻¹ on each plate in triplicate to measure inter-plate variation. I read the plates at 405 nm and with 595 nm correction using a Multiskan Ascent microplate reader (Thermo Scientific, Milford, MA, USA). Average intra-plate coefficients of variation ranged from 6–12%, and the inter-plate coefficient of variation was 8%.

I collaborated with the Centre d’Etude Biologique de Chizé-CNRS, France, to determine PRL levels in blood plasma samples using a heterologous competitive radio-immuno assay following the method outlined in Cherel et al. (1994). All reactants were diluted with 0.025 M barbital-bovine serum albumin buffer. Standard PRL samples ranging from 62.5–8,000 pg/25 µl and 15 µl of murrelet plasma were incubated with 250 µl labeled chicken PRL and 250 µl antibody solution at 4 ºC for 24 hr. Anti-antibody solution was added to each tube, which were then incubated for an additional day. The tubes were centrifuged, the supernatants discarded, and an automatic gamma counter (Wizard gamma counter, PerkinElmer, Waltham, MA, USA) measured the radioactivity
of the precipitate directly. The lowest detectable PRL level was 0.72 ng ml\(^{-1}\) and the intra-assay coefficient of variation was 5%. The recovery mean in samples spiked with standard PRL was 84%. The recovery mean refers to the accuracy of measuring an analyte correctly after spiking samples with a known amount of the analyte (Koch and Peters 1999). All samples were run in duplicate in a single assay.

**Feathers.** I extracted and measured CORT in breast and secondary feathers following the procedure outlined in Bortolotti et al. (2008; 3 assays for all samples). I removed the calami from all feather samples before they were measured (mm), weighed (mg), and placed into 15 ml conical tubes. Data from Lattin et al. (2011) and unpublished data from the Breuner lab indicate that length is a better standardization than weight; additionally, unpublished data from the Breuner lab suggests minimizing variation in length across feathers. Therefore, I standardized all secondary feather clips to 10 mm and used 2 breast feathers from each sampled individual (~40–50 mm total). I added 5 ml of methanol and 50 \(\mu\)l 3H-CORT (2000 cpm/50\(\mu\)l, for recoveries) to each sample and placed all capped tubes into a sonicating water bath at room temperature. After 30 min, I placed the samples into a 50 ºC water bath for an overnight incubation. The next day, I separated the methanol from the feathers using vacuum filtration and evaporated the methanol off the CORT sample with nitrogen gas. I reconstituted the remaining CORT residues into 500 \(\mu\)l phosphate-buffered saline with gelatin and refrigerated the samples overnight. After refrigeration, I ran a radioimmunoassay (RIA) on 200 \(\mu\)l of each sample, adding 100 \(\mu\)l 1:100 dilution antibody and 100 \(\mu\)l 3H-CORT (4000 cpm/100 \(\mu\)l) to all samples. I used a 9 point standard curve ranging from 7.81–2000 pg/100\(\mu\)l CORT. I included an external standard of 500 pg ml\(^{-1}\) in each RIA. I incubated the assay at 4 ºC.
overnight. I separated bound CORT from unbound CORT with the addition of dextran-coated charcoal, which I then centrifuged for 10 min at 2000 rpm after incubating for 12 min. Supernatants were poured into scintillation vials for counting. I read the samples using a Tri-Carb 2900 TR Liquid Scintillation Analyzer (PerkinElmer, Waltham, MA, USA) and adjusted concentrations using results from recoveries (mean recovery was 90%). The inter-assay coefficient of variation was 1.5% and the intra-assay coefficients of variation ranged from 4–5%.

The average mass of the 79 samples of black-tipped breast feathers used in this study (2/individual murrelet) was 2.76 mg (SE = 0.05), with a range from 1.68–4.15 mg (2009–2012). The combined feathers averaged 45.65 mm in length (SE = 0.31) and ranged from 40.00–51.00 mm. The 56 secondary feathers included in this analysis weighed 1.14 mg on average (SE = 0.03) and ranged from 0.67–1.55 mg (2010–2012).

**GIS Methods**

**Remotely-sensed data.** I used both regional and local remotely-sensed environmental indices to predict variation in hormone concentrations of Kittlitz’s murrelets throughout the year. I included 2 local indices of ocean productivity: chlorophyll a concentration (Chl-a; mg m⁻³) and sea surface temperature (SST; ° C). Chl-a provides an index of phytoplankton biomass in the ocean, which is responsible for the production of approximately half of the total net primary productivity on Earth (Behrenfeld et al. 2006). This metric was not available during the winter months (December–February) due to excessive cloud cover and polar darkness, which limits vegetal plankton growth. Sea surface temperature is another important component of marine productivity, with cooler temperatures associated with more nutrient upwelling
and greater primary productivity (Behrenfeld et al. 2006). As ocean temperatures have risen concurrently with the warming climate, both spatial and temporal shifts in ocean productivity have been documented (Moline et al. 2008, Thompson et al. 2012), which could lead to spatial and temporal mismatches between primary producers and upper trophic levels. Indeed, recent studies have indicated that as sea surface temperature increases, both seabird survival and reproduction decrease (for review, see Sydeman et al. 2012).

I included the winter average of ice extent over the northern pole (WIE) as our region-wide productivity index. In the northern latitudes, Arctic sea ice plays a key role in the structuring of the marine ecosystem. WIE in a given year can be used as a broad-scale climate index signifying whether years are warm or cool (Alexander et al. 1996, Stabeno et al. 2010). In particular, the seasonal advance and retreat of Arctic sea ice hugely impacts many aspects of the northern marine environment, including light penetration, sea temperature and salinity, heat absorbance, moisture exchange, and access to the water surface (Alexander et al. 1996). High latitude Arctic sea ice supports and sustains complex multi-trophic communities; whereas lower latitude Arctic sea ice communities must annually reestablish themselves, resulting in a spring burst of productivity. Increasing global temperatures have reduced both the area and thickness of multiyear ice, which has then been replaced with seasonal ice. This seasonal ice is much thinner, and as a result, is more easily melted. As this seasonal sea ice melts, more ocean surface is exposed, which leads to increased absorption of light and heat, creating in a positive feedback loop of ever decreasing ice and increasing ocean temperatures (Arrigo et al. 2008). Similar to sea surface temperature, changes in the timing and extent of
winter sea ice has also led to mismatches between the lower and upper trophic levels, again resulting in reduced reproductive success and abundances (Moline et al. 2008).

I obtained mean values of Chl-α and SST for the time periods and spatial extent corresponding to each area of the Kittlitz’s murrelet seasonal distributions (Figure 3-2) using the Spatial Analyst Zonal tool in ArcMap 10.0. I acquired Chl-α concentrations from the Goddard Space Flight Center OceanColor Group (http://oceancolor.gsfc.nasa.gov/) and SST values from the NASA Jet Propulsion Laboratory (http://www.jpl.nasa.gov/), and accessed the raster files using Marine Geospatial Ecology Tools (Roberts et al. 2010). I used monthly composite Level-3 MODIS-Aqua 4-km resolution data for both metrics to account for cloud cover and to obtain a relative measure of productivity for the entire time period. I obtained WIE data from the National Snow and Ice Data Center (nsidc.org).

**Seasonal distributions.** In order to identify the spatial and temporal boundaries for estimating SST and Chl-α concentrations, I defined the seasonal distributions of Kittlitz’s murrelets as a coarse representation of the geographic limits within which the species may be found during defined parts of the year. I created seasonal distribution polygons in ArcMap10.0 (ESRI 2011; Figure 3-2). Because all birds included in this study were captured during the breeding season, I am most confident in this distribution. However, I was not able to follow the sampled birds throughout space and time; therefore the pre-breeding, post-breeding, and wintering distributions are assumptions based observational (Kuletz, USFWS, unpublished data) and literature-derived information.

The pre-breeding season distribution included observations from March–May over 5 years and encompassed 2 distinct geographic areas: coastal Gulf of Alaska (Pre-
GOA) and an area in the Bering Sea east of St. Matthew Island and west of Nunivak Island (Pre-BS). The post-breeding season distribution included observations made during September and October over 5 years and also included 2 distinct geographic areas: one area extending from Nunivak Island south towards Bristol Bay and west to the Pribolof Islands (Post-BB) and the other extending along the northern coast of Alaska in the Chukchi Sea (Post-CS). There were limited winter observations (December–February), so we centered the winter distribution over the Bering Sea, which is where Kittlitz’s murrelets are believed to overwinter (Winter; Day et al. 1999). I included the area between St. Lawrence, Nunivak, and St. Matthew islands in this seasonal distribution because recent observations from icebreaker surveys suggest this as an important overwintering area for the species. All birds included in the current study were captured in or near Icy Bay; therefore, the breeding season distribution included Icy Bay, nearby Yakutat Bay, and the portion of the Gulf of Alaska directly adjacent to these two areas (Breeding).

**Statistical Analysis**

I performed all analyses using R version 3.0.3 (R Core Team 2014). I standardized all continuous explanatory variables to z-scores and loge-transformed plasma CORT and PRL to meet assumptions of normality, which I evaluated via inspection of standardized residuals and Q-Q plots. All reported means and standard errors of response and explanatory variables are untransformed. I used Akaike’s Information Criterion (Akaike 1973) corrected for small sample sizes (AICc; Hurvich and Tsai 1989) to select the best model of the candidate model set.
Hormones and breeding initiation. To understand the relationship between stress physiology, parental investment, and breeding initiation, I developed a generalized linear model (GLM) for each hormone and sample type in which I regressed either CORT or PRL against the proportion of the population that initiated breeding in the current season (breeding proportion). Additionally, in the July and post-breeding season feather analyses, I included a parameter for the proportion of the population that initiated breeding in the subsequent breeding season (future breeding). I inferred breeding initiation from the subset of murrelets fitted with VHF transmitters each season (Kissling et al. In review a, Kissling et al. In prep).

Factors influencing hormone variation. Circulating plasma CORT and PRL vary naturally throughout the annual cycle (Romero 2002). Therefore, to evaluate the relative contribution of ocean productivity metrics and biological variables on hormone concentrations, I developed separate GLM model sets for each hormone and time period (4 plasma model sets: CORT-May, CORT-July, PRL-May, PRL-July; 2 feather model sets: CORT- Pre-Breeding, CORT- Post-Breeding). Due to data limitations, I only included bivariate models in the breast feather analysis and univariate models in the secondary CORT feather analysis.

In all model sets, I included parameters for the average SST and Chl-a values for the time period reflected in the sample and previous time periods (to test for carry-over effects), WIE, sex, brood patch score, mass (g, index of body condition; Labocha and Hayes 2012), and year. In all plasma model sets, I included the date of capture (day) to control for differences in hormone concentrations within time periods. In just the PRL
analysis, I included CORT as an explanatory variable to test if stress potentially was suppressing parental behavior in this population.

Hormone concentrations in blood plasma respond rapidly to acute stressors, such as capture or handling, so to achieve baseline levels, it is important to draw blood within 3 minutes of capture (Romero and Romero 2002, Chastel et al. 2005). Harsh weather and sea conditions in the field prohibited the attainment of this goal; therefore, I expected the plasma CORT levels to be higher and PRL levels to be lower than actual baseline concentrations. To control for variation in time between capture and processing, I included it as a variable (minutes) in each model set.

RESULTS

Breeding Initiation
Pre-breeding season feather CORT (from breast feathers) was negatively correlated with breeding proportion (adjusted $R^2 = 0.40$, $\beta = -0.21$, SE = 0.03; Figure 3-3A). Therefore, higher levels of stress during the pre-breeding season reflected lower levels of breeding propensity during the upcoming breeding season. Additionally, post-breeding season feather CORT (from secondaries) was negatively correlated with future breeding (adjusted $R^2 = 0.34$, $\beta = -0.21$, SE = 0.04; Figure 3-3B). Thus, higher concentrations of CORT during the post-breeding period reflected lower breeding propensity during the subsequent breeding season. In July, PRL was correlated with future breeding (adjusted $R^2 = 0.17$, $\beta = 0.26$, SE = 0.08; Figure 3-3C), with higher PRL concentrations associated with higher breeding propensity in the following breeding season. There was no relationship between breeding proportion and May plasma CORT (adjusted $R^2 = 0.01$), May PRL (adjusted $R^2 = 0.01$) or July plasma CORT (adjusted $R^2 = 0.02$).
Factors Influencing Hormone Variation

**Corticosterone.** Total circulating plasma CORT concentrations of murrelets captured during May ranged from 4.32–151.00 ng ml$^{-1}$, with a mean of 33.81 ng ml$^{-1}$ (SE = 2.61, $n = 80$, 2008–2012). Average CORT levels were highest in May 2008 and lowest in 2010 (Figure 3-4A). Model selection results testing relationships between CORT and explanatory variables were inconclusive and provided little support for any model. Models showed poor precision on parameters for all covariates, indicating that nothing I measured explained the observed variation in plasma CORT during this period (adjusted $R^2 = 0.04$).

The average total CORT concentration decreased to 21.60 ng ml$^{-1}$ (SE = 1.68) in July with a range of 4.87–56.80 ng ml$^{-1}$ ($n = 45$, 2008–2011). Average CORT levels in July were lowest in 2008 and highest in 2010 (Figure 3-4B). Model selection results indicated 3 well-supported models, which included parameters for day, mass, minutes, and July Chl-a concentration. I found that day, mass, and minutes best explained the observed variation in July plasma CORT (adjusted $R^2 = 0.17$). Higher CORT levels were associated with earlier capture dates ($\beta = -0.15$, SE = 0.08), lower body mass ($\beta = -0.17$, SE = 0.08), and longer time spans between capture and processing ($\beta = 0.21$, SE = 0.08).

CORT concentrations in black-tipped breast feathers, which are grown prior to the breeding season, ranged from 1.53–9.17 pg mm$^{-1}$, with a mean value of 3.91 pg mm$^{-1}$ (SE = 0.15; Figure 3-5). Model selection results suggested 2 models with substantial support (Table 3-2A), but average spring SST in the Pre-GOA and Pre-BS distributions best explained the observed variation in breast feather CORT (adjusted $R^2 = 0.56$). Higher
CORT levels were correlated with cooler SST in both areas (Pre-GOA: $\beta = -0.96$, SE = 0.11; Pre-BS: $\beta = -1.06$, SE = 0.11).

The average CORT concentration for secondary feathers, which are grown during the post-breeding season, was 15.57 pg mm$^{-1}$ (SE = 0.84), with a range from 8.36–34.93 pg mm$^{-1}$ ($n = 56$, 2010–2012; Figure 3-5). Model selection resulted in 1 model with substantial support, but an additional 2 models indicated non-zero correlations between the explanatory variables and secondary feather CORT (Table 3-2B). The most-supported model included the parameter for year (adjusted $R^2 = 0.33$), with lower CORT levels associated with 2011($\beta = -0.52$, SE = 0.10) and 2012 ($\beta = -0.32$, SE = 0.10). Although the other 2 models included covariates that were correlated with secondary feather CORT, both had relatively large $\Delta AIC_C$ values (> 9), and had a smaller effect on CORT levels compared to the year model ($\beta_{SST\ (Pre-BB)} = -0.16$, SE = 0.04, $\beta_{Chl-a\ (Fall\ BB)} = -0.15$, SE = 0.04).

**Prolactin.** The average PRL concentration for murrelets captured in May was 27.55 ng ml$^{-1}$ (SE = 2.61) with a range of 8.54–72.06 ng ml$^{-1}$ ($n = 78$, 2008–2012). Average prolactin levels were lowest during May 2009 and highest during May 2012 (Figure 3-4C). Model selection indicated 1 model with substantial support, which included just the parameter for CORT concentration. Higher PRL levels were associated with higher CORT ($\beta = 0.11$, SE = 0.05, adjusted $R^2 = 0.06$).

In July, the average PRL concentration ranged from 4.15–59.24 ng ml$^{-1}$ with a mean of 22.31 ng ml$^{-1}$ (SE = 1.68, $n = 44$, 2008–2011). Average PRL was lowest in 2008 and highest in 2010 (Figure 3-4D). There were 3 well-supported models in our model set. The first model included parameters for sex and year; the second included both of these
parameters with the addition of CORT; and the third included sex and CORT. I found that sex and year best explained the observed variation in July PRL (adjusted $R^2 = 0.25$). Both terms were positively correlated with PRL, indicating that higher PRL was associated with female sex ($\beta = 0.41$, SE = 0.16) and higher levels of prolactin in 2009 ($\beta = 0.21$, SE = 0.23), 2010 ($\beta = 0.52$, SE = 0.22), and 2011 ($\beta = 0.53$, SE = 0.19).

**DISCUSSION**

I used physiological measures to examine the relationships between stress, parental investment, breeding propensity, and environmental conditions experienced by Kittlitz’s murrelets throughout the year. Overall, higher feather CORT during the pre- and post-breeding seasons were correlated with lower rates of breeding propensity during the following breeding season. Further, variation in CORT and PRL concentrations were associated with both environmental (e.g., SST) and biological (e.g., sex) factors.

**Breeding Initiation**

In Kittlitz’s murrelets, high feather CORT reflected lower breeding propensity in the following breeding season; this relationship is found in both the breast feathers (when predicting the immediate breeding season) and the secondary feathers (when predicting the breeding season the following year). These relationships seem to suggest a trade-off between stress and future reproduction, and indicate carry-over effects in this species. Given the strong relationship between food availability and patterns of CORT secretion in seabirds (Angelier et al. 2007, Kitaysky et al. 2007, 2010), these data suggest that food availability during molt may be an important determinant of subsequent breeding success. During the post-breeding period, Kittlitz’s murrelets primarily forage on small fishes in offshore waters, while in the pre-breeding period, individuals mainly feed on
macrozooplankton (Hatch 2011). Scarce or highly variable resources during these periods may lead to up-regulation of CORT in the body and subsequent suppression of breeding or parental behaviors.

Higher late-breeding season PRL (July) was associated with higher breeding propensity in the following breeding season. Over the breeding season, nocturnal activity levels of Kittlitz’s murrelets (as inferred by radar observations) steadily increase until peaking in late July (Cragg 2013). These results and unpublished data collected in Icy Bay, Alaska suggest that non-breeding Kittlitz’s murrelets may be exhibiting courtship behaviors and prospecting for future mates or nest sites during this period of the year (Cragg 2013, MLK, unpublished data). This is consistent with the correlation we found between July PRL and the breeding proportion in the following season.

Taken all together, it appears that Kittlitz’s murrelets, like many other avian species (e.g., Marra and Holberton 1998, Dale and Leonard 2011) may use the late- and non-breeding seasons to prepare for subsequent reproductive events. However, with both the breeding proportion and future breeding proportion terms, I am assuming the experiences of the radio-tagged murrelets represent the experiences of all of the individual murrelets in the population. Due to the high temporal and spatial variability of Kittlitz’s murrelet abundance and challenges associated with the capture method, the recapture probability of Kittlitz’s murrelets across years in Icy Bay was very low (0.04, Kissling et al. In review b). Therefore, the population in one breeding season may not represent the population in subsequent breeding seasons. I emphasize that these models are coarse in nature. However, I believe the results described here are a first step to understanding how stress may impact the breeding ecology of Kittlitz’s murrelets, a topic
which warrants more rigorous study. Further, all significant relationships between hormone concentrations and breeding propensity were predictive. Therefore, these results may be a productive place to focus further research and potentially guide management actions for Kittlitz’s murrelets.

**Factors Influencing Hormone Variation**

*Corticosterone*. Similar to other bird species, the Kittlitz’s murrelet exhibited higher levels of circulating plasma CORT at the beginning of the breeding season (May) relative to the end of the breeding season (July; Romero 2002). On average, females demonstrated higher plasma CORT concentrations than males within both periods (May and July) and across all years, with the exception of July 2010. However, differences in plasma CORT by sex were not substantial enough to improve model fit, likely because both males and females participate in incubation and chick provisioning (Day et al. 1999). Therefore, both sexes would be expected to increase activity levels and energy use during the breeding season, presumably leading to higher plasma CORT concentrations (Wingfield et al. 1998, Romero 2002).

Though nothing I measured explained the observed variation in May plasma CORT concentrations, we found that time between capture and processing, date of capture, and body mass best explained the variation in July plasma CORT, although there was still a large amount of unexplained variation ($R^2 = 0.17$). The Kittlitz’s murrelets in Icy Bay breed asynchronously (Kissling In prep); therefore, interpretation of the date of capture is difficult. I found that lower CORT levels were associated with capture dates that occurred later in the breeding season, which is a pattern consistently found across
avian species (Romero 2002). Thus, perhaps lower CORT levels reflect reduction in chick-provisioning activities as young begin to fledge from the nest (Day et al. 1999).

Contrary to findings from the closely related marbled murrelet (B. marmoratus; McFarlane-Tranquilla 2001) but consistent with most other studies (Breuner 2010), I found a negative relationship between CORT and body mass. I observed a decline in the mean body mass of both male and female Kittlitz’s murrelets over the course of the breeding season, a pattern that has been previously observed in this species (Hatch 2011) and others (e.g., McFarlane-Tranquilla 2001, Coulson 2010). Mean female mass decreased from 250 g (SE = 4) in May to 208 g (SE = 4) in July, while mean male mass decreased from 243 g (SE = 4) in May to 224 (SE = 3) in July. In the spring, females may be developing or carrying an egg that is ~20-25% of the female’s body weight (Day et al. 1999), therefore the majority of the seasonal mass loss observed in females presumably is attributable to the laying or abortion of the egg.

High energetic costs incurred from prolonged fasting during their 24–72 hr incubation shifts (Lawonn 2012, MLK, unpublished data) or from commuting between the ocean and their nest (Hatch 2011), could also be causing the decline in male mass and part of the decline of female mass. During the incubation and chick-rearing phases, Kittlitz’s murrelets may be unable to consume or assimilate enough energy to balance their overall energy budget (Hatch 2011), causing metabolism of fat reserves and, in turn, lower body mass. Therefore, the negative relationship we found between July plasma CORT and body mass may be indicative of lower body condition caused by the increased energy expenditure associated with breeding activities. However, the reduction of body mass throughout the breeding season may be an adaptive strategy. High body mass could
be a disadvantage for species that use a flapping flight mode (as the Kittlitz’s murrelet does) to make multiple flights between the ocean and their nest or during large seasonal movements (Freed 1981, Coulson 2010). In either scenario (imbalanced energy budgets or adaptive loss of body mass), CORT secretion would be expected to increase in the body to promote mobilization of stored energy reserves (Wingfield et al. 1998, Romero 2002).

The strongest relationship between hormone concentrations and explanatory variables occurred during the pre-breeding season ($R^2 = 0.56$). Pre-breeding season feather CORT levels (black-tipped breast feathers) were negatively correlated with the average spring SST values in the spring distribution areas (Figure 3-2); thus, higher CORT was associated with lower SST. Lower SST is associated with higher ocean productivity (Behrenfeld 2006), and so I predicted that lower SST would predict lower CORT. It is possible that Kittlitz’s murrelets incur higher thermoregulatory costs when resting on cooler water, as is seen across other seabird species (Richman and Lovvorn 2011), and this may have led to elevated CORT. Further, because the Kittlitz’s murrelet is relatively small, this species would be expected to experience greater mass-specific heat loss in cooler water temperatures compared to larger-bodied species, such as penguins, diving ducks, or cormorants (de Vries and van Eerden 1995, Richman and Lovvorn 2011). Therefore, the negative relationship observed between SST and CORT may pertain to the higher metabolic activity necessary to maintain body temperatures when resting on and diving in cooler waters.

The negative correlation between pre-breeding season SST and CORT may also be attributed to spring phytoplankton bloom dynamics. Although cooler waters are
generally associated with higher productivity (Behrenfeld et al. 2006), both increasing 
light availability and water column stability (resulting from increasing SST in the spring) 
are important factors influencing the onset of the spring phytoplankton bloom in the Gulf 
of Alaska (Henson 2007). Warmer sea surface temperatures and earlier stratification lead 
to earlier and more intense spring blooms (i.e. higher Chl-a concentrations; Henson 2007, 
Mundy et al. 2010). Additionally, Brown et al. (2011) found that warmer sea surface 
temperatures enhance phytoplankton growth rates. Both results suggest greater 
phytoplankton growth and abundance during warmer SST conditions, which potentially 
provides increased foraging resources for the macrozooplankton on which Kittlitz’s 
murrelets primarily feed during the pre-breeding season (Hatch 2011).

Post-breeding season CORT was most strongly correlated with year, which 
suggests unexplained annual variation. However, CORT was also negatively correlated 
with SST and Chl-a concentrations in the Post-BB distribution, though these models did 
not have substantial support. Thus, I am not able to draw any firm conclusions to explain 
post-breeding CORT variation, though I acknowledge that inter-annual variation across 
years was important.

Prolactin. As with CORT, females exhibited higher PRL concentrations on 
average than males within both periods and across all years, except for May 2012. These 
differences did not improve model fit in May, when both males and females develop a 
brood patch and share the burdens of incubating the egg (Day et al 1999). Interestingly, 
there was not a relationship between PRL and brood patch score. Kissling et al. (In 
review a) also was unable to establish a relationship between brood patch score and 
breeding propensity for Kittlitz’s murrelets, emphasizing that brood patches can be
difficult to interpret and are not always reliable indicators as to the reproductive status of murrelets (McFarlane-Tranquilla et al. 2003, Kissling et al. In review a).

Although the positive relationship between May PRL and CORT was not expected, the relationship conforms to the view of CORT as the primary mediator of allostasis. Recent studies suggest that, rather than hindering reproductive performance, up-regulation of plasma CORT triggers behavioral and physiological adjustments that may actually enhance current reproductive efforts (Moore and Jessop 2003, Love et al. 2004). Elevation of circulating plasma CORT mobilizes energy stores so an individual is better able to overcome the increased metabolic demands associated with breeding and parental care (Wingfield et al. 1998, Romero 2002, Love et al. 2004, Chastel et al. 2005). Therefore, I believe that the stress-induced CORT levels exhibited by these Kittlitz’s murrelets were not elevated enough or for a prolonged enough length of time to depress PRL and thus suppress parental expression.

In July, higher PRL was associated with female sex and year. The inclusion of the year parameter indicates that unexplained inter-annual variability was important for explaining July PRL concentrations, and therefore, I may not have measured the variables important to hormone secretion during this period.

Conclusions
Understanding the drivers of variation in population demographics requires long-term, consistent collection of data, which is often financially and logistically burdensome. Further, direct quantification of prey abundance, availability, and quality is difficult to assess and is not practical over large spatial and temporal scales. Physiological measurements, such as CORT levels from plasma or feathers and PRL from plasma, can
be used to understand conditions experienced by individuals throughout the year, from which population demographics may be predicted or inferred (Satterthwaite et al. 2012). These results demonstrate the importance of continued research to understand the mechanisms linking stress physiology, foraging ecology, and breeding ecology of Kittlitz’s murrelets.

Overall, it appears that feather CORT concentrations better reflected environmental conditions than plasma CORT concentrations, especially in this system where rapid plasma samples were very difficult to obtain. Feathers integrate and accumulate stress hormones over a longer time-span than plasma. Therefore, feather CORT may provide a more useful and appropriate temporal scale of stress for comparison with general measurements of ocean productivity. Further research will be necessary to understand the direct linkages between foraging ecology and stress physiology of Kittlitz’s murrelets.

I used both regional and local remotely-sensed environmental indices to predict variation in hormone concentrations of Kittlitz’s murrelets. Ocean productivity metrics are inherently correlated. Thus, I selected 3 metrics based on a priori mechanistic hypotheses and predictions (described in Methods section) and that commonly are related to aspects of seabird biology (e.g., Satterthwaite et al. 2012, Thompson et al. 2012). I did not include any large-scale climate indices, such as the Pacific Decadal Oscillation or the Arctic Oscillation, because these processes operate on multi-decadal time scales (Mantua et al. 1997, Thompson and Wallace 1998), while these data span 5 years (2008-2012) and do not encompass any climate regime shifts.
I encountered several challenges in this analysis, such as incomplete knowledge regarding the seasonal distributions of the Kittlitz’s murrelets sampled in this study. The seasonal distributions used for this study likely are not the only locations in which Kittlitz’s murrelets can be found during the non-breeding season. However, I used the best available data to create the seasonal distributions in order to define spatial and temporal boundaries for estimating the remotely-sensed ocean productivity metrics. I suggest that future studies incorporate the ocean productivity metrics from locations of birds tracked through time and space.

A further challenge was the lack of individual-level covariates that influence stress and parental investment in other species, such as age, breeding phenology, and breeding experience (e.g., Angelier et al. 2009b, Goutte et al. 2010). The cryptic life-history strategies of the Kittlitz’s murrelets preclude researchers’ ability to collect these data. However, I suggest that future research consider sampling CORT and PRL from radio-tagged individuals to compare concentrations of known breeders against known non-breeders. In the future, known-breeders could also be targeted for re-sampling throughout the breeding season. This may not be feasible for Kittlitz’s murrelets nesting in glaciated landscapes, such as Icy Bay, but could be considered for murrelets nesting in non-glaciated habitats, such as in the Kodiak Archipelago.

These results provide new insight regarding when Kittlitz’s murrelets may make their breeding decisions, and how stress might influence this decision. These results provide evidence that conditions during the late- non-breeding seasons may drive future reproductive decisions of Kittlitz’s murrelets. Additionally, higher circulating CORT levels within the breeding season seemed to enhance parental investment, as opposed to
suppressing reproduction. While breeding propensity is low in this population, success is not (Kissling et al. In review a). Therefore, high CORT may be inhibiting breeding initially (Wingfield et al. 1998), but once the decision to breed is made, elevated CORT levels may promote the attempt or rise in response to increased activity levels.
LITERATURE CITED


Figure 3-1. Collection of blood plasma and 2 feather types (breast and secondary feathers) at capture (May or July) enabled insights into the physiological status of Kittlitz’s murrelets (*Brachyramphus brevirostris*) captured in Icy Bay, Alaska (2008–2012) for 4 distinct periods of the year: pre-breeding (green), early and late breeding (May and July; yellow), and post-breeding (green).
Figure 3-2. Seasonal distributions of Kittlitz’s murrelet (Brachyramphus brevirostris) as inferred from non-breeding season observations, 2007–2012. All murrelets were captured in Icy Bay, Alaska (black box). These distributions describe the spatial and temporal extent used to estimate sea surface temperature and chlorophyll $a$ concentrations to explain variation in hormone levels of Kittlitz’s murrelets throughout the annual cycle. Colors of the seasonal distributions correspond to the colors of the annual timeline figure for Kittlitz’s murrelets (Figure 3-1).
Figure 3-3. Pre-breeding season (A) and post-breeding season (B) CORT levels were negatively correlated with breeding initiation rates during the upcoming breeding season, whereas late-breeding season PRL (July; C) was positively related with breeding initiation rates during the subsequent breeding season for Kittlitz’s murrelets (*Brachyramphus brevirostris*) captured in Icy Bay, Alaska, 2008–2012.
Figure 3-4. Average plasma hormone concentrations (± SE) for Kittlitz’s murrelets (*Brachyramphus brevirostris*) captured during May and July in Icy Bay, Alaska: A) May CORT (2008–2012); B) July CORT (2008–2011); C) May PRL (2008–2012); D) July PRL (2008–2011). Dashed horizontal lines indicate the average value for that month across all years.
Figure 3-5. Average feather hormone concentrations (± SE) for Kittlitz’s murrelets (*Brachyramphus brevirostris*) captured in Icy Bay, Alaska. Inter-annual variation in pre-breeding season black-tipped breast feather CORT is shown in the top panel (2009–2012), while inter-annual variation in post-breeding season secondary feather CORT is showed in the lower panel (2010–2012). Dashed horizontal lines indicate the mean value for each feather type across all sampled years. Due to differences in structure and density, comparisons cannot be made across feather types. Instead, I could evaluate variation within a sampling period and population variation within a sampling period across years.
Table 3-1. The samples used for evaluating the relationships between ocean productivity, stress (CORT), and parental investment (PRL) of Kittlitz’s murrelets (*Brachyramphus brevirostris*) captured in Icy Bay, Alaska, 2008–2012.

<table>
<thead>
<tr>
<th>Period reflected</th>
<th>Sample type</th>
<th>Hormone(s) measured</th>
<th>Years collected</th>
<th>Sample Size</th>
</tr>
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<tbody>
<tr>
<td>Pre-breeding</td>
<td>Breast feather</td>
<td>CORT</td>
<td>2009</td>
<td>20</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>2010</td>
<td>20</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>2012</td>
<td>19</td>
</tr>
<tr>
<td>Early-breeding</td>
<td>Plasma</td>
<td>CORT, PRL</td>
<td>2008</td>
<td>14</td>
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<td></td>
<td></td>
<td></td>
<td>2009</td>
<td>19</td>
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<td></td>
<td></td>
<td>2012</td>
<td>17</td>
</tr>
<tr>
<td>Late-breeding</td>
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<td></td>
<td>2011</td>
<td>13</td>
</tr>
<tr>
<td>Post-breeding</td>
<td>Secondary feather</td>
<td>CORT</td>
<td>2010</td>
<td>18</td>
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<td></td>
<td></td>
<td></td>
<td>2012</td>
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Table 3-2. Model selection results of the feather CORT analyses for Kittlitz’s murrelets (*Brachyramphus brevirostris*) captured in Icy Bay, Alaska, during May and July 2009–2012. Well-supported variables in the A) pre-breeding feather analysis were sea surface temperature (SST) and in both of the pre-breeding distributions (Pre-BS and Pre-GOA), and year; and the B) post-breeding feather analysis were year, and SST or Chl-α for the Post-BB distribution.

<table>
<thead>
<tr>
<th></th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>K&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Deviance</th>
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<tr>
<td>A. Black-tipped Breast Feathers</td>
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<tr>
<td>SST (Pre-BS) + SST (Pre-GOA)</td>
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<td>Year</td>
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<td>B. Secondary Feathers</td>
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<tr>
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<td>4</td>
<td>18.51</td>
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<td>SST (Post-BB)</td>
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<tr>
<td>Chl-α (Post-BB)</td>
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<sup>a</sup>K = Number of Parameters