

WATERBIRDS

JOURNAL OF THE WATERBIRD SOCIETY

VOL. 29, NO. 4

2006

PAGES 407-524

Testing the Junk-food Hypothesis on Marine Birds: Effects of Prey Type on Growth and Development

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Abstract.—The junk-food hypothesis attributes declines in productivity of marine birds and mammals to changes in the species of prey they consume and corresponding differences in nutritional quality of those prey. To test this hypothesis nestling Black-legged Kittiwakes (*Rissa tridactyla*) and Tufted Puffins (*Fratercula cirrhata*) were raised in captivity under controlled conditions to determine whether the type and quality of fish consumed by young seabirds constrains their growth and development. Some nestlings were fed rations of Capelin (*Mallotus villosus*), Herring (*Clupea pallasii*) or Sand Lance (*Ammodytes hexapterus*) and their growth was compared with nestlings raised on equal biomass rations of Walleye Pollock (*Theragra chalcogramma*). Nestlings fed rations of herring, sand lance, or capelin experienced higher growth increments than nestlings fed pollock. The energy density of forage fish fed to nestlings had a marked effect on growth increments and could be expected to have an effect on pre- and post-fledging survival of nestlings in the wild. These results provide empirical support for the junk-food hypothesis. Received 25 March 2006, accepted 21 July 2006.

Key words.—chick growth, forage fish, Black-legged Kittiwake, lipid, Tufted Puffin.

Waterbirds 29(4): 407-414, 2006

Following a climate regime shift in the North Pacific Ocean during the late 1970s, marine fish communities in the Gulf of Alaska were completely reorganized (Francis *et al.* 1998; Anderson and Piatt 1999). The relative abundance of forage species such as Capelin (*Mallotus villosus*) and Pacific Herring (*Clupea pallasii*) declined while that of predatory groundfish such as Walleye Pollock (*Theragra chalcogramma*) increased. Concurrent with changes in fish communities, the diet composition of several piscivorous predators changed markedly (Merrick *et al.* 1987; Piatt and Anderson 1996; Benson and Trites 2002). Some predators switched from diets dominated by capelin or herring to diets dominated by juvenile Walleye Pollock and other gadids (Piatt and Anderson 1996). Marked changes in breeding success and

population structure of several marine bird and mammal species were observed following these changes in diet (Merrick *et al.* 1987; Piatt and Anderson 1996; Merrick *et al.* 1997). The consequences of shifting to a new prey base may have included significant changes in net energy gain.

In Alaska, attention has been focused on post-acquisition prey quality. For both marine mammals and seabirds, the “junk-food hypothesis” suggests that the replacement of high-lipid forage species, such as capelin, with low-lipid pollock and other gadids (the “junk food”) is directly responsible for observed changes in predator populations and productivity in Alaska (Alverson 1992; Anderson and Piatt 1999; Benson and Trites 2002). Juvenile pollock have much lower energy densities than other fish commonly

found in diets of seabirds and marine mammals in the Gulf of Alaska. During the seabird breeding season the energy content of capelin, Pacific Sand Lance (*Ammodytes hexapterus*), and herring can be twice that of juvenile pollock, depending on sex and age class (Van Pelt *et al.* 1997; Anthony *et al.* 2000). If a nestling diet of low-lipid prey results in reduced chick growth and development, then population dynamics may be affected if lighter or slower growing chicks experience reduced survival.

In view of the widespread interest in the junk-food hypothesis, we performed an experiment to test the hypothesis that differences in prey type translate directly into differences in growth and development of seabird nestlings. We predicted that nestlings fed diets of high-lipid fish would grow and develop more rapidly than those fed the same biomass of low-lipid fish. We further predicted that these diet-related differences would occur regardless of seabird taxon. The use of captive seabird nestlings provided a unique opportunity to test these predictions because it allowed the elimination of confounding variables that would have occurred in a study of wild birds, such as predation, variability in provisioning rates, extremes in ambient temperature, etc.

METHODS

Black-legged Kittiwake (*Rissa tridactyla*) and Tufted Puffin (*Fratercula cirrhata*) nestlings were used in captive feeding trials conducted at the Kasitsna Bay Laboratory, University of Alaska Fairbanks, during 1996 and 1997. All nestlings (14 of each species in 1996 and 12 of each species in 1997) were collected from colonies in Cook Inlet, Alaska. The age of each bird at capture was estimated using regression equations for head/bill length and wing length vs. age (kittiwakes; David B. Irons, unpublished data) or culmen length and body mass vs. age (puffins; John F. Piatt and Marc D. Romano, unpublished data). Kittiwakes were estimated to be 3-10 days post-hatch, and puffins were estimated to be 4-18 days post-hatch at the time of their capture. All birds were held indoors at 16-20°C in individual cages throughout the feeding trials.

Fish used in the diet treatments for this experiment included capelin, Pacific Sand Lance, Pacific Herring and Walleye Pollock. All capelin (68-103 mm standard length [SL]) and sand lance (56-148 mm SL) were captured in beach seines or cast nets in Kachemak Bay, Alaska during June and July 1996. The herring (129-141 mm SL) were purchased during May and June 1997 from a commercial baitfish supplier in Anchorage, Alaska. Pol-

lock (estimated age class 2+; 164-265 mm SL) were collected by trawl during two research cruises in Prince William Sound, Alaska in May 1996 and May 1997. Additional pollock (estimated age class 1+; 143-170 mm SL) were collected during a research cruise in the Bering Sea in June 1997. The additional fish were fed to puffins in 1997 because an insufficient amount of age class 2+ pollock was collected during the original trawl. All fish were stored frozen (-20°C) until they were fed to nestlings.

Samples of fish fed to chicks were analyzed for proximate composition. Specimens were weighed and measured individually, then dried to constant mass in a convection oven at 60°C to determine water content. Whole, dried fish were ground, and lipid content was determined by solvent extraction in a Soxhlet apparatus with hexane/isopropyl alcohol 7:2 (v:v) as the solvent system (Radin 1981). Lean dry fish samples were ashed in a muffle furnace at 600°C for 12 hours to calculate ash-free lean dry mass (ca. 94% protein; Montevecchi *et al.* 1984) by subtraction. Energy content of diets was calculated from the proximate composition (percent water, lipid, ash-free lean dry matter, and ash) of fish along with published energy equivalents of these fractions (39.3 kJ/g lipid; 17.8 kJ/g protein for uricotelic vertebrates; Schmidt-Nielsen 1997).

During 1996, kittiwake chicks were randomly assigned to one of two diet groups (N = 7 per treatment), each receiving a daily ration of either 100 g of age class 2+ Walleye Pollock, or 100 g of sand lance. In 1997, kittiwake chicks were randomly assigned to diet groups (N = 6 per treatment) receiving either 100 g/day of age class 2+ pollock, or 100 g/day of herring. Under natural circumstances, Black-legged Kittiwake nestlings will receive approximately 100 g of food each day (Baird 1994). All chicks were fed their respective experimental diets beginning at 13 days post-hatch until the experiment was terminated at 31 days post-hatch, which represents the mean age that nestlings in the wild will attain peak weight prior to fledging (Baird 1994). Before beginning feeding trials, each bird was fed an *ad libitum* diet of approximately equal amounts of the prey types used in the respective years (i.e., sand lance and pollock in 1996 and herring and pollock in 1997).

Puffin chicks collected in 1996 were randomly assigned to one of two diet treatment groups (N = 7 per treatment), with each bird receiving a daily ration of 80 g of age class 2+ pollock or 80 g of capelin. During 1997, puffin chicks were randomly assigned to diet treatment groups (N = 6 per treatment), of either 100 g/day of age class 1+ pollock or 100 g/day of herring. The daily ration was increased to 100 g in 1997 because the growth performance of puffin nestlings that received 80 g of pollock in 1996 was well below the growth of birds in the wild (Piatt and Kitaysky 2002). All puffin chicks were fed their respective experimental diet beginning at 19 days post-hatch until the experiment was terminated at 40 days post-hatch, which represents the earliest likely fledging date for birds in the wild (Piatt and Kitaysky 2002). Before the feeding trial began, each bird was fed an *ad libitum* diet of approximately equal amounts of the prey types used in the respective years.

Diet rations were fed to the birds as four, equal-sized meals daily (25 g four times/day for all kittiwakes and for puffins in 1997, 20 g four times/day for puffins in 1996). Feeding commenced at about 1000 h and the remaining three meals were spaced evenly throughout the remainder of the day. Under natural conditions, nestlings of both species are fed approximately four times/

day, throughout the entire day (Baird 1994; Piatt and Kitaysky 2002). All meals were thawed then weighed on an electronic balance (± 0.1 g).

Variables measured for kittiwake and puffin chicks in both years of the study included: (1) body mass (measured to ± 0.1 g), and (2) flattened wing length (measured to ± 1 mm). All variables were measured daily between 0800 h and 1000 h, before the first feeding of the day.

Data on the energy content of kittiwake diets were compared using the Kruskal-Wallis H test and multiple comparisons were performed with the Kruskal-Wallis Z test. The Kruskal-Wallis tests were used because the data failed a Modified-Levene Equal-variance test ($P < 0.001$). Following log transformation, energy contents of puffin diets were compared with t-tests. Data on the energy, lipid and protein content of fish fed to the birds was compared using the Kruskal-Wallis H test and multiple comparisons were performed with the Kruskal-Wallis Z test. Nonparametric tests were used because the data failed a Modified-Levene Equal-variance test ($P < 0.001$).

Four measures of growth were compared between birds on the respective diet treatments, body mass and wing length at the termination of the experiment and the growth increment of body mass and wing length during the experiment. The growth increment was defined as the final body mass or wing length of each chick minus the body mass or wing length for that chick at the start of the feeding trials. All four measures of growth for kittiwake chicks were compared among diet treatments with a one-way ANOVA and the Bonferroni test for multiple comparisons as the data met all assumptions. Significance for the kittiwake comparisons was set at $P = 0.05$. The four measures of growth for puffin chicks were compared between equal biomass diet groups (i.e., 100 g/day herring group was compared to the 100 g/day pollock group and the 80 g/day capelin group was compared to the 80 g/day pollock group) with t-tests. Due to the large number of t-tests performed on the puffin data set a Bonferroni adjustment was used, resulting in a significance level of $P = 0.0125$ for all puffin data.

All animal care and use procedures were evaluated and approved, prior to the experiment, by the Oregon State University, Animal Care and Use Committee.

RESULTS

There was a significant difference in energy content (% wet mass; d.f. = 4, $P < 0.001$) and lipid content (% wet mass; d.f. = 4, $P < 0.001$), but not in protein content (% wet mass; d.f. = 4, n.s.), among fishes used in the feeding experiments (Fig. 1). The energy content and lipid content of age class 2+ pollock was significantly less than that of herring (energy $P < 0.001$; lipid $P < 0.001$), capelin (energy $P < 0.001$; lipid $P < 0.001$) and sand lance (energy $P < 0.001$; lipid $P < 0.001$). Age class 1+ pollock had a lower energy content ($P < 0.001$) and lipid content than herring ($P < 0.001$), but a higher ener-

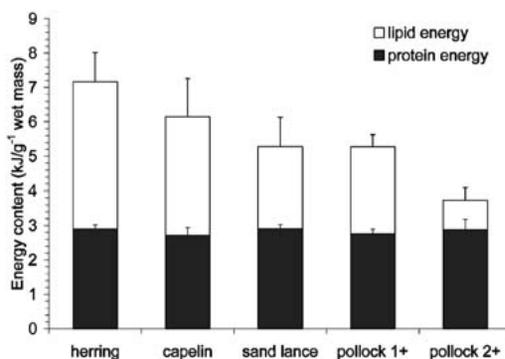


Figure 1. Mean energy content (kJ/g^{-1} wet mass) of fish species used in Black-legged Kittiwake and Tufted Puffin captive feeding experiments. The relative energy contributions of protein (black bar; + 1 SE) and lipid (white bar; + 1 SE) to the total energy/g of each fish species are shown.

gy content ($P < 0.001$) and lipid content ($P < 0.001$) than age class 2+ pollock.

Black-legged Kittiwakes

The daily rations fed to kittiwake nestlings differed in energy density (kJ/g wet mass; d.f. = 2, $P < 0.001$; Fig. 2). The energy density of both herring and sand lance rations fed to kittiwakes was greater than the pollock ration ($P < 0.001$ for both; Fig. 2) and the energy density of the herring ration was greater than the sand lance ration ($P < 0.001$; Fig. 2). Growth data from kittiwakes fed 100 g/day of pollock in the two years of

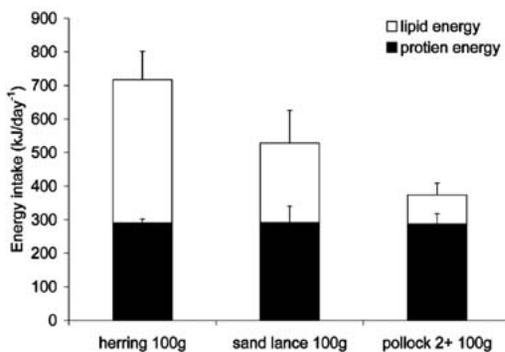


Figure 2. Mean daily energy intake of Black-legged Kittiwake nestlings raised on controlled diets of 100 g/day of Pacific Herring, Pacific Sand Lance or age class 2+ Walleye Pollock. The relative energy contributions of protein (black bar; + 1 SD) and lipid (white bar; + 1 SD) to total energy of the daily ration are shown.

the study were pooled because no between-year differences were found for the energy density of age class 2+ pollock used in the study ($t = 0.216$, d.f. = 40, n.s.). Additionally, no between-year difference was found in the final body mass ($t = 0.569$, d.f. = 11, n.s.) or final wing length ($t = 1.307$, d.f. = 11, n.s.) of kittiwake chicks raised on the pollock diets.

The mean body mass of kittiwakes at the end of the feeding trials was greater for birds fed herring ($P < 0.001$) or sand lance ($P < 0.001$) than those fed pollock (Fig. 3). Kittiwakes that were fed herring also had greater final body mass than those fed sand lance ($P < 0.01$; Fig. 3). The growth increment of body mass for kittiwake nestlings on the herring diet was significantly greater than those on the sand lance ($P < 0.001$) and pollock diets ($P < 0.001$). In addition, kittiwakes fed sand lance had significantly greater body mass growth increment than those fed pollock ($P < 0.001$; Fig. 3).

There was no difference in final wing length between kittiwakes fed herring and those fed sand lance (n.s.; Fig. 4). However, the mean final wing length of kittiwakes was greater for birds fed herring ($P < 0.001$) or sand lance ($P < 0.001$) compared to birds fed pollock (Fig. 4). Wing growth increment was significantly greater for kittiwakes fed herring ($P < 0.001$) or sand lance ($P < 0.001$) than for those fed pollock, but not significantly different between birds fed herring or sand lance diets (n.s.; Fig. 4).

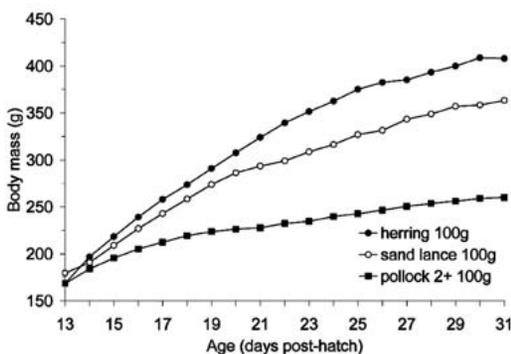


Figure 3. Mean daily growth in body mass of Black-legged Kittiwakes raised on controlled diets of 100 g/day of Pacific Herring, Pacific Sand Lance or age class 2+ Walleye Pollock.

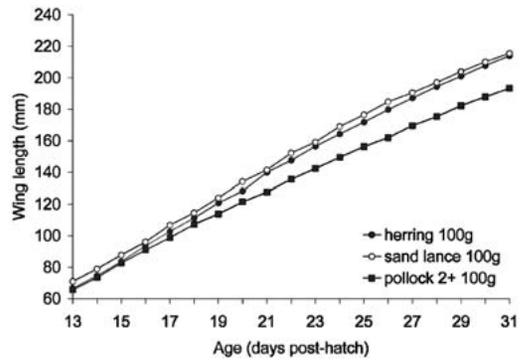


Figure 4. Mean daily growth in wing length of Black-legged Kittiwakes raised on controlled diets of 100 g/day of Pacific Herring, Pacific Sand Lance or age class 2+ Walleye Pollock.

Tufted Puffins

The mean energy density of the 100 g/day herring diet fed to puffins was greater than the 100 g/day, age class 1+ pollock diet ($t = 10.429$, d.f. = 42, $P < 0.001$). Mean energy density was also greater for the 80 g/day capelin treatment than for the 80 g/day age class 2+ pollock treatment ($t = 10.822$, d.f. = 33, $P < 0.001$; Fig. 5).

Mean body mass at the termination of the experiment was significantly greater for puffins reared on herring than for those raised on age class 1+ pollock ($t = 8.096$, d.f. = 10, $P < 0.001$; Fig. 6). Puffins raised on capelin had greater final body mass than

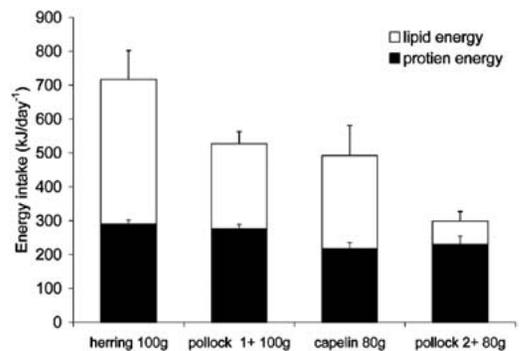


Figure 5. Mean daily energy intake of Tufted Puffin nestlings raised on controlled diets of 100 g/day of Pacific Herring, or age class 1+ juvenile Walleye Pollock, or raised on an 80 g/day of Capelin or age class 2+ juvenile Walleye Pollock. The relative energy contributions of protein (black bar; + 1 SD) and lipid (white bar; + 1 SD) to total energy of the daily ration are shown.

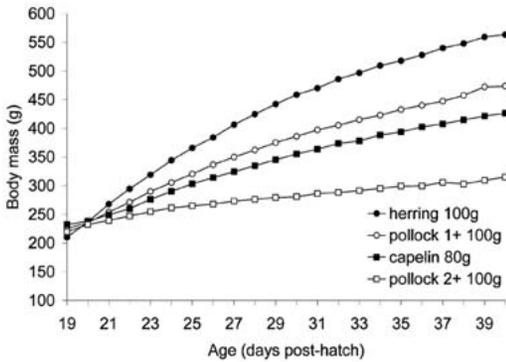


Figure 6. Mean daily growth in body mass of Tufted Puffins raised on controlled diets of 100 g/day of Pacific Herring, or age class 1+ juvenile Walleye Pollock, or raised on 80 g/day of Capelin or age class 2+ juvenile Walleye Pollock.

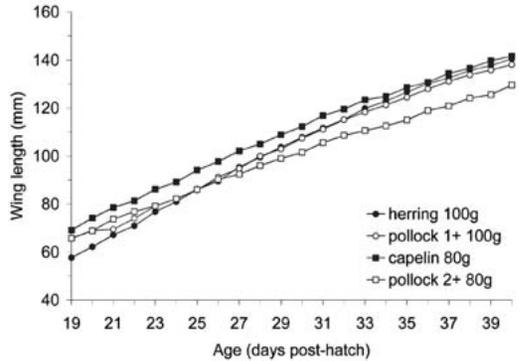


Figure 7. Mean daily growth in wing length of Tufted Puffins raised on controlled diets of 100 g/day of Pacific Herring, or age class 1+ juvenile Walleye Pollock, or raised on 80 g/day of Capelin or age class 2+ juvenile Walleye Pollock.

those raised on age class 2+ pollock ($t = 12.739$, d.f. = 12, $P < 0.001$; Fig. 6).

Tufted Puffins fed herring had a greater increment of body mass growth than those fed age class 1+ pollock ($t = 6.238$, d.f. = 10, $P < 0.001$; Fig. 6), and puffins raised on a capelin diet had a greater increment of body mass growth than puffins raised on age class 2+ pollock ($t = 7.952$, d.f. = 12, $P < 0.001$; Fig. 6).

There was no significant difference in the mean final wing length of puffins fed herring and those fed age class 1+ pollock ($t = 0.792$, d.f. = 10, n.s.; Fig. 7). Puffins fed capelin had a greater mean final wing length than puffins fed age class 2+ pollock ($t = 4.494$, d.f. = 12, $P < 0.001$; Fig. 7). Puffins fed herring had greater increment of wing growth than puffins fed age class 1+ pollock ($t = 3.578$, d.f. = 10, $P < 0.01$; Fig. 7) despite there being no difference in final wing length between the two groups. Puffins fed capelin also had greater increment of wing growth than puffins fed age class 2+ pollock ($t = 3.865$, d.f. = 12, $P < 0.01$; Fig. 7).

DISCUSSION

In this study nestling seabirds fed high-lipid fish received more energy than nestlings fed the same mass of low-lipid fish, resulting in significant differences in growth of body mass and wing length. The metabolizable energy content of lipid is more than twice that

of protein for uricotelic vertebrates such as birds (39.3 kJ/g lipid vs. 17.8 kJ/g protein; Schmidt-Nielsen 1997). The protein content of forage fish species used in the feeding trials was similar and interspecific differences in lipid content of the fish explained nearly all the variation in energy density between diet treatments (Fig. 1). The assimilation efficiency of seabirds is positively related to the fat content of food items (Brekke and Gabrielsen 1994). As a result, nestlings reared on high-lipid prey ingest more energy per unit of biomass and metabolize it more efficiently than nestlings reared on low-lipid prey.

While large differences in the growth of body mass of nestlings fed different diets was observed in this study, the difference in growth of wing feathers between diet treatments was much less extreme. These results suggest that undernourished seabird chicks may preferentially allocate assimilated nutrients to wing growth instead of mass gain. This developmental trade-off, which increases the chance that underweight young will at least be able to fledge, has been observed previously in other seabirds (Øyan and Anker-Nilssen 1996; Dahdul and Horn 2003). Feathers, comprised largely of protein, may be less affected by the energy density of prey items as long as sufficient protein intake is maintained.

In addition to its effect on growth and development, prey type may also affect the

stress level of seabird nestlings. Baseline levels of corticosterone are significantly higher in kittiwakes nestlings fed pollock than in those fed an equal biomass of sand lance or herring (Kitaysky *et al.* 1999). While short-term increases in secretion of corticosterone may have beneficial effects for adult animals during stressful situations (Wingfield *et al.* 1997), chronic elevation of corticosterone can have negative effects on immune systems and neurological functions (Saplonsky 1992), and cause severe impairment of foraging ability in newly fledged offspring (Kitaysky *et al.* 2003). While the level of corticosterone in blood plasma is inversely correlated with daily energy intake in Black-legged Kittiwake nestlings, Tufted Puffin chicks can reduce corticosterone secretion in response to nutritional deficits and thus avoid the detrimental effects of chronic corticosterone elevation (Kitaysky *et al.* 2005).

Diets consisting of a single prey species serve to highlight differences in the quality of prey with respect to seabird nestling growth in a lab environment (Heath and Randall 1985; Dahdul and Horn 2003), but a nestling diet comprised of a single species would be unusual in a natural setting, thus captive studies may tend to over estimate the importance of one prey type over another. In the wild, adult seabirds may have the opportunity to provision their young with a variety of prey species depending on availability. Atlantic Puffins (*Fratercula arctica*) can switch from capelin to sand lance to provision their young, with no apparent reduction in hatching or fledging success when compared to puffins who provision their nestlings primarily with capelin (Baille and Jones 2003). A high-lipid alternative prey such as sand lance is not always available to foraging adults though. Common Murres (*Uria aalge*) forced to provision young with a low-energy prey experience very low breeding success despite maintaining similar provisioning rates from previous, successful years when high-lipid prey is available (Wanless *et al.* 2005). Pigeon Guillemot (*Cepphus columba*) pairs in Prince William Sound, Alaska that provision their young with primarily high-lipid fishes have shown higher reproductive success than

pairs that deliver mostly low-lipid prey to the nest (Golet *et al.* 2000).

Our controlled, experimental study supports the junk-food hypothesis that walleye pollock do not meet the nutritional needs of rapidly growing seabird nestlings nearly so well as lipid-rich forage fish like herring, capelin and sand lance. The results of this experiment add support and perspective to field studies which have shown that diet quality can affect the development time and fledging mass of birds in the wild (Lance and Roby 1998; Golet *et al.* 2000; Österblom *et al.* 2001). Some field studies further suggest that shorter development time or higher mass at fledging can translate into greater post-fledging survival in the wild (Perrins *et al.* 1973; Coulson and Porter 1985; Magrath 1991), although this is not always the case (Harris and Rothery 1985). Nestling growth rate has been shown to have a significant positive effect on the number of Black-legged Kittiwakes chicks that survive and return to the colony after fledging (Coulson and Porter 1985). In contrast, post-fledging survival of Common Murre chicks is not affected by body condition at fledging (Harris *et al.* 1992), although murre fledglings receive considerable post-fledging assistance from at least one parent (Manuwal and Carter 2001).

Seabirds in the wild possess a variety of biological and behavioral adaptations that allow chicks to fledge even when they are malnourished. Nestlings may lower their resting metabolic rate, decrease activity patterns, slow or halt growth, live off fat reserves, or fledge at less than optimal mass (Kitaysky 1996). Chicks can stimulate adults to deliver more food (Kitaysky *et al.* 2001; Harding *et al.* 2002) and in some species, adults can maintain constant chick feeding rates by adjusting their foraging effort (Suryan *et al.* 2000; Litzow *et al.* 2002). However, all of these compensatory mechanisms come at some cost to the chick or adult (Suryan *et al.* 2002; Davis *et al.* 2005), which may ultimately influence survival. In recent decades, walleye pollock and other low-lipid prey items have comprised as much as 50-90% of prey biomass delivered to nestling seabirds at certain colonies in Alaska (Hatch and Sanger 1992;

Dragoo *et al.* 2004; John F. Piatt unpublished data). Prolonged reliance on a diet comprised primarily of low-lipid prey could eventually overwhelm compensatory mechanisms of nestlings and adults. This could ultimately translate into population level effects for species in which post-fledging survival is affected by development time or fledging mass.

ACKNOWLEDGMENTS

Primary funding for this research was provided by the Exxon Valdez Oil Spill Trustee Council as part of the Alaska Predator Ecosystem Experiment (APEX), Project #96163N. Additional funding and logistic support was provided by the Alaska Science Center of the USGS, the Alaska Maritime National Wildlife Refuge, and the Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University. We are grateful to A. Nielsen, M. Kosmerl, J. Pierson, D. Black, J. Figurski, R. Kitaysky, A. Morris and B. Smith for assistance in the field and lab. We are grateful to Martin Robards, Gary Drew and two anonymous reviewers for constructive review of this manuscript. Jill Anthony helped design the protocol for proximate composition analysis. We are indebted to Alexander Kitaysky for advice on study design and care of captive seabirds.

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Associate Editor: Ken Morgan.