Can oceanic prey effects on growth and time to fledging mediate terrestrial predator limitation of an at-risk seabird?

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Abstract. Most seabird species nest colonially on cliffs or islands with limited terrestrial predation, so that oceanic effects on the quality or quantity of prey fed to chicks more often determine nest success. However, when predator access increases, impacts can be dramatic, especially when exposure to predators is extended due to slow growth from inadequate food. Kittlitz’s Murrelet (Brachyramphus brevirostris), a rare seabird having experienced serious declines, nests solitarily on the ground in barren, often alpine areas where exposure to predators is generally low. Nestling growth rates are exceptionally high and nestling periods very short relative to other Alcidae. This strategy reduces duration of exposure to predators, but demands adequate deliveries of high-energy prey. In an area where foxes can access nests, we investigated whether varying energy content of prey fed to chicks could alter growth rates and resulting duration of predator exposure, and whether prolonged exposure appreciably reduced nest success. From 2009 to 2016, we monitored 139 nests; 49% were depredated (almost all by foxes) and 25% fledged. Prey fed to nestlings were 80% Pacific sand lance (Ammodytes personatus) and 19% capelin (Mallotus villosus), with capelin having 2.3× higher energy content per fish. In a year of slow chick growth, increased sand lance energy density of 31% (4.29–5.64 kJ/g, within published values), or increased proportion of capelin in the diet from 5.6% to 27.2%, would have allowed maximum chick growth. Maximum growth rates were attainable by delivering only 1.9 capelin/d versus 5.5 sand lance/d. Slow growth increased time to fledging by up to 5 d, decreasing survival by 7.7% (0.142–0.131). Breeding propensity of Kittlitz’s Murrelet averages only 20%, so even small changes in nest success could affect populations. Although nest success was limited mainly by predation, oceanic effects on prey quantity and quality had overriding impacts in one year (2015 heat wave), and small but substantive effects in other years by mediating exposure to predation. Climate warming that decreases availability of high-energy forage fish, or increases expansion of predators into nesting habitats, may disproportionately affect this sensitive species and others with predator-accessible nests and demands for energy-rich prey.

Key words: chick growth rate; chick provisioning; Kittlitz’s Murrelet; Kodiak Island; nest predation; ocean climate change; prefl edging period; seabird breeding success.

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INTRODUCTION

Seabirds commonly nest on cliffs, in burrows, or on islands with few land-based predators, so that effects of predation on breeding success typically receive less attention than effects of oceanic prey availability (Anthony et al. 2000, Litzow et al. 2002, Wanless et al. 2005, Hedd et al. 2006, Romano et al. 2006, Hatch 2013). However, when land-based predators gain access to nests, predation can become a major limitation on breeding success (Towns et al. 2011, Iverson et al. 2014). For the Kittlitz’s Murrelet (Brachyramphus brevirostris) on western Kodiak Island, Alaska, high rates of nest predation by red foxes (Vulpes vulpes) suggest that land-based predators and not ocean conditions control nest success (Lawonn et al. 2018). However, if the quantity or quality of prey delivered to chicks is limited by ocean conditions, reduced growth rates can extend the nestling period and indirectly increase the chicks’ exposure to predators. In this paper, we explore interactions between oceanic prey quantity and quality, chick growth rates, duration of the nestling period, and land-based predation.

The Kittlitz’s Murrelet is a long-lived (~15 yr) alcid of the North Pacific. Unlike most alcids, Kittlitz’s Murrelets nest non-colonially, with nests found up to 75 km inland from the coast. They lay a single egg in mountain or coastal upland habitats, usually dominated by scree, talus, or barren ground, at elevations from 128 to 2249 m and on slopes of 0–66° (Fig. 1; Felis et al. 2016, Day et al. 2017, Lawonn et al. 2018a). During the 20–40 d of the nestling period, parents deliver single planktivorous fish to chicks 1–12 times per day (Kaler et al. 2011, Lawonn et al. 2018b).

Several studies suggest that predation on eggs or young is a major factor limiting Kittlitz’s Murrelet nest success in some areas (Kaler et al. 2009, Lawonn et al. 2018a). Other alcid species avoid predation by nesting on cliffs, in burrows, in crevices among rocks, or high in trees. In contrast, Kittlitz’s Murrelets nest in exposed sites on the ground and avoid avian and mammalian predators by relying on cryptic coloration and widely dispersed nest sites in inaccessible habitat supporting little or no vegetative cover (typically alpine scree; Fig. 1). Compared to other semiprecocial alcids (Sealy 1973), Kittlitz’s Murrelet has among the highest growth rates and lowest fractions of adult mass at fledging, and as a result the shortest period between hatching and fledging (Lawonn et al. 2018). This strategy presumably offsets the potentially high vulnerability of Kittlitz’s Murrelet nests to predation, by minimizing the duration of exposure to predators (Litzow et al. 2002, Romano et al. 2006). However, this strategy will not be effective if predators acquire greater access to the murrelets’ nest sites, or if ocean conditions limit the quantity or quality of prey needed to support high growth rates.

Abundance and species composition of forage fish exhibit considerable spatiotemporal variation in the North Pacific and are sensitive to both short- and long-term oceanographic changes (Wespestad 1991, Agler et al. 1999, Anderson and Piatt 1999, Hedd et al. 2006, Hatch 2013, Shearn-Bochsler et al. 2014). There are also wide fluctuations in lipid and energy content within and among prey species that can strongly affect seabird reproductive success (Anthony et al. 2000, Litzow et al. 2002, Wanless et al. 2005, Romano et al. 2006, Gorman et al. 2018, von Biela et al. 2019). Energetics analyses indicate that Kittlitz’s Murrelets incur exceptionally high energy costs in raising young up to 75 km from the coast and up to 2250 m above sea level (Hatch 2012). The high costs of each foraging trip may make Kittlitz’s Murrelets delivering single prey items more dependent than other seabirds on energy-dense forage fish for their young.

A recent analysis for Kittlitz’s Murrelets suggested a population-wide decline of 31% per annum from 1989 to 2000, for an overall decline of 95% from 602,000 to 33,600. With annual survival of about 0.80 (Kissling et al. 2015), available data suggest that annual fecundity is far too low to sustain the population (Day and Nigro 2004, Kaler et al. 2009, Lawonn et al. 2018). Based on 191 Kittlitz’s Murrelets radio-marked in Icy Bay, Alaska before the breeding season, Kissling et al. (2016) reported a breeding propensity of only 20% (range 5–45% over 6 yr). Such low breeding propensity places great importance on factors that limit reproductive success of individuals that do attempt to nest. In three studies from 2005 to 2012 (total of 204 nests), 74% of nests failed due to nest predation, chick death, or chick abandonment (Felis et al. 2016). Major declines in
Kittlitz’s Murrelet abundance corresponded to an oceanic regime shift in 1989, followed by declines in forage fish availability through at least 2000 (Hare and Mantua 2000, Mueter et al. 2007, Hatch 2013). These results suggest that high nest predation rates, together with inadequate prey quantity or quality, could be major contributing factors in the decrease and lack of recovery of this species.

The U.S. Fish and Wildlife Service recently declined to list Kittlitz’s Murrelet under the Endangered Species Act (Federal Register 2013). This ruling recognized that climatic shifts in ocean conditions can significantly affect the prey of Kittlitz’s Murrelet, but concluded that such changes in prey would not threaten the persistence or recovery of murrelets. One reason was lack of sufficient evidence that abundance of Kittlitz’s Murrelets or their prey oscillated with climate-driven oceanic shifts, with most information indicating that murrelets can accommodate such changes by switching prey or altering their distribution. Another reason was lack of evidence that changes in ocean conditions have limited delivery of high-quality meals to chicks or will in the future (Federal Register 2013). However, more recent information suggests that interactions between land-based predation and growth rates driven by ocean conditions may be important to maintaining nest survival rates needed to maintain or recover the population.

For Kittlitz’s Murrelets on Kodiak Island, Alaska, we examined the following questions: (1) What are the main causes of nest failure for this at-risk species nesting in remote alpine scree on Kodiak Island? (2) Could variations in energy content of the same or different fish species delivered to chicks explain observed variations in growth rate and time to fledging? (3) Could observed variations in duration of the nestling period affect overall nest success by altering the duration of exposure to terrestrial predators?

**METHODS**

**Study area**

Kodiak Island is in the northern Gulf of Alaska, separated from the Alaska Peninsula by about 35 nmi across Shelikof Strait (Fig. 2). Our study area encompassed 7 km² of low- to mid-elevation ridges and peaks with large, contiguous areas of broken rock and scree comprised largely of igneous ultramafic rock. This substrate has scarce nutrients and high concentrations of heavy metals that together prevent growth of most plants (Alexander et al. 2006). Areas searched for Kittlitz’s Murrelet nests (Fig. 2) were 5–11 km from the ocean, at elevations from 80 to 470 m.

**Nest searches and procedures at the nest**

Each year from 2009 to 2015, the four study sites (Fig. 2) were searched for murrelet nests by a team of 3–4 people. In 2016, the crew was increased to 5–7 people split into two teams. Crews systematically searched scree hillsides.
with slopes >20°, focusing on steeper slopes and larger patches of ultramafic rock. On the first round of searching (early to mid-June), 4–8 d were spent at each study site. Each site was searched again in late June, and nest searching continued until late July. Total area searched per year (not including repeated searches) averaged 2.33 km² (range 1.64–3.15 km²). Crews began at the lowest elevation of a slope and searched progressively higher horizontal strips until reaching the top of the slope (for details, see Lawonn et al. 2018b). All nests found were logged with a GPS unit.

When a nest was found, we used nitrile gloves to minimize human scent around the nest. Hatching date was estimated from egg flotation, assuming a 30-d incubation period (Rizzolo and Schmutz 2007, Day et al. 2017). A camera painted to blend with the substrate was mounted near the nest and camouflaged with rocks (see next section). Starting in 2014, a temperature data logger (Thermochron iButtons, Embedded Data...
Nest cameras and checks

Incubation shifts, hatching, adult brooding, chick meal deliveries, predations, fledging, nest fate, and any other events at the nest were quantified from camera images. We placed still-image, motion-triggered cameras (Reconyx, Holmen, Wisconsin, USA; Primos, PC900 or PC90) 1–3 m from active nests to monitor nest activity. Experiments showed that camera placement had no detectable effect on nest success (Lawonn et al. 2018b), and cameras were set on every nest studied starting in 2011 (only every other nest before that). In 2011, three cameras were set to 1-min intervals; out of 199 meal deliveries recorded, only one visit was shorter than 3 min, indicating a 3-min interval was adequate to film >99% of visits by parents to the nest (Lawonn et al. 2018b). Thereafter, all nest cameras were set to trigger after detecting animal motion (3 images at 1-s intervals), as well as at standard 3-min intervals from discovery of the nest to fledging.

Nest fate was determined from later analysis of camera images and physical evidence present during the final nest check when the camera was retrieved. A nest was considered abandoned if adults left an egg unattended and never returned to the nest. A large fecal ring at the nest, accompanied by down shed by the chick just before fledging, was taken as evidence of a successful nest (Piatt et al. 1999). Depredation was assumed if there was no chick present on the first nest check, and hatching was determined by the presence of chick excreta and egg fragments.

Estimating fish length

Camera images taken at nests from discovery through fledging or failure were reviewed after the field season. For each meal delivery, we recorded the date, time, and prey species to the extent possible depending on the quality of the images. Fish length was estimated as a ratio to the head length of the adult delivering the fish. An adult head length of 57.3 mm (from a female adult captured at a nest on Kodiak Island in 2015) was multiplied by each ratio to estimate the length of each fish delivered. All films from early in the study were reviewed again and fish lengths estimated by this standardized method. Fish length estimates were made for 2009–2015 by a single observer and in 2016 by a different observer. To test for consistency of estimates, the 2016 observer repeated all the measurements during that year. The mean head length-to-fish length ratio differed by only 0.0198 (1.135 mm), which was not significant (paired t-test, n = 407 fish, P = 0.13). The 2016 observer then re-measured ratios for a random sample of deliveries from each nest in 2013 (20 deliveries from each of 9 nests, n = 180 fish) to test equivalence between the two observers. The mean difference in head length-to-fish length ratio between observers, 0.1319 (7.56 mm), was significant (P < 0.01), so we corrected the 2016 data by that average difference.

Estimating chick growth

For each nest with at least one later measurement of chick growth, we used a formula from Hoyt (1979) to estimate egg mass at laying (g) from egg length (cm) and egg width (cm):

\[
\text{eggmass} = 0.548 (\text{length} \times \text{width})^2.
\]  

Chick mass at hatching was then estimated by assuming 15% (SD = 1%) water loss during incubation regardless of incubation period (Alcidae; Ar and Rahn 1980) and that the shell on average comprised 7.9% of total egg mass (Charadriiformes; Whittow 1980).

Based on chick measurements from 2009 to 2016, we used a 3-parameter logistic model in program JMP (SAS Institute, Cary, North
Carolina, USA) to estimate growth curves (Ricklefs 1983, Tjorve and Tjorve 2010). Using estimated mass at hatching (preceding paragraph) and chick body mass measurements, we calculated a growth rate for each year and a combined growth rate for all years. Growth rates were not calculated separately for each individual, because even for the subset of chicks that survived to fledging there were only three measurements per chick for fitting a nonlinear sigmoidal curve. Growth rate \( K \) represents the slope of the tangent at the inflection point as a measure of instantaneous growth rate. We combined data from 2009 and 2010 due to small sample sizes. Data for 2015 were not available because only a single nest lasted to the first growth measurement. One chick from 2011 and two from 2013 were removed from analyses, as their growth rates (2013) or calculated total energy required (2011) were significant outliers at least 2.5 standard deviations below the mean (outlier tests, \( P \leq 0.05 \); Grubbs 1969).

**Estimating fish energy content**

Only fish length could be estimated from camera images, so we used models of Kittlitz’s Murrelet chick energy needs to estimate prey energy content relative to the wide range of measured values reported in the literature. From calculations of the energy needed to sustain observed growth between measurement periods and the number and lengths of prey delivered during the same periods, we estimated the average energy content of prey needed by a given chick in a given day. We calculated daily maintenance requirements \( E_{\text{maint}} \) (kJ) of chicks by multiplying allometric estimates of resting metabolic rate \( \text{RMR, kJ/h} \) for chicks of any bird species given its mass \( M_c \) (g) by 24 h (Weathers 1996).

\[
E_{\text{maint}} = 24 \times \text{RMR} = 24 \times 10 \exp[-1.1357 + (0.845 \times \log_{10}M_c)].
\]  
\[(2)\]

This equation does not account for possible costs of thermoregulation, which are addressed in the section below entitled Testing impact of variations in ambient temperature.

We assumed a constant rate of daily mass gain from hatching to the first growth measurement and between later growth measurements. Using a standard cost associated with the gain in tissue mass, 6.6944 kJ/g (Furness 1978), we estimated the energy cost of chick growth for each day \( C_{\text{growth}} \) (kJ). We assumed an assimilation efficiency (AE) for prey fish of 0.85 (Konarzewski et al. 1993, Brekke and Gabrielsen 1994, Oka 2011). We estimated the daily energy requirements \( \text{DER, kJ} \) needed during the period between hatching and each growth measurement for each chick as.

\[
\text{DER} = \frac{E_{\text{maint}} + C_{\text{growth}}}{\text{AE}}.
\]  
\[(3)\]

In each year, DER was averaged over all nests for each sequential day of development.

We used formulas from Elliott and Gaston (2008) to estimate the mass of each of the two main prey species (Pacific sand lance \( \text{Ammodytes personatus} \) and capelin \( \text{Malloletes villosus} \)) to estimate the mass of each of the two species observed in a given year. For fish length \( L_{\text{fish}} \) (dm), fresh mass \( M \) (g) of sand lance \( (M_{\text{sand}}) \) and fresh mass of capelin \( (M_{\text{cap}}) \),

\[
M_{\text{sand}} = 2.26 \times L_{\text{fish}}^{2.96}
\]  
\[(4)\]

\[
M_{\text{cap}} = 4.18 \times L_{\text{fish}}^{3.77}
\]  
\[(5)\]

To estimate the energy density \( \text{kJ/g fresh mass} \) of fish required to sustain observed chick growth in a given year \( (\text{EC}_{\text{req}}) \), we divided the total DER \( (\text{kJ}) \) during all observation days by the total fresh mass of fish delivered \( (g) \) during that same time. This approach yielded equal energy densities \( \text{kJ/g} \) for sand lance and capelin, but specifically accounted for differences in mass per unit length (and thus energy per unit length) of the two species.

**Sand lance energy content or diet fraction of capelin needed for maximum growth**

We investigated whether differences in annual chick growth rates \( K \) could be explained by annual changes in either energy density of sand lance or prey species composition (sand lance vs. capelin). We used data from 2013 \( (n = 8 \text{ nests}) \), which exhibited the highest daily energy required for growth \( \text{DER}_{\text{max}} = 149.1 \text{ kJ/d} \), and growth rate \( K = 0.241 \text{ d}^{-1} \) second only to
2009–2010. We calculated how much change in either sand lance energy density or species composition would be needed for chicks to reach DERmax in each other year, depending on the number, proportion, mass, and energy content required of fish delivered in those years (see above section Estimating fish energy content; ECreq = total energy required divided by total grams delivered). We used the formula.

\[
\text{DER}_{\text{max}} = \left( \frac{P_{\text{sand}} \times M_{\text{sand}} \times EC_{\text{sand}}}{\left( N_{\text{del}} \times P_{\text{cap}} \times M_{\text{cap}} \times EC_{\text{cap}} \right)} \right)
\]

where DERmax = daily energy requirements (kJ) of murrelet chicks in 2013, Ndel = daily mean number of fish delivered (determined from camera images) in the given year, Psand = proportion of sand lance in the number of fish delivered in the given year, Msand = mean mass of sand lance in the given year (from Eq. 4), ECsand = annual mean energy content of sand lance (kJ/fish) required in the given year, Pcap = proportion of capelin in the number of fish delivered in the given year, Mcap = mean mass of capelin in the given year (from Eq. 5), and ECcap = mean energy content of capelin (kJ/fish) required in the given year. To evaluate how much change in energy content of sand lance (ECsand) would be needed to achieve DERmax in each year, in Eq. 6 we set ECcap = mean energy content of fish required (kJ/g, total energy required divided by total grams delivered) in the given year and solved for ECsand. The range of estimated values of ECsand was then compared to the range of published values to determine whether the estimated changes were within reasonable bounds. To evaluate how much change in species composition of prey would be needed to achieve DERmax in each year, in Eq. 6 we set Pcap = 1 – Psand and solved for Psand.

Testing impact of variations in ambient temperature

Eq. 2 for costs of maintenance does not include possible costs of thermoregulation. The only microclimate variable that we measured was temperature. To determine whether variation in ambient temperature at the nest could affect the energy required by chicks, we analyzed temperatures taken at equivalent sites near the nest, every 10 min, over the same time period for which chick energy requirements where calculated. We calculated the mean temperature and the proportion of time when a chick was outside its thermoneutral zone. We assumed a lower critical temperature for the thermoneutral zone of 9°C reported for a similar species, Scrippsi’s Murrelet (Synthliboramphus scrippsi, formerly Xantus’s Murrelet Synthliboramphus hypoleucus). For each 10-min increment that a chick experienced an ambient temperature below thermoneutrality, we increased RMR by 2.3% for each 0.5°C below the lower critical temperature (Fig. 8 in Eppley 1984).

Modeling nest survival

We estimated daily survival rate of Kittlitz’s Murrelet nests in program MARK using methods described by Dinsmore et al. (2002), which account for effects of nests that were not found (nests that fail early are less likely to be found) but whose fate could affect overall survival estimates. We calculated a daily survival rate for each year, during egg and chick stages separately, and for all years combined. We evaluated candidate models in MARK using Akaike’s information criterion. We included date of nest initiation and nest age as covariates to assess their relationship with survival. These analyses were intended to test whether nest survival and resulting population trajectories might be affected by the energy content of prey delivered to chicks, by altering growth rate, resulting time to fledging, and the consequence duration of exposure to terrestrial nest predators.

RESULTS

Nest fate

We found 139 active Kittlitz’s Murrelet nests in western Kodiak Island from 2009 to 2016 (Table 1), of which 53% hatched and 25% fledged. Predation rates were higher during the incubation stage compared to the nestling stage. For the 65 eggs that did not hatch, 74% (48) were depredated, while for the 40 chicks that hatched but did not fledge, 50% (20) were depredated. Total nest losses to predators (incubation and nestling period combined) varied among years from 19% to 76%, with a mean for all nests of 49% (51% if averaged among years; Fig. 3). We identified the predator responsible for nest depredation at 44 of 68 (65%) depredated nests.
Red fox and Black-billed Magpie (*Pica hudsonia*) depredated 93% (*n* = 41) and 7% (*n* = 3) of nests, respectively. Across the study, parents abandoned 12% of nests, but abandonment rates varied from 5% to 31% in different years. All abandonments occurred during incubation. Over all years, 20 of the 40 chicks (50%) that hatched but did not fledge died at the nest from what initially were unknown causes. For 9 of 10 chick carcasses that were tested, saxitoxin, a neurotoxin produced by certain species of marine dinoflagellates (USGS 2012, Shearn-Bochsler et al. 2014) was considered the cause of death.

**Nestling period, chick growth, and fish delivered**

Over all study years, the mean nestling period for chicks with known hatching and fledging dates (*n* = 34) was 23.4 d, with yearly means varying by as much as 5 d from 22 to 27 d (Table 1). Mean estimated mass at fledging differed among years (Fig. 4A) by as much as 27% (37 g, 136.4–173.2 g). Here and in subsequent text, we often compare values for 2011 and 2013, which were years with opposite extremes of chick growth rates (Fig. 5) and when sample sizes were relatively high (Table 2). In 2011, chicks took on average 5 d longer to fledge at a smaller mass than did chicks in 2013, 27 d at 136 g vs. 22 d at 155 g (Table 1). The growth rate coefficient *K* differed among all study years by a factor of 1.8 (0.137–0.246 d⁻¹; Table 2). Average chick growth rate in 2013 (0.241 d⁻¹) was 18% higher than the

| Year | Total no. nests | Hatched | Fledged | Nestling period (d) | Mass at fledging (g) |
|------|----------------|---------|---------|---------------------|---------------------|
| 2009 | 12             | 5       | 42      | 1                   | 22.0                |
|      |                | 8       |         |                     | 148.4 ± 9.4         |
| 2010 | 15             | 9       | 60      | 4                   | 21.5 ± 0.5          |
|      |                | 27      |         |                     | 148.4 ± 9.4         |
| 2011 | 22             | 14      | 64      | 4                   | 26.5 ± 1.5          |
|      |                | 18      |         |                     | 136.4 ± 7.1         |
| 2012 | 21             | 14      | 67      | 10                  | 22.8 ± 1.3          |
|      |                | 48      |         |                     | 154.7 ± 5.0         |
| 2013 | 16             | 12      | 75      | 8                   | 21.8 ± 1.8          |
|      |                | 50      |         |                     | 155.1 ± 7.6         |
| 2014 | 23             | 10      | 43      | 4                   | 23.0 ± 0.0          |
|      |                | 17      |         |                     | 173.2 ± 26.3        |
| 2015 | 13             | 3       | 23      | 0                   | 0                   |
| 2016 | 17             | 7       | 41      | 3                   | 26.5 ± 1.5          |
|      |                | 18      |         |                     | 162.2 ± 33.3        |
| All  | 139            | 74      | 53      | 34                  | 23.4 ± 2.0          |
| years|                | 25      |         |                     | 149.5 ± 4.2         |

**Notes:** Grand means are averaged over all nests (not years). Only nests with documented hatching and fledging dates were used to calculate the nestling period.

Table 1. Nest fate and mean (±SD) nestling period and mass at fledging for Kittlitz’s Murrelets on Kodiak Island, Alaska.

![Fig. 3](https://www.esajournals.org/doi/abs/10.1890/17-0329.6)  

Fate of Kittlitz’s Murrelet nests on Kodiak Island, Alaska, in different years.
average growth rate over all years (0.205 d⁻¹; Fig. 4C), and 36% higher than in 2011 (0.177 d⁻¹); however, chicks received 14% more fish per day in 2011 than in 2013 (4.8 vs. 4.2 fish/d; Table 3). In addition to greater numbers of fish needed to fledge a chick in the year of slower growth (2011), sand lance were on average 6% longer in that year (Table 3). These anomalies suggest that the lower proportion of capelin in 2011 (7% vs. 15%), or perhaps lower energy density (kJ/g) of sand lance in the same year, led to slower growth in 2011 (Fig. 5). For Kittlitz’s Murrelets on Kodiak Island, the slower the growth rate, the longer the time to fledging (Fig. 4B), thereby increasing the duration of exposure to predation.

Numbers, length, and energy content of fish delivered

For nests in which chicks were monitored by cameras for at least 3 d, there were no differences among years in the average number of fish delivered per day (ANOVA, F₆,₃₈ = 1.02, P = 0.43; 2015 was not included in this analysis due to small sample size; Table 3). Sand lance and capelin together comprised 99.5% of identified fish delivered in each year. Based on literature values reviewed by Cauffope and Heymans (2005), energy density (kJ/g fresh mass) ranged from 3.2 to 6.5 for sand lance and 3.5–7.0 for capelin. However, in the size ranges delivered to Kittlitz’s
Table 2. Results of logistic growth analyses of the body mass (g) of Kittlitz’s Murrelet chicks on Kodiak Island, Alaska.

| Year | $n_1$ | $n_2$ | Growth rate ($K \pm SE$) | $r^2$ | Asymptote ($a \pm SE$) | Inflection point ($b \pm SE$) |
|------|------|------|----------------------|------|----------------------|----------------------|
| 2009 | 1    | 3    | 0.246 ± 0.044         | 0.938| 148.4 ± 9.4          | 5.3 ± 0.8            |
| 2010 | 3    | 10   | 0.246 ± 0.044         | 0.938| 148.4 ± 9.4          | 5.3 ± 0.8            |
| 2011 | 10   | 29   | 0.177 ± 0.022         | 0.934| 136.4 ± 7.1          | 6.3 ± 0.8            |
| 2012 | 9    | 32   | 0.206 ± 0.018         | 0.968| 154.7 ± 5.0          | 6.6 ± 0.5            |
| 2013 | 8    | 24   | 0.241 ± 0.036         | 0.927| 155.1 ± 7.6          | 5.0 ± 0.7            |
| 2014 | 4    | 13   | 0.137 ± 0.032         | 0.930| 173.2 ± 26.3         | 9.7 ± 2.9            |
| 2015 | 5    | 18   | 0.158 ± 0.046         | 0.877| 162.2 ± 33.3         | 8.0 ± 3.2            |
| All  | 40   | 129  | 0.205 ± 0.015         | 0.904| 149.5 ± 4.2          | 6.1 ± 0.4            |

Notes: $n_1$ = number of individual chicks for which growth measurements were obtained, $n_2$ = total number of growth measurements (including mass at hatching). Growth formula was $M = a/[1 + \exp\left\{ -K \times (\text{chick age} - b) \right\}$ where, $M$ = chick mass (g), $a$ = asymptote (g), $K$ = growth rate coefficient (day$^{-1}$), and $b$ = inflection point of curve (day; see Ricklefs 1983:422). Due to small sample sizes, 2009 and 2010 were combined for this analysis. No chicks fledged in 2015.

Table 3. Mean (±SE) numbers and lengths of fish delivered to Kittlitz’s Murrelet chicks on Kodiak Island, Alaska, as measured in images from nest cameras.

| Year | Total number of fish/d (mean ± SE) | Total number of fish | Fish length (mm) | Sand lance (%) | Sand lance$^\dagger$ | Capelin$^\ddagger$ |
|------|----------------------------------|---------------------|-----------------|---------------|------------------|------------------|
|      |                                  | Sand lance          |                 |               |                  |                  |
| 2009 | 4.1 ± 0.5                        | 88                  | 10              | 90            | 134.9 ± 1.0 a    | 133.2 ± 3.0 ab   |
| 2010 | 4.7 ± 1.1                        | 130                 | 7               | 95            | 136.9 ± 1.1 a    | 132.3 ± 4.5 ab   |
| 2011 | 4.8 ± 1.0                        | 707                 | 54              | 93            | 138.0 ± 0.4 a    | 134.3 ± 1.3 a‡   |
| 2012 | 4.2 ± 0.7                        | 504                 | 157             | 76            | 139.1 ± 0.6 a    | 125.2 ± 1.1 b‡   |
| 2013 | 4.2 ± 0.9                        | 523                 | 88              | 85            | 130.0 ± 0.7 b    | 139.7 ± 1.6 c‡   |
| 2014 | 3.8 ± 0.6                        | 203                 | 102             | 67            | 123.7 ± 1.0 c    | 123.6 ± 1.3 b    |
| 2015 | 2.0 ± 1.4                        | 15                  | 4               | 79            | 116.9 ± 4.0 cd   | 88.5 ± 7.7‡c    |
| 2016 | 4.2 ± 0.8                        | 236                 | 149             | 61            | 118.7 ± 1.2 d    | 106.5 ± 1.5‡c   |

Notes: Total number of fish per day includes only nests for which at least 3 chick-days were monitored by cameras and excludes the day of hatch. Sand lance and capelin comprised 99.0–100% of fish identified in each year, and 99.5% overall (other species included 0.3% herring and 0.1% salmon); 13% of fish were not identified due to poor image clarity. In the total number of fish delivered per day, 2015 ($n$ = 2 nests, neither surviving past day 4) differed from some other years (one-way ANOVA, $P = 0.02$. With 2015 removed, there were no differences among years ($P = 0.43$).

$^\dagger$ Within species, means that share the same letter among years do not differ, Tukey–Kramer HSD tests, $P < 0.05$.

$^\ddagger$ Within year, different from sand lance, t-test, $P < 0.05$.

Murrelet chicks (60–188 mm; Table 3), the much thicker-bodied capelin had an average 2.3 times (range = 1.2–3.3 times) greater mass, and therefore greater energy content per fish, than did sand lance of equal length (Eqs. 4 and 5). Average length of sand lance and capelin delivered to murrelet chicks did not differ in some years, and when it did differ the direction of difference was not consistent and was mostly less than 11% (Table 3). On average, chick meals consisting of capelin had much higher total energy content than did chick meals consisting of sand lance.

**Energy needs and fish required**

Total daily energy requirements for Kittlitz’s Murrelet chicks ranged from 117 to 149 kJ/d (Table 4). We chose to illustrate growth curves using data from two years with relatively high sample sizes (>100 chick-days in each year) and with exceptionally low (2011) and high (2013) chick growth rates. Mass estimated from length (Eqs. 3 and 4) indicated a difference of only 2.6 g/d (9%) in total fresh mass of fish delivered in 2011 (29.4 g/d) vs. 2013 (26.8 g/d; t-test, $P = 0.55$). The proportion of sand lance delivered as chick meals was higher in 2011 (93%) than in 2013 (85%; Table 3). For chicks in 2011 to achieve the same growth rate and time to fledging as in 2013, the energy density of sand lance would have had to increase by 31% from 4.29 to 5.64 kJ/g fresh mass (Table 4). Both values are within the range of published means for the energy density of sand lance (3.2–6.5 kJ/g fresh mass; Caufﬁpô and Heymans 2005).
Despite having similar average energy density (kJ/g fresh mass), the greater mass per unit length of capelin resulted in capelin having about 2.3 times the total energy content of sand lance of the same length. Thus, an increase in capelin in the diet from 5.6% to 27.2%, or from 0.25 to 1.21 individual fish per day, could also have enabled the higher growth rate and shorter time to fledging observed in 2013 (Table 4).

Calculations for other years and for all years combined (Table 4) indicated that variation in energy density of sand lance, in the proportion of capelin in the diet, or some combination of both could enable or preclude maximum chick growth rates, depending on annual variation in the energy density of sand lance or the relative availability of capelin. For example, in 2013 when average length, and thus mass, of capelin chick meals was greatest (Table 3), Kittlitz’s Murrelet parents could have delivered as few as 1.9 capelin per day to their chick and still meet the energy provisioning rate required for maximum chick growth rate, compared to the 5.5 sand lance needed to achieve the same growth rate.

**Impacts of variation in temperature**

The question arises as to whether annual energy demands of murrelet chicks might have been affected by costs of thermoregulation that varied among years. Ambient temperature measurements at equivalent nest sites were available only in 2014 and 2016 (no nests survived to provide growth rates in 2015). For those murrelet nests with temperature measurements that could be used to calculate chick energy requirements, mean temperature differed by only 0.4°C between 2014 (n = 3) and 2016 (n = 3; ANOVA, P < 0.01). Means for individual nests ranged from 13.3°C to 14.4°C (SD = 3.2°C–7.7°C). For those individuals, there was no relationship between total daily energy required and either the mean or variance of ambient temperatures at the nest site ($r^2 < 0.04$, $P > 0.71$). The lower critical temperature reported for Scripp’s Murrelet at age 12 d was 9°C (Fig. 8 in Eppley 1984), so mean nest site temperatures were well within the presumed thermoneutral zone for Kittlitz’s Murrelet chicks. For the 6 individuals for which data were available for both nest site temperatures and calculations of energy requirements, temperatures were below thermoneutrality during an average 10% of the total time monitored by an average of only 0.7°C. Assuming a 2.3% increase in RMR for each 0.5°C increment a chick was below thermoneutrality (Fig. 8 in Eppley 1984), our estimates of daily energy required would increase

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**Table 4.** Estimated energy intake required by Kittlitz’s Murrelet chicks (kJ/g) for observed growth rates on Kodiak Island, Alaska, the energy density (kJ/g fresh mass) of sand lance delivered in a given year needed to achieve observed or maximum observed growth rates (e.g., $K = 0.241$ in 2013; Table 2), the observed proportion of capelin in numbers of fish delivered to chicks in each year, and the proportion of capelin of the lengths observed in each year (Table 3) that would enable maximum growth, given the higher energy content per unit length of capelin (2.3 × that of sand lance).

| Year | Energy needed for observed growth (kJ/d) | Energy in sand lance needed for observed growth (kJ/g) | Energy in sand lance needed for max growth (kJ/g) | Observed capelin in diet (%) | Capelin in diet needed for max growth (%) |
|------|------------------------------------------|-----------------------------------------------------|--------------------------------------------------|-----------------------------|------------------------------------------|
| 2009 | 143.0                                    | 7.50                                                | 7.90                                             | 9.3                         | 13.1                                      |
| 2010 | 140.5                                    | 5.99                                                | 6.41                                             | 6.4                         | 12.4                                      |
| 2011 | 117.0                                    | 4.29                                                | 5.64                                             | 5.6                         | 27.2                                      |
| 2012 | 138.3                                    | 4.98                                                | 5.57                                             | 22.6                        | 34.7                                      |
| 2013 | 149.1                                    | 5.53                                                | 5.53                                             | 12.8                        | 12.8                                      |
| 2014 | 136.3                                    | 6.23                                                | 7.61                                             | 36.2                        | 46.2                                      |
| 2016 | 125.8                                    | 7.71                                                | 9.85                                             | 23.4                        | 56.2                                      |
| All years | 135.7                                    | 6.03                                                | 6.93                                             | 16.1                        | 28.3                                      |

Notes: Capelin in the diet needed for maximum growth assumes the length and energy density of sand lance actually observed in each year. No chicks fledged in 2015.
† Percentages of observed capelin in the diet do not exactly match values in Table 3 because a smaller sample of fish was delivered during the periods for which incremental measurements of chick body mass were available for Table 4.
by an average of just 1.0% (range 0–1.7%). According to these estimates of thermostatic costs, our estimates of the energy density of fish required by Kittlitz’s Murrelet chicks might have been underestimated by about 1.0% or 0.06 kJ/g fresh mass of fish, an order of magnitude lower than all differences among the 8-study years (Table 4).

Table 5. Daily survival rates of Kittlitz’s Murrelet nests on Kodiak Island, Alaska, calculated in Program Mark by methods described in Dinsmore et al. (2002).

| Year | Daily survival rate | Likelihood of survival | Difference |
|------|---------------------|------------------------|------------|
|      | Rate ± SE           | 95% CI                 | To day 52  | To day 57† |          |
| 2009 | 0.947 ± 0.016       | 0.906–0.971            | 0.060      | 0.056      | 0.005     |
| 2010 | 0.965 ± 0.010       | 0.938–0.981            | 0.159      | 0.147      | 0.012     |
| 2011 | 0.962 ± 0.009       | 0.941–0.976            | 0.135      | 0.125      | 0.010     |
| 2012 | 0.981 ± 0.006       | 0.965–0.989            | 0.363      | 0.336      | 0.027     |
| 2013 | 0.976 ± 0.008       | 0.952–0.988            | 0.281      | 0.260      | 0.021     |
| 2014 | 0.949 ± 0.011       | 0.921–0.967            | 0.065      | 0.060      | 0.005     |
| 2015 | 0.921 ± 0.021       | 0.869–0.954            | 0.014      | 0.013      | 0.001     |
| 2016 | 0.955 ± 0.012       | 0.926–0.973            | 0.092      | 0.085      | 0.007     |
| All years | 0.962 ± 0.004   | 0.954–0.968            | 0.142‡      | 0.131      | 0.011     |

Notes: Likelihood of survival from hatching to annual mean fledging age of 52 d after nest initiation in 2013, and 57 d after nest initiation in 2011, is presented to indicate how much extending the time to fledging over this range would affect annual survival (the difference).

† A daily survival rate of 0.984 was used to calculate survival between day 52 and 57 to account for the increase in survival with chick age. This survival rate was calculated from a nest survival model that incorporates chick age and time of season, the value chosen is a survival estimate during the last day of the nestling period for nests with an average hatch date.

‡ Survival calculated using egg stage survival (0.96220) × chick stage survival (0.96425).
In summary, ambient temperatures at nest sites appeared to be very similar between the two years when measurements were taken, and there was negligible effect of temperature differences among nests on patterns of estimated fish energy required by chicks. Thus, it is unlikely that annual variations in nest site temperatures appreciably contributed to among-year differences in the estimated energy requirements reported here, and by extension the estimated energy content of fish consumed. Weather variables we did not measure, such as wind speed, precipitation, or radiation, may have had effects on chick thermostatic costs that we could not account for. Therefore, we cannot conclude that fish energy content alone explained variations in chick growth rates independently of micrometeorological factors. However, our results do show that variations in fish energy content that are well within reported values are adequate to explain observed differences in growth rate.

**Chick survival and time to fledging**

Both apparent (Fig. 6) and modeled (Table 5) survival rates of Kittlitz’s Murrelet nests varied greatly among years. As noted in the above section Nest fate, the main cause of failure for nests that did not fledge was predation by red fox; predation accounted for 65% of nest losses on average, ranging from 36 to 93% among years (Fig. 3). Daily survival rate (DSR) during the egg stage (0.962 ± 0.005) decreased with nest age and was slightly less than DSR during the chick stage (0.964 ± 0.006). DSR for the chick stage also increased with nest age, resulting in low mortality rates for nestlings later in the chick stage (DSR = 0.984 ± 0.006). Nests were less likely to succeed over the 30-d egg stage (31.5%) than during the mean 23.4 d of the chick stage (42.8%; Table 5).

Higher chick growth rates, as observed in 2013, could potentially decrease the mean time to fledging by as much as 5 d compared to growth rates such as those observed in 2011 (Table 1, Fig. 6). Delays in fledging due to low growth rates in 2011 and 2016 would reduce apparent survival by 5–10% owing to extended exposure to red fox predation. To evaluate such effects on modeled survival rates, we used a higher daily survival rate of 0.984 for days 52–57 of the total nest period to account for the increase in survival with chick age. This survival rate was calculated from a nest survival model that incorporated chick age and time of season, and the estimate chosen was for the last day of the nestling period for nests with an average hatch date (7 July). Extending the nestling period by 5 d, as seen in annual means from this study, could decrease overall nest survival from 14.2% to 13.1% (Table 5), a relative decrease of 7.7%. For a species whose propensity to breed may average only 20%, and is much lower in some years (range = 5–45% among 6 yr; Kissling et al. 2016), this seemingly small difference could be important. Thus, although terrestrial predation is the main limitation to Kittlitz’s Murrelet egg and chick survival on Kodiak Island, duration of exposure to predation can be mediated to an extent by oceanic effects on the availability and quality of prey, and their resultant impact on chick growth rates.

**DISCUSSION**

For Kittlitz’s Murrelets nesting on Kodiak Island, variation in energy density of sand lance, or differences in total energy content of capelin vs. sand lance, could explain the observed variations in chick growth rate and associated nestling period. Low growth rates extended the nestling period and thus the period of exposure to predators, with the maximum annual exposure duration reducing overall nest survival by 7–8% over the minimum annual exposure duration. This indirect effect of oceanic prey conditions on terrestrial predation rates was far less than direct effects of predation on eggs and young throughout the nesting period. The low breeding propensity of Kittlitz’s Murrelet (Kissling et al. 2016), however, increases the importance of even small changes in nest success for achieving the reproductive output needed to maintain the population. Nevertheless, when predation pressure on nests is as high as was observed on Kodiak Island, the postulated Kittlitz’s Murrelet strategy of growing very rapidly to reduce exposure to predation is no longer adequate, especially with increasing oceanic temperatures that reduce the quantity and quality of prey in ways that further increase exposure to predation.

**Diet and growth rates in other areas**

Our findings are consistent with studies in other locations. In the Aleutian Islands, Kittlitz’s...
Murrelet chicks were fed lower quality prey (40% hexagrammids, 36% sand lance, 24% gadids and rockfish) compared to Kodiak (80% sand lance, 19% capelin, <1% herring and salmonids) or to Icy Bay along the northeast Gulf of Alaska (58% sand lance, 21% capelin, 9% smelt, 6% herring, 6% snake prickleback; Federal Register 2013; R. Kaler, unpublished data). These differences in prey quality apparently influenced rates of chick provisioning (9.8 fish/d in the Aleutians vs. 4.0 fish/d at Kodiak Island and 3.0 fish/d at Icy Bay) and contributed to low fledgling mass (about 50% of adult body mass in the Aleutians vs. 63% at Kodiak Island and Icy Bay). On Agattu Island, where most Aleutian nests were monitored, the mean (±SD) nesting period was 30.6 ± 5.6 d compared to 23.4 ± 2.0 d on Kodiak Island (Table 1; Federal Register 2013; R. Kaler, unpublished data). Chick growth rates are available for only one year on Agattu Island, but were 53% lower (0.096 d−1) than on Kodiak Island (overall mean of 0.205 d−1). Of the 79 nests with known fates in the Aleutians, 40% failed due to chick starvation or exposure, 24% were depredated, and 11% were abandoned after eggs failed to hatch. These data from the Aleutians concur with our findings on Kodiak Island that chick diet strongly influences growth rates, fledgling mass, and nest success of Kittlitz’s Murrelets, as has been found in a range of other seabird species (Brekke and Gabrielsen 1994, Kitaysky et al. 2003, 2010, Lyons and Roby 2011, Shoji et al. 2012).

**Effects of prey quantity and quality**

Substantial inter-annual variation in average chick growth rates could be explained by the energy content of prey delivered to Kittlitz’s Murrelet chicks. Although the energy density (J/g fresh mass) of sand lance and capelin is similar (Anthony et al. 2000), the much higher energy content per unit length of thicker-bodied capelin made them a much better prey type for a species that transports one prey item at a time to the nest site.

Across North America and Western Europe, reproductive success of seabirds has often been tied to availability of capelin or sand lance in a given year (Barrett and Krasnov 1996, Rindorf et al. 2000, Litzow et al. 2002, Hedd et al. 2006, Hatch 2013). In the northeastern Pacific, there are wide annual fluctuations in local abundance of these forage fish species, as well as long-term trends related to ocean climate (Anderson and Piatt 1999, Brown 2002). Following a shift from a cooler to a warmer ocean climate regime, capelin declined dramatically from high abundance in the early 1970s to very low numbers in the 1980s (Anderson and Piatt 1999, Zador and Frandsen 2016, Sydeman et al. 2017). Although stocks of sand eels (Ammodytes marinus) in Europe are monitored regularly in regard to their commercial harvest, congenic sand lance in the North Pacific are not commercially harvested and their inshore habitats are not regularly sampled (cf. Blackburn and Anderson 1997). Thus, it is unknown how long-term trends in sand lance might be related to Kittlitz’s Murrelet population trends. Pacific herring (Clupea pallasi), a forage fish species with high energy content similar to that of capelin and sand lance (Anthony et al. 2000), whose availability can have major effects on seabird growth and fledging success (Barrett and Krasnov 1996, Breton and Diamond 2014), also declined from high to very low abundance in the 1980s (Anderson and Piatt 1999) and has not recovered. Juvenile herring are a known prey of Kittlitz’s Murrelet (Federal Register 2013; Day et al. 2017), but were not detected at >1% of prey items in this study.

Variation in abundance and lipid content of prey fish can depend strongly on water temperature per se, as well as on food availability for forage fishes under differing ocean conditions (Robards et al. 2002, Danielson et al. 2016, Sousa et al. 2016, Sreenivasan and Heintz 2016, Cope- man et al. 2017, Sydeman et al. 2017, Wright et al. 2017). Given that variation in the energy content of even high-lipid prey can cause variation in growth rates of Kittlitz’s Murrelet, and that both capelin and herring have declined appreciably in abundance, it is likely that future conditions affecting the availability and energy density of sand lance (Wright et al. 2017) may be important to the population trajectory of Kittlitz’s Murrelet.

**Effects of episodic extreme events**

In 2015, we located only 16 Kittlitz’s Murrelet nests in our Kodiak Island study area, nest abandonment rates were higher than in any other year of the study, only three nests hatched, and no nests fledged young. Poor nest success
coincided with the greatest marine heat wave ever recorded in the northeastern Pacific, beginning in 2014 and extending into 2016 (Di Lorenzo and Mantua 2016, Walsh et al. 2018). Record-setting sea surface temperatures were as much as 3°C higher than average in the Gulf of Alaska and in 2015 corresponded with the lowest nest survival documented during the eight years of our study on Kodiak Island. During 2015, seabird productivity in the northern Gulf of Alaska was below average for almost all common species, Black-legged Kittiwakes (Rissa tridactyla) exhibited widespread breeding failures, and colony abandonment was recorded for Common Murres (Uria aalge) for the first time in over 35 yr of monitoring (Dragoo et al. 2016).

In March 2015, a seabird die-off began in the Gulf of Alaska which continued into spring 2016. The temporal and spatial scale of the die-off was unprecedented, with the number of dead birds estimated to be in the hundred thousands, mainly Common Murres (Piatt et al. 2020). Carcasses necropsied from several locations in the Gulf of Alaska indicated starvation as the cause of death in all cases. This finding suggested that the die-off was related to changes in the abundance, distribution, or quality of forage fish in response to the record warm sea surface temperatures (USFWS 2016, von Biela et al. 2019). This was not the first such occurrence (Piatt and van Pelt 1997), although effects in earlier instances were not as severe or pervasive. Moreover, additional heat waves are expected and may already be developing (Cornwall 2019a, b).

Beyond the failure of all Kittlitz’s Murrelet nests found on Kodiak Island in 2015, we continued to detect potential effects of the 2014–2016 heat wave during the 2016 nesting season. Double the search effort for nests resulted in fewer...
nests (17) being found than average (18), nest success (18%) was lower than average (25%), and lengths of both sand lance and capelin were shorter than in all preceding years except 2015 (Tukey–Kramer HSD, P < 0.05). These extreme years suggest that if warming continues, ocean conditions could overshadow the impact of high terrestrial predation rates on Kittlitz’s Murrelet nest success, or at least intensify effects of extended exposure to nest predators.

**Predation, ocean conditions, and the future of Kittlitz’s Murrelet**

Kittlitz’s Murrelets have an extreme breeding strategy relative to 14 other species of semi-preocial alcids: They have among the fastest chick growth rates, the shortest nesting periods, and among the lowest percentages of adult mass at fledging (Fig. 7). This strategy reduces the duration of exposure to nest predation and may function effectively in high alpine and other areas where predator numbers are low. However, studies in more accessible areas have revealed very high predation rates on murrelet nests by red foxes on Kodiak Island and by avian predators in the Aleutians (Glaucous-winged Gull, *Larus glaucescens*; Common Raven, *Corvus corax*; Federal Register 2013). On Kodiak Island, predation by red foxes was by far the main cause of nest failure, even in years with high chick growth rates and reduced duration of the nestling period. The red fox continues to expand its range and numbers northward and to higher elevations, perhaps in response to milder winters and increased vegetation in Arctic and alpine habitats (Hersteinsson and Macdonald 1992, Bartoń and Zalewski 2007, Fuglei and Ims 2008). Rising predation rates are affecting a range of tundra-nesting birds, for which nesting in the Arctic where predation has historically been low (McKinnon et al. 2010) has become a poor strategy as predators have increased and alternative lemming prey have declined (Kubelka et al. 2018).

Such climate-related changes will likely expose Kittlitz’s Murrelet nests to greater predation pressure (Federal Register 2013), together with warmer ocean conditions that reduce prey availability or quality for chicks, prolong exposure of nests to predation, and cause intermittent breeding failure. As proposed for tundra nesters (Kubelka et al. 2018), our study suggests that previously successful antipredator strategies may actually facilitate population declines as predator numbers increase in concert with deteriorating prey conditions. The situation at Kodiak Island may presage a future in which the unusual breeding strategy of Kittlitz’s Murrelet renders it especially vulnerable to climate-driven changes in both nest predation rates and availability of high-energy prey.

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