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Abstract

The marbled murrelet (*Brachyramphus marmoratus*) is a federally threatened seabird that continues to decline throughout its range. Murrelets utilize late-successional and old growth coastal forest as nesting habitat, and forage in the marine environment. Murrelet adults invest heavily in raising a single young per year, and chicks are dependent on adults for all their nutrition during the 27- to 45-day nestling period. Rates of nestling growth and development are highly sensitive to food quality and quantity. We developed a nutritional model that examined the effects of missed feedings for murrelet chicks. Six dietary scenarios were developed to simulate murrelet chick feeding: a high-quality, intermediate, and low-quality diet, with one or two feedings missing from each diet. Five of the six scenarios resulted in insufficient energy for marbled murrelet chicks, with only the high-quality diet able to provide sufficient energy with one missed feeding. The intermediate and low-quality diets with missed feedings were not able to meet the metabolic requirements of the developing chick, and over time would likely result in growth stunting and starvation. Future conservation actions should focus on avoiding disruptive activities at places and times when adult murrelets are likely to be engaged in meal deliveries to chicks, and on improving forage conditions for murrelets.

Keywords: Marbled murrelet, *Brachyramphus marmoratus*, disturbance, feeding, chicks

Introduction

Marbled murrelets (*Brachyramphus marmoratus*) (hereafter murrelets) are small, US federally threatened seabirds of the Alcidae family. They are highly cryptic and nest in large trees, usually within older-aged conifer coastal forest from Alaska to central California (Nelson 1997, Raphael 2006). Murrelets consume a diversity of marine prey species from near-shore areas, including small fish and invertebrates, and fly up to 100 km inland to nest and take prey items to their young (Nelson 1997, Hull et al. 2001). They utilize a flexible foraging strategy (Hunt 1995) and constantly adapt to changes in prey size and distribution (Kuletz 2005), choosing prey based on either their availability or their energetic value

(Carter and Sealy 1990). Murrelets are especially sensitive to declines in forage quality because they have high metabolic energy demands (Hull et al. 2001). They invest heavily in a single offspring per year, resulting in a high parental investment per young (Ydenberg 1994). Reproductive success is dependent on food availability, predation risk, and nest site availability (Divoky and Horton 1995, Peery et al. 2004). Of these factors, food availability is often the most sensitive to environmental change, and variation in marine conditions can result in altered levels of food availability for adults and chicks (Weathers 1996, Peery et al. 2004). Changes in food availability can also interact with changes in the terrestrial environment to affect nesting (Betts et al. 2020).

Murrelets eat a wide variety of prey including fish such as Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), Pacific sand lance (*Ammodytes personatus*), smelt species (Osmeridae), and rockfish species (*Sebastes* spp.), and invertebrates such as squid (e.g., *Dory-*

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teuthis opalescens), krill (Euphausiacea), and shrimp (Mysida) (Burkett 1995, Fountain et al. 2023). Adult diets vary between the pre- and post-breeding periods (Becker et al. 2007) and also differ markedly from nestling diets. Nestlings are primarily fed age 1+ fish between 60 and 130 mm long, whereas adults also eat larval fish between 30 and 60 mm long, and even smaller invertebrates (Burkett 1995, Kuletz 2005). These larger fish may be less abundant and more difficult to obtain than the smaller fish and invertebrates consumed by adults, and may be available in different places or at different times of the day (Carter 1984, Carter and Sealy 1990, Burkett 1995). Fish species fed to nestlings vary by location and over time and may undergo marked shifts within a single breeding season (Strong et al. 1993, Kuletz 2005, Janssen et al. 2011).

Evidence from stable isotope studies shows that murrelet diets have changed over the last century or more, with a decline in the trophic level of prey items (Becker and Beissinger 2006, Norris et al. 2007, Gutowsky et al. 2009). This indicates that high trophic level, energy-rich fishes, such as herring and northern anchovy, now make up a smaller proportion of the murrelet diet than they did previously, whereas low and mid-trophic prey, such as krill and sand lance, have increased in proportion. In the Puget Sound region, Pacific sand lance now comprise a larger proportion of the marbled murrelet nestling diet than they did historically (Gutowsky et al. 2009). This is significant because sand lance have the lowest energetic value of the fishes that marbled murrelets commonly feed on. For example, a single northern anchovy has nearly six times the energetic value of a sand lance of the same size (Gutowsky et al. 2009). These long-term changes in trophic level have been associated with decreases in reproductive success and declining populations of murrelets across their geographic range (Becker and Beissinger 2006, Norris et al. 2007, Gutowsky et al. 2009).

Food availability and diet quality influence individual murrelet reproductive success and may be a limiting factor to the lifetime reproductive output of murrelets (Becker et al. 2007). The dietary shift toward lower trophic level prey has

important energetic consequences for egg production (Becker and Beissinger 2006, Janssen et al. 2009), nestlings, (Gutowsky et al. 2009) and fledgling success (Becker et al. 2007). Murrelets are more likely to occupy nesting habitat during good ocean conditions and more likely to vacate nest stands following poor ocean conditions (Betts et al. 2020). This is likely because murrelets forego breeding if they cannot find sufficient food resources in preparation for breeding (Peery et al. 2004), and females eating a diet that promotes good body condition are more likely to produce eggs (Janssen et al. 2009). There is no simple association between trophic level of prey consumed by adults and reproductive success, presumably because adults can obtain adequate nutrition by eating a few high-value prey items or by eating many lower-value, but more readily available, prey items (Becker et al. 2007, Janssen et al. 2009). Murrelet parents foraging for chicks have less flexibility and may not be able to compensate for a lack of high-value fish with a larger number of lower-value feedings, due to the time and energy costs associated with inland flights (Gutowsky et al. 2009). This may be why poor food availability is associated with reduced reproductive success, even when murrelets increase foraging effort (Ronconi and Burger 2008). The inability to compensate may especially be the case when nests are located far from foraging areas. Although available data do not indicate that nesting farther inland reduces nesting success (Hull et al. 2001, Barbaree et al. 2014, Lorenz et al. 2017), murrelets are more likely to vacate far inland sites than those closer to the coast (Betts et al. 2020) perhaps because time and energy budgets do not allow for long flights between foraging and nesting areas when the only fish available are nutrient-poor and many deliveries would be required for chick survival.

Feeding and Nutritional Ecology of Murrelet Chicks

Chick growth and development changes with food supply and is the breeding parameter most sensitive to food availability within other alcid species (Baillie and Jones 2004). Murrelet chicks hatch after 27–30 days and grow rapidly, gaining 5–15 g

per day during the first nine days after hatching (Simons 1980, Hirsch et al. 1981, Nelson and Hamer 1995). To fuel this rapid rate of growth, chicks receive an average of 3.2 meals per day (range 1–8 meals on any given day; Nelson and Hamer 1995) from their parents. We would not expect daily feedings at the high end of this range to be a regular occurrence; to our knowledge, there has only been one single observation of a chick being fed eight times in one day, and while that chick was fed seven times in a day more than once, the average was four feedings per day (Jones 1993, Nelson and Hamer 1995). Subsequent information indicates that chick feedings may often be less frequent than previously reported, with a range of 0–6 meals per chick per day and individual chicks receiving a daily average of 1.3 to 3.2 feedings in Oregon (Dachenhaus et al. 2022) and 2.4 feedings per day averaged across sampled nests in British Columbia (Bradley et al. 2002). Note that these observed feeding rates may not meet the nutritional needs of murrelet chicks, and in the case of the chick fed an average of 1.3 times per day, the chick died, likely of starvation (Dachenhaus et al. 2022). It is not clear whether this represents a change over time in nestling feedings, as sample sizes are generally small, and the studies showing fewer than three feedings on average occurred 20 years apart (Bradley et al. 2002, Dachenhaus et al. 2022).

Feedings are most common at dawn and dusk (Nelson and Hamer 1995), with morning flights accounting for up to 80% of dawn/dusk provisioning events (Barbaree 2011, Lorenz et al. 2019). Parents fly inland to provision nestlings for 27 to 45 days, until fledging (Nelson and Hamer 1995, Dachenhaus et al. 2022) or until chicks are between 58 and 71% of adult mass (Nelson 1997). Both adults feed young and generally carry a single fish. On average, over the course of a 27 to 40 day nestling period, nestling murrelets require a total of 38 herring to 255 capelin to support fledging (Kuletz 2005). Note that the youngest murrelet chicks would not likely be able to consume a 23 g herring, so a diet consisting entirely of herring in this size class represents a hypothetical extreme, rather than a strictly realistic scenario. Overall, chick rearing success can be predicted by the

number of food deliveries by adults while the chick is in the nest (Bradley et al. 2004).

There are several factors that influence murrelet chicks' vulnerability to energy deficits. First, seabird chicks exhibit a larger surface area per unit body mass than adults (Visser 1998). As a result, low ambient temperatures can result in high thermoregulatory costs to chicks. Therefore, energy can be easily diverted to maintenance of body temperature and away from growth, particularly when the chick is very small and heat losses to surface area are significant. Second, metabolic priorities are different for young birds than adults (Janssen et al. 2011, Elliott et al. 2014). As a result of the ontogenetic changes that occur in water content, fat, protein ratios, muscle gain, and thyroid function as chicks grow, there is a continuous increase in the proportion of metabolically active mass, which tends to be energetically expensive to maintain (Weathers and Siegel 1995). In this case, the chick body is allocating available energy to both maintenance of existing tissue as well as to the production of new biomass until fledging (Roby 1991). In addition, the caloric deficit from missed feedings is sometimes further exacerbated by a decrease in food deliveries from murrelet parents, especially female parents, prior to fledging (Nelson and Hamer 1995, Bradley et al. 2002, Barbaree 2011). If food is limited for the chick during nesting, poor growth, delayed fledging, increased mortality, and nest abandonment can occur. If a chick meal is lost, it is not clear that murrelet parents will engage in additional flights or foraging to compensate for the lost meal, or that they will be successful if they attempt to do so (Speckman et al. 2004). For the growing chick, altered or delayed development may be the only available response to such fluctuations in food resources. When decreases in food intake occur, chick growth is compromised so that maintenance, thermoregulation, and activity remain unaffected (Schew and Ricklefs 1998). In addition, growth only occurs within a certain time window and terminates at a specific age. The patterns of growth and prioritization seen in murrelets during times of food scarcity are consistent with the tenets of the adaptive growth hypothesis, which predicts that individual nestlings preferentially allocate

resources to growth of high-priority body components (Janssen et al. 2011), such as those for flight and feeding. For example, both bill length and wing length are prioritized because they are crucial for prey capture during the first week of independence in the absence of post-fledging parental care. Wing growth is essential to reach independence because failure to reach the ocean on the first flight is usually fatal (Janssen et al. 2011).

In the context of assessing the effects of human activities for murrelets, a disturbance event is considered significant when activity causes a murrelet to delay or avoid nest establishment, delay an exchange of incubation duties, flush away from an active nest site, or abort a feeding attempt during the nestling phase. These responses are considered significant because they have the potential to result in reduced hatching success, fitness, or survival of juveniles and adults (Teachout 2015). There are myriad stimuli that can be perceived as negative and therefore can activate a stress response in murrelets. Murrelets tend to nest in areas that are less affected by the human footprint, but their exposure to anthropogenic activities has increased over time (Raphael et al. 2016a). Murrelet presence in marine areas is also greater in areas with fewer anthropogenic influences (Raphael et al. 2016b). Human activities and presence near nest trees have caused adult murrelets to delay nestling feedings or abort attempts to feed their chick by dropping the fish and flying away when startled or disturbed (Hamer and Nelson 1998, Long and Ralph 1998). At sea, fish-holding murrelets preparing to fly inland have been observed swallowing the fish intended for their nestling in response to disturbance by small boats (Speckman et al. 2004). In addition to missed feedings, nestlings subjected to disturbances may also experience behavioral and physiological consequences, some of which involve increased energy expenditure. Murrelet chicks spent less time resting during experimental disturbance with chainsaws than before or after the disturbance (Hébert and Golightly 2006). Numerous studies of other bird species have documented physiological responses to noise, aircraft overflight, human presence, or handling. Responses include increased heart rate, in some cases for up to three hours after disturbance

(Weimerskirch and Guionnet 2002, Ellenberg et al. 2013), increased body temperature for up to six hours after disturbance (Regel and Putz 1997), and stress hormone responses (Ellenberg et al. 2007). In one case, mallard (*Anas platyrhynchos*) chicks exposed to four weeks of experimental noise treatments exhibited a 4.6% reduction in biomass and altered skeletal growth relative to control chicks, even though they were fed the same diet (Fleming et al. 1996).

To look at the potential impacts of disturbance on nesting murrelets, we examined the energetic consequences of missed feedings for developing murrelet chicks. The assumption behind this nutritional model was that something disturbed the murrelet parent, and the fish intended for the chick was dropped as a result. Furthermore, we assumed the murrelets did not engage in compensatory feedings when a meal was lost, and the loss of a fish represented a significant energy deficiency in the daily consumption of a developing chick. We examined the energetic consequences for a developing chick of one or two missed meals of different nutritional quality to examine whether missed feedings due to anthropogenic disturbance could have serious nutritional and developmental consequences to individual murrelet chicks.

Methods

Nutritional Model: Energetic Consequences of Missed Feedings for Murrelet Chicks

We developed three possible feeding scenarios to examine the nutritional effects of missed feedings for murrelet chicks. The high-quality diet comprised three herring and offered a nutritional reward of $411 \text{ kJ}\cdot\text{day}^{-1}$; the intermediate-quality diet comprised two sand lance and one herring and provided $273 \text{ kJ}\cdot\text{day}^{-1}$ of energy; and the low-quality diet comprised three sand lance and provided $204 \text{ kJ}\cdot\text{day}^{-1}$ of energy. The range of $261\text{--}303 \text{ kJ}\cdot\text{day}^{-1}$ is the peak daily metabolized energy for a chick needed to support basic metabolic and growth demands (Kuletz 2005) and was used for all chick metabolic calculations. In addition, we assumed an 80% assimilation rate for all foods consumed (Kitaysky 1999, Niizuma and Yamamura 2004, Table 1).

TABLE 1. Data used for calculations of the energetic consequences of missed feedings for marbled murrelet chicks. Data come from published literature for energy consumed per day per chick and the energetic values for herring and sand lance, and utilized the standard equation for assimilation efficiency of consumed foods. Energetic values, both for energy consumed by the chick and energetic value of each fish, are reported with the assimilation efficiency applied.

Factor	Value used	References
Energy consumed $\cdot d^{-1} \cdot chick^{-1}$	261–303 $\text{kJ} \cdot d^{-1}$	Kuletz 2005
Assimilation efficiency*	80%	Kitaysky 1999, Niizuma and Yamamura 2004
Energetic value for herring (23g)	137 $\text{kJ} \cdot fish^{-1}$	Vermeer and Devito 1986, Anthony et al. 2000, Kuletz 2005, Romano et al. 2006
Energetic value for sand lance (12g)	68 $\text{kJ} \cdot fish^{-1}$	Van Pelt et al. 1997, Anthony et al. 2000, Kuletz 2005, Romano et al. 2006

*Assimilation efficiency = (metabolizable energy \cdot gross energy intake $^{-1}$) \times 100 (Engelmann 1966)

Results

High-Quality Diet

The first diet examined within this nutritional model represented a high-quality diet. This diet represented the best scenario for growing murrelet chicks and was energetically very dense, but may be hard to achieve in the current marine environment (Becker and Beissinger 2006, Gutowsky et al. 2009, Dachenhaus et al. 2022). The high-quality diet comprised three herring consumed throughout the day (Table 2, Table 3). Each herring (at 23 g) had an energetic value of 137 kJ (Kuletz 2005). The three herring provided 411 kJ for developing chicks, which exceeds the maximum daily requirement for chick development by over 100 kJ. For seabirds, this excess of energy can result in faster development and shorter time at the nest before fledging (Visser 2002). When one fish was not delivered to the waiting murrelet chick on the high-quality diet, the chick still consumed two herring that day, resulting in 274 kJ. This value is still within the range of 261–303 $\text{kJ} \cdot \text{day}^{-1}$ that supports basic metabolic needs and growth for the chick. If two fish were dropped and not delivered to the chick, the chick only received energy from one herring that day, resulting in only 137 kJ consumed. This represented 45–52% of the daily needs of the chick.

Intermediate-Quality Diet

The second diet comprised two sand lance and one herring for the three feedings given to chicks daily. The combination of two sand lance and one herring resulted in an energy content of 273 kJ, which is at the lower end of the range of the daily metabolic needs for murrelet chicks and only 10 $\text{kJ} \cdot \text{day}^{-1}$ above the minimum value required for metabolic maintenance. When one fish was dropped, two different energy situations could result as the fish not delivered could be either a sand lance or a herring (Table 2, Table 3). If a sand lance was dropped, then the chick would consume 205 kJ that day. However, if the single missed feeding was a herring, then the chick would consume 136 kJ that day. Both values are below the energetic threshold at which chicks can meet their basic needs, and hover around 60% of the total energy needed each day to support basic metabolism. The loss of two intermediate-quality feedings within a day could either result in the loss of two sand lance, or one sand lance and one herring. This would result in an energetic intake of 137 kJ at a maximum and 68 kJ at a minimum for that day. The 68 kJ value, generated from the loss of one sand lance and one herring, would result in the chick only eating a single sand lance, which represents only 22–26% of their required energy that day.

Low-Quality Diet

The third diet represented what would be available in an area that had a significant change to food

TABLE 2. Calculations showing total potential energetic values that come from the consumption of the high-quality, intermediate-quality, and low-quality diet for marbled murrelet chicks, and what energetic values are available to chicks when one fish or two fish are dropped during feeding for the high-quality, intermediate-quality, and low-quality diets.

Diet quality	When one fish is dropped during feeding	When two fish are dropped during feeding
High 3 herring = 411 kJ	274 kJ available	137 kJ available
Intermediate 2 sand lance + 1 herring = 273 kJ	136–205 kJ available	68–137 kJ available
Low 3 sand lance = 204 kJ	136 kJ available	68 kJ available

TABLE 3. Energetic values associated with marbled murrelet chick diets. Nine feeding scenarios (3 diet qualities by 3 feeding quantities) were evaluated. High-quality diets were only composed of herring. Intermediate-quality diets were composed of a combination of two sand lance and one herring; a diet quantity of 2 resulted in one sand lance and one herring (upper values) or two sand lance (lower values); and a diet quantity of 1 resulted in one herring (upper values) or one sand lance (lower values). Low-quality diets were only composed of sand lance. Diet quantity represents the number of forage fish available to a chick. Energetic values for forage fish and daily metabolic needs for chicks (261–303 kJ·d⁻¹) were based on Kuletz (2005). The value for kJ·d⁻¹ lost represents energetic differences from the high-quality diet of three prey items. For sufficiency, Y indicates energy values meet the daily needs of a chick; N indicates energy values do not meet the daily needs of a chick.

Diet quality	Prey species	Diet quantity	kJ·d ⁻¹ available	kJ·d ⁻¹ lost	kJ·d ⁻¹ sufficiency
High	3 herring	3	411	0	Y
		2	274	137	Y
		1	137	274	N
Intermediate	2 sand lance + 1 herring	3	273	138	Y
		2	136–205	206–275	N
		1	68–137	274–343	N
Low	3 sand lance	3	204	177	N
		2	136	275	N
		1	68	343	N

availability, or a bad year for foraging within the expected variation of marine food availability where sand lance are the primary prey species for nestlings. The low-quality diet comprised three sand lance. Combined, the three sand lance provided 204 kJ of energy, which is 67–78% of the energy needed for basic maintenance and growth on a daily basis. The loss of one sand lance would reduce the consumed energy to 136 kJ, which is 45–52% of daily metabolic need (Table 2). The loss of two fish would have resulted in 68 kJ consumed that day and would represent 22–26% of daily required energy to support basic metabolism.

Discussion

A missed feeding is a very significant event in the development period of a nestling marbled

murrelet. Access to adequate nutrition for chicks with each feeding is key to their growth and survival. Of the three diets (high quality, intermediate quality, and low quality), the only diet that could still meet the metabolic requirements of a murrelet chick with the loss of a single feeding was the high-quality diet. Only the high-quality diet could meet the metabolic needs of a growing chick with the loss of one feeding. With two feedings lost, the intermediate and low-quality diets would presumably result in malnutrition and growth stunting (Sears and Hatch 2008) for each day they remained at this level of intake, and death by starvation if experienced for a high enough proportion of their nestling period. Murrelet chicks fed the intermediate or low-quality diets would likely suffer from significant energetic

deficiencies with the loss of only a few feedings. As a result of the lower energetic density of sand lance compared to herring, a murrelet would have to consume two to three times as many sand lance to get the same energy they would by consuming one herring (Kuletz 2005). Overall, five of the six missed-feeding scenarios analyzed would be detrimental to the murrelet chick and, if continued for multiple days, would provide inadequate nutrition to support metabolism and growth necessary to fledge (Kuletz 2005). The results of this model demonstrate that human activities that result in disturbance near the nest area or at sea have the potential to result in malnourishment for fast-growing murrelet chicks. This exercise demonstrated the potential for malnutrition and potentially starvation in murrelet chicks, as well as delayed fledging and possible death, as a result of restricted food consumption following anything that causes missed feedings.

The consumption of insufficient energy can have both short- and long-term effects for developing murrelet chicks. In the absence of available research on food deprivation to marbled murrelet chicks, we present the results of other avian nutritional studies as proxies to determine the effects of caloric restrictions on marbled murrelet chicks, with emphasis on studies of other alcids where available. Food restriction results in effects throughout the body of bank swallow (*Riparia riparia*) chicks, including notable reductions in body mass, intestinal mass, pectoral muscle mass, fat reserves, body temperature, and resting metabolic rate (Brzek and Konarzewski 2004). Stunting and changes to the developmental sequence begins when these chicks are given 74% of their energetic intake for three days (Brzek and Konarzewski 2004), demonstrating that even at nearly three-quarters of their normal energy intake, there can be significant effects. This level of intake is comparable to our low-quality diet scenario when the murrelet chick receives all three meals, indicating that when these chicks are fed mainly sand lance, they likely require an above-average number of feedings to develop normally. A study of another alcid, the rhinoceros auklet (*Cerorhinca monocerata*), found that a 50% reduction in dietary intake through the

latter two-thirds of chick development resulted in permanent growth stunting (Sears and Hatch 2008). In our intermediate and low-quality diet scenarios, the loss of one meal resulted in daily energy intake falling to around half of metabolic need, and we would expect these disruptions in growth to begin even after a single missed feeding. European starling (*Sturnus vulgaris*) chicks at 8 days old, fed a weight-maintenance diet that supported metabolism but not growth, dropped to 80% of the normal tarsus growth rate by day one, and were at 40% tarsus growth rate by day three (Schew 1995). Additionally, wing growth was reduced to 60% normal growth rate by day three (Schew 1995). After one day of a diet that only supported weight maintenance, Japanese quail (*Coturnix japonica*) chicks slowed the rate of wing growth to as little as 20%, and tarsus growth to as little as 15%, of the growth in the control group, and after three to ten days on this diet, when it occurred early in development, the pace of growth did not fully recover after normal feeding was resumed (Schew 1995). Within the first day of energetic restriction, oxygen consumption decreased, body temperature dropped, growth of all tissues except the brain ceased, and the rate of maturation decreased (Schew 1995). When growth is slowed but maturation is not similarly delayed, the ontogenetic trajectory deviates from its normal course, and the chick could fail to attain normal adult size before maturity closes off the growth phase. For carrion crows (*Corvus corone corone*), slowed growth without delayed maturation resulted in permanent stunting and reduced fitness (Richner et al. 1989). Furthermore, in alcids, including Kittlitz's murrelets (*Brachyramphus brevirostris*), horned (*Fratercula corniculata*) and tufted (*F. cirrhata*) puffins, crested (*Aethia cristatella*) and parakeet (*A. psittacula*) auklets, and rhinoceros auklets, reductions in nutritional intake often result in delayed fledging in addition to altered growth patterns (Harfenist 1995, Kitaysky 1999, Knudson et al. 2020).

Starvation represents the most extreme consequence of energy deprivation for animals. Starvation often follows extended periods of inadequate energetic consumption. To maintain physiological function during starvation, energy comes from the

oxidation of body lipids and proteins following glycogen storage exhaustion. For the little auk (*Alle alle*), another small alcid species, chicks were estimated to have lipid mass capable of supporting approximately one to three days of fasting, depending on chick age and prior food availability (Taylor and Konarzewski 1989). Lipids are a high-density energy source that can be used in the longer term, but when those are exhausted, proteins, which have a much lower energy density and cannot support metabolism as readily, are used as an energy source (Kurpad and Aeberli 2013). Mortality most often occurs following a critical threshold of protein depletion (Caloin 2004). For example, Emperor penguin (*Aptenodytes forsteri*) chicks typically undergo a period of fasting during their post-fledging molt, and if their body mass falls below a critical threshold of 4 kg, or approximately one-third of their mass at fledging, they are highly likely to die of starvation (Putz and Plotz 1991). For alcids (horned and tufted puffins, and crested and parakeet auklets), this is likely to occur whenever the rate of feeding is too low to support a minimal resting metabolic rate for an extended period (Kitaysky 1999).

How juvenile animals allocate their energy reserves during starvation to meet the conflicting demands of allocating energy to support skeletal growth, tissue maturation, and the deposition of fat is not often studied (Gownaris and Boersma 2021). Studies of starvation patterns in Magellanic penguins (*Spheniscus magellanicus*) demonstrate that chicks are more likely to suffer energetic constraints during the period before chicks begin to thermoregulate (Boersma and Stokes 1995, Gownaris and Boersma 2021). During this early period, vulnerability to starvation can occur if chicks miss a meal (Gownaris and Boersma 2021). Chicks that are most vulnerable to starvation are those that were unable to achieve adequate body size to support metabolism and subsequent fledging. This is especially true for those that begin periods of energy deprivation with lower adiposity levels. In summary, how much a chick is fed, how often it is fed, and the composition of the chick's diet all influence how a chick allocates its energy, and how prone to starvation it will be as a result (Gownaris and Boersma 2021).

Additionally, there is a strong relationship between peak levels of daily metabolized energy during the growth period as a function of mass, and the metabolic effect of an accelerated change in mass for a rapidly growing seabird chick (Visser 2002). As a result, the effect of insufficient energetic intake in the first 15 days could be more detrimental than in the second 15-day period for marbled murrelets. Because the first 15 days represent a critical time of growth for murrelets (Nelson and Hamer 1995), and metabolic demands per gram of body weight are elevated to support rapid growth, the effects of food deprivation and their subsequent effects into adulthood are more significant within this time period. Often called a "critical period" in nutrition, it is a period in the development of the bird that can influence fledgling survival, as well as adult morphology and fitness (Klasing 1998, Ohlsson et al. 2002) because of the rapid rate of growth and associated development. Therefore, caloric insufficiency, as seen with the loss of even one fish meal within the intermediate and low-quality diet, occurring within the first 15 days of the nesting period would be much more influential to chick development and stature than if it occurred in the second 15-day period of nesting. We note that a newly hatched, 35 g chick likely cannot physically eat a 23 g herring, so the daily delivery of three or even more smaller fish in the early nestling phase should be particularly important to components of the chick's long- and short-term fitness.

Prey availability and quality varies in time and space, and further changes in marbled murrelet prey resources are occurring due to climate change and other anthropogenic causes. Sand lance in the Salish Sea may be smaller for their age class than those in the Gulf of Alaska (Matta and Baker 2020), and the size estimates used in our model come from Gulf of Alaska sand lance populations (Van Pelt et al. 1997, Anthony et al. 2000, Kuletz 2005, Romano et al. 2006). Furthermore, during marine heat waves, sand lance of the ages consumed by murrelet chicks are reduced in size and nutritional value (von Biela et al. 2019), and while marine heat waves have always occurred, they are likely to become more common in the future (IPCC 2019). Naturally occurring climate

regime shifts have caused the collapse of some forage fish populations within the range of murrelets (Anderson and Piatt 1999, Chavez et al. 2003), and the effects of anthropogenic climate change, including increased water temperatures, acidification, and deoxygenation, are expected to result in additional reductions in forage fish populations (Thayer et al. 2008, Ainsworth et al. 2011). Overfishing and reduction in the quantity or quality of spawning habitats also contribute to lower abundance of important forage fish species such as herring and sardine (Becker and Beissinger 2006, Levin et al. 2016). Availability of other prey species, such as rockfish, is becoming more variable as climate change increases the variability of ocean conditions (Sydeman et al. 2013). Additionally, marbled murrelets may experience intensified competition for the prey that are available, as warming water increases the metabolic demands of the predatory fish that share the same forage base (Piatt et al. 2020).

Current murrelet reproductive rates are low, typically lower than the rates required for the average individual murrelet to replace itself over its lifetime, a prerequisite for population stability. One radiotelemetry study reported a fecundity rate estimate of 0.027, or 2.7 female chicks produced per year for every 100 females of breeding age (Peery et al. 2004). Other radiotelemetry studies provided information on the number of successful fledging events per radio-tagged murrelet (e.g., Bradley et al. 2004, Peery et al. 2004, Lorenz et al. 2019). Combining this information with the methods of Peery et al. (2004) results in fecundity rates ranging from 0.021 to 0.063 female fledglings per adult female (Hébert and Golightly 2006, Lorenz et al. 2017). Ratios of juveniles to older birds at sea are also generally lower than the minimum ratio of 0.176 that appears to be required for population stability (Beissinger and Peery 2007). For example, Lorenz and Raphael (2018) report a long-term average juvenile ratio of 0.067 in the San Juan Islands of Washington. Decreased prey availability and reduced prey quality are likely factors contributing to poor murrelet reproduction (Peery et al. 2004, Ronconi and Burger 2008), and changes in diet may have contributed to population declines over the last

150 years (Becker and Beissinger 2006, Norris et al. 2007, Gutowsky et al. 2009). In the context of declining nutrition, missed feedings caused by disturbance are likely to have increasingly poor outcomes for individual chicks, and in aggregate, for murrelet populations.

To reduce the likelihood of disrupting chick feedings when construction or timber harvest activities occur in or adjacent to murrelet nesting habitat, these activities could be timed to occur when nestlings are not present. If that is not possible, these activities could be restricted to the mid-day period when chick feedings occur less frequently. Similarly, marine construction occurring in and around important foraging and staging areas during the nesting season could be curtailed when murrelets are present, especially during pre-dawn and pre-dusk periods when murrelets are likely to be holding fish to carry inland (Thoresen 1989, Burkett 1995). Conservation measures aimed at restoring prey populations or increasing their resilience to climate change could also improve foraging conditions and reduce the severity of the consequences of a missed feeding. In addition, studies to better understand time-energy budgets, more refined detail on nest-visitation rates, and an analysis of what foods are currently being fed and in what quantity to murrelet chicks across their range would inform future work toward the recovery of murrelets. Much work remains to understand the population dynamics of marbled murrelets and their nutritional ecology following disturbance events.

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