DIET AND POSTNATAL GROWTH IN RED-LEGGED AND BLACK-LEGGED KITTIWAKES: AN INTERSPECIES CROSS-FOSTERING EXPERIMENT

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Abstract.—Red-legged Kittiwakes (*Rissa brevirostris*) and Black-legged Kittiwakes (*R. tridactyla*) are morphologically similar, breed in mixed colonies, and nest at the same time, but they exhibit substantial differences in diet, rate of nestling provisioning, and foraging distribution. We cross-fostered nestlings of the two species to test the competing hypotheses that growth in mass of kittiwakes is constrained by diet (i.e. composition, provisioning rate, and quality) or by inherent species-specific physiology. Survival and body mass of cross-fostered nestlings at 30 to 32 days posthatching did not differ from those of conspecific controls. Black-legged Kittiwake fledglings had higher lean mass than Red-legged Kittiwake fledglings regardless of whether they were raised by foster or natural parents. However, nestlings of both species raised by Red-legged Kittiwakes were 50% fatter at 30 to 32 days posthatching than those raised by Black-legged Kittiwakes. Regurgitations from nestlings raised by Red-legged Kittiwakes consisted primarily of lanternfish and contained about twice the lipid (percent dry mass) as regurgitations from nestlings raised by Black-legged Kittiwakes. Consequently, growth rate of lean tissue was genetically and/or physiologically constrained, whereas rate of fat deposition was constrained by diet. We hypothesize that the adaptive significance of lanternfish in diets for Red-legged Kittiwake nestlings is manifest in higher prefledging and/or postfledging survival. Interspecific differences in energy density of food and food provisioning rates balanced each other so that rates of energy provisioning were similar. *Received 14 January 1999, accepted 9 August 2000.*

Food supply affects rates of nestling growth and development in numerous species of seabirds that vary in geographic distribution, mode of development, and feeding ecology (Ashmole 1971, Wehle 1983, Schreiber 1994). In addition, growth can differ markedly within a population from year to year. The apparent intraspecific plasticity in growth rates of seabirds has been interpreted as an adaptive response to changing environmental conditions that influence food availability. Despite intraspecific variation in growth, however, many of the interspecific differences in growth patterns are genetically based (Ricklefs 1979, Prince and Ricketts 1981). These growth characteristics presumably are shaped by natural selection to fit the long-term expectation of the food supply and other factors (e.g. predation, sibling competition).

The two species of kittiwake are morphologically similar, but Black-legged Kittiwakes (*Rissa tridactyla,* 434 g) are larger than Red-legged Kittiwakes (*R. brevirostris,* 377 g; Byrd and Williams 1993). Where the two species breed sympatrically, the timing and duration of breeding events are similar. Red-legged Kittiwakes have a slightly longer incubation period (Hunt et al. 1981) and lay a one-egg clutch, whereas Black-legged Kittiwakes lay one to three eggs (Byrd and Williams 1993). Nestlings of the two species exhibit different patterns of growth that can be explained by differences in adult body size (Lance and Roby 1998).

In the Pribilof Islands, nestling Black-legged Kittiwakes are fed mostly juvenile walleye pollock (*Theragra chalcogramma*) and sandlance (*Ammodytes hexapterus*; Hunt et al. 1981, Dragoo 1991, Lance and Roby 1998) with a lipid content of 1 to 8% wet mass (Van Pelt et al. 1997). Red-legged Kittiwakes feed their young mostly lanternfishes (especially northern lanternfish [*Stenobrachius leucopsarus*]; Hunt et al. 1981,

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Dragoo 1991, Lance and Roby 1998), which contain about 13 to 17% lipid by wet mass (Nevenzel et al. 1969, Van Pelt et al. 1997). Much of the lipid in lanternfishes is in the form of wax esters (Nevenzel et al. 1969), a refractory lipid. Thus, nestling Red-legged Kittiwakes presumably are fed an energy-dense diet. Red-legged Kittiwake nestlings receive meals at about one-half the rate of Black-legged Kittiwake nestlings, but meal size for the two species is similar (Lance and Roby 1998). Consequently, Red-legged Kittiwakes are fed about one-half the wet mass of food per day as are Black-legged Kittiwakes.

Lack (1968) hypothesized that the small clutch size, slow growth, and long nestling periods of pelagic seabirds resulted from constraints on food supply. If Red-legged and Black-legged kittiwakes exhibit major differences in diet, provisioning rates, and foraging ecology, how can nestlings of the two species have similar growth rates? The primary objective of our study was to identify factors constraining reproduction in the two species of kittiwake. In particular, we tested the hypothesis that interspecific differences in nestling feeding frequency, daily food intake, and diet composition are manifest in differences in growth rate, allocation of energy to lean mass and fat deposition, and fledging success. We used an interspecific cross-fostering experiment to test this hypothesis, an approach that has proved to be a powerful tool for testing hypotheses about factors constraining reproduction in seabirds (Prince and Ricketts 1981, Shea and Ricklefs 1985, Roby et al. 1997).

Interspecific cross-fostering of nestlings allows discrimination between species-specific genetic constraints (i.e. adult body size; Lance and Roby 1998) and nutritional constraints on nestling growth. We had two alternative hypotheses and predictions: (1) if growth rates are determined by genetic constraints, then growth of cross-fostered nestlings should be similar to that of conspecific controls; and (2) if growth rates are determined by diet, then growth of cross-fostered nestlings should be different from that of conspecific controls.

If growth is related to diet, then additional hypotheses and predictions can be generated. First, if the rate of food delivery constrains growth (Lack 1968, Ashmole 1971), then cross-fostered Red-legged Kittiwake nestlings should exhibit higher growth rates and attain higher peak mass than conspecific controls, and growth of cross-fostered Black-legged Kittiwake nestlings should be retarded compared with that of Black-legged Kittiwake controls. Second, if growth is constrained by the lipid and energy content of the diet (Roby 1991), then Black-legged Kittiwake nestlings raised by Red-legged Kittiwake foster parents should exhibit higher growth rates and attain higher peak mass than conspecific controls, and growth of cross-fostered Red-legged Kittiwake nestlings should be retarded compared with that of Red-legged Kittiwake controls. Third, if other essential nutrients limit growth (Ricklefs 1979), or if dietary lipids (i.e. wax esters) are poorly digested (Roby et al. 1986), then growth of Black-legged Kittiwake nestlings raised by Red-legged Kittiwake foster parents should be retarded compared with controls. Last, if each species is adapted to its specific diet, then growth of cross-fostered nestlings should be retarded compared with respective conspecific controls. The present study investigates how the predominance of lanternfishes in Red-legged Kittiwake diets influences (1) nestling growth and development, (2) patterns of fat storage in nestlings, and (3) survival of nestlings to fledging age.

METHODS AND MATERIALS

Cross-fostering experiment.—We studied Red-legged and Black-legged kittiwakes on St. George Island, Alaska (56°35′N, 169°35′W), in the southeastern Bering Sea from 14 June to 25 August 1993. Nests of both species were distributed from 3 to 100 m above high tide on vertical cliffs and were accessed by ladder from the beach or by using ropes to rappel from the top of the cliff. We marked 305 kittiwake nests (129 Red-legged and 176 Black-legged) early in the incubation period. Marked nests were examined daily during the hatching period to determine hatching date. Of nests that hatched young (40 Red-legged and 38 Black-legged), we assigned 30 randomly chosen nests, 15 of each species, to the experimental group and the remainder to the control group for each species. Owing to high egg loss on study plots, several nests that contained newly hatched nestlings (four Black-legged and two Red-legged) were added to the cross-fostering experiment.

Cross-fostering was accomplished within three days after hatching by switching hatchlings of similar ages between the 15 pairs of nests. At the time of cross-fostering, all nests used in the experiment had one nestling. Early in the season, a few Black-legged

Kittiwake control nests contained two nestlings; however, all beta nestlings died within three days after hatching, prior to the cross-fostering experiment. Disruption of parental activities at the nest was minimized using this protocol because parents were highly attentive to their nestlings during the first few days posthatching. Nestlings were switched by carefully inserting the foster hatchling beneath the brooding parent. Previous switching experiments with procellariiforms indicated that parents do not distinguish their own newly hatched nestlings from foster nestlings, and that nestlings will accept food from adults other than their natural parents (Prince and Ricketts 1981, Ricklefs et al. 1987). In addition, Cullen (1957) reported that Black-legged Kittiwake parents do not learn to recognize their own nestlings until the nestlings are about four weeks old.

We monitored growth of control and cross-fostered nestlings by measuring mass and wing length at three-day intervals from hatching until 30 to 32 days posthatching. We collected diet samples opportunistically from nestlings that regurgitated during periodic weighing and measuring (Lance and Roby 1998). Nestlings were not forced to regurgitate. This resulted in collecting an average of 2.05 ± SD of 1.24 regurgitations from any given nestling over the course of the nestling period. Although we had no controls, we do not believe this level of meal collection caused significant stress that would have affected nestling growth. We discontinued weighing and measuring nestlings at 30 to 32 days posthatching because older nestlings can fledge prematurely if handled (Baggot 1992). Nestlings were placed in a nylon bag and weighed using Pesola spring scales (±0.5 g up to 100 g, ±1 g up to 300 g, and ±2.5 g above 300 g). We measured wing length (maximum length of flattened wing from bend of wrist to tip of longest primary) to the nearest 1 mm.

We calculated nestling survival for each species in the two treatments using the Mayfield method (Mayfield 1975, Johnson 1979) and methods described in Lance and Roby (1998). Data on age-specific body mass of nestlings, separated by species and treatment, were fit to logistic growth models using a nonlinear least-squares curve-fitting routine (SAS 1990) and methods outlined in Ricklefs (1983) and Lance and Roby (1998).

Nestling body composition.—We collected all cross-fostered nestlings to preclude potential hybridization owing to imprinting on the foster parents (Harris 1970, Harris et al. 1978). Collection procedures conformed with protocols of the Institutional Animal Care and Use Committee and the AOU (1988) for conducting research on wild birds. Nestlings from both species and treatments were collected 30 to 32 days posthatching, placed in plastic bags, and frozen at −20°C for determination of body composition.

Carcasses were partially thawed, weighed (±0.1 g) to determine fresh mass, plucked, and the stomach contents removed. Carcasses were then dried to constant mass in a convection oven at 60°C and reweighed to determine water content. Dried carcasses were homogenized by passing them through a small electric meat grinder several times. Three aliquots (ca. 2.5 g) were taken from each homogenized carcass and the fat extracted using a Soxtec HT 12 soxhlet apparatus and petroleum ether as the solvent (Dobush et al. 1985). If the coefficient of variation (CV) of the three-aliquot mean was less than 1.0%, the extraction was considered representative of the entire carcass; if the CV exceeded 1.0%, the carcass was further homogenized and three additional aliquots extracted.

We calculated body composition by the following equations:

$$TBW = (FCM - SC) - DCM, \qquad (1)$$

where *TBW* is total body water, *FCM* is fresh carcass mass, *SC* is stomach contents, and *DCM* is dried carcass mass;

$$TBF = (MFC/100)\, DCM, \qquad (2)$$

where *TBF* = total body fat, and *MFC* is mean fat content as a percentage of dry mass; and

$$LDBM = DCM - TBF, \qquad (3)$$

where *LDBM* is lean dry body mass.

The cross-fostering experiment was a two-by-two design that allowed testing for differences in growth parameters as well as assigning any differences to a species (genetic) or diet (nutritional) effect. Data were ranked because the variables may not have met assumptions of ANOVA (Zar 1984). Small sample sizes precluded testing for significant departures from normality and homogeneity of variances. Total mass, lean dry mass, and total fat reserves of nestlings 30 to 32 days posthatching were analyzed using a two-way ANOVA on ranked values of the response variable (Zar 1984, SYSTAT 1992).

Comparisons of total body fat can be misleading, because a larger bird may have higher total body fat simply as a consequence of being large. Therefore, we calculated a fat index as the ratio of total body fat to lean dry body mass to correct for differences in body size. Because the fat index is a ratio, data were square-root arcsine transformed before two-way ANOVA.

We estimated potential fledgling survival time in the absence of feeding by expressing fat reserves as the ratio of the energy equivalent of fat (39.3 kJ per g; Schmidt-Nielsen 1990) to the daily maintenance energy requirements of nestlings. Although we did not measure energy expenditure of nestlings, such measurements have been made for Black-legged Kittiwakes based on indirect calorimetry (Gabrielson et al. 1992). We used a value of 380 kJ per day (calculated for 34-day-old Black-legged Kittiwake nes-

tlings) to estimate survival times for both species of kittiwake nestlings.

Composition of nestling diets.—We investigated the biochemical composition and energy density of kittiwake diets using two approaches: (1) analysis of proximate composition of nestling regurgitations in the laboratory, and (2) multiplying the proportions of prey taxa in the diet by the energy density of those prey items. We used two methods because (1) all regurgitations were collected from nestlings, which may have altered the composition of the meal between time of ingestion and collection; and (2) conversely, fresh prey captured by adults may have been altered prior to delivery to the nest.

Regurgitations were analyzed for taxonomic composition (Lance and Roby 1998) and dried to constant mass in a convection oven at 60°C to determine water content. Lipids were extracted by the method described above for carcasses. Lean dry food samples were ashed in a muffle furnace at 500°C for 24 h to calculate ash-free lean dry mass. To estimate energy density of nestling regurgitations, we assumed that ash-free lean dry mass consisted only of protein (Ricklefs et al. 1980a). Energy content of nestling regurgitations, or fresh fish prey per gram wet mass, was calculated from composition (percent water, lipid, protein, ash) and the energy equivalents of these fractions (lipid = 39.3 kJ per g, protein = 17.8 kJ per g; Schmidt-Nielsen 1990). Energy content of nestling meals was calculated from the proximate composition of forage fishes and their proportions in the diets of the two species. Samples of forage fish representative of kittiwake diets were analyzed for biochemical composition. Methods were similar to those for analysis of nestling regurgitations, except that a mixture of 7:2 N-hexane : 2-proponol was used as the solvent (Van Pelt et al. 1997).

We estimated nestling feeding rates based on parental exchanges at the nest 20 to 32 days posthatching. Data on feeding rates and meal sizes were collected from broods of one nestling. Average daily rates of provisioning were estimated by monitoring nests for 2 to 6 h, with effort subdivided into 2-h blocks distributed throughout the daylight hours (0600 to 2400 AST). Only exchanges that included a feeding event (regurgitation of a food bolus from adult to nestling) were included in estimates of feeding rates (see Lance and Roby 1998).

RESULTS

Nestling survival.—Daily survival rates of Red-legged Kittiwakes did not differ between control and cross-fostered nestlings for the early (0 to 5 days; $Z = 0.36$, $P = 0.71$) or mid- to late (6 to 30 days; $Z = 0.27$, $P = 0.79$) nestling periods (Table 1). Likewise, survival did not differ between control and cross-fostered

TABLE 1. Mayfield daily survival rates ($\pm$SE) of experimental and control Red-legged Kittiwake and Black-legged Kittiwake nestlings on St. George Island, Alaska, in 1993.

Nestling age	No. nests	No. exposure days	Daily survival	Success[a]
Red-legged Kittiwake control				
0 to 5 days	25	140	0.97 ± 0.01	0.84
6 to 30 days	21	437	0.99 ± 0.01	0.71
Overall	—	—	—	0.60
Red-legged Kittiwake cross-fostered				
0 to 5 days	16	51	0.98 ± 0.02	0.89
6 to 30 days	15	311	0.98 ± 0.01	0.67
Overall	—	—	—	0.59
Black-legged Kittiwake control				
0 to 5 days	20	102	0.94 ± 0.01	0.70
6 to 30 days	21	437	0.99 ± 0.01	0.87
Overall	—	—	—	0.61
Black-legged Kittiwake cross-fostered				
0 to 5 days	16	68	0.99 ± 0.01	0.91
6 to 30 days	15	315	0.98 ± 0.01	0.62
Overall	—	—	—	0.57

[a] Fraction of nestlings surviving.

Black-legged Kittiwakes for the early ($Z = 1.41$, $P = 0.16$) or mid- to late ($Z = 1.58$, $P = 0.11$) nestling periods (Table 1). Survival rates to 30 days posthatching were similar both for cross-fostered (59%) and control (60%) Red-legged Kittiwake nestlings and for cross-fostered (57%) and control (61%) Black-legged Kittiwake nestlings (Table 1).

Nestling growth: Body mass.—Nestling body mass for both species and treatments were plotted as a function of age (Figs. 1A,B). Mass of Red-legged Kittiwake control nestlings at 30 to 32 days posthatching ($\bar{x} = 350 \pm$ SD of 57 g, $n = 13$) was nearly identical to that of cross-fostered Red-legged Kittiwakes ($\bar{x} = 349 \pm 40$ g, $n = 10$), and mass of Black-legged Kittiwake control nestlings ($\bar{x} = 418 \pm 31$ g, $n = 13$) did not differ from that of cross-fostered Black-legged Kittiwakes ($\bar{x} = 411.7 \pm 59.8$ g, $n = 9$). Black-legged Kittiwake nestlings had a higher mass at 30 to 32 days posthatching than did Red-legged Kittiwake nestlings regardless of whether they were raised by natural or foster parents ($F = 25.46$, df = 1 and 41, $P < 0.001$). Nestling mass at 30 to 32 days posthatching as a percentage of average adult mass did not differ between Black-legged (96.4%) and Red-legged (92.9%) kittiwakes ($F = 0.55$, df = 1 and 24, $P = 0.46$).
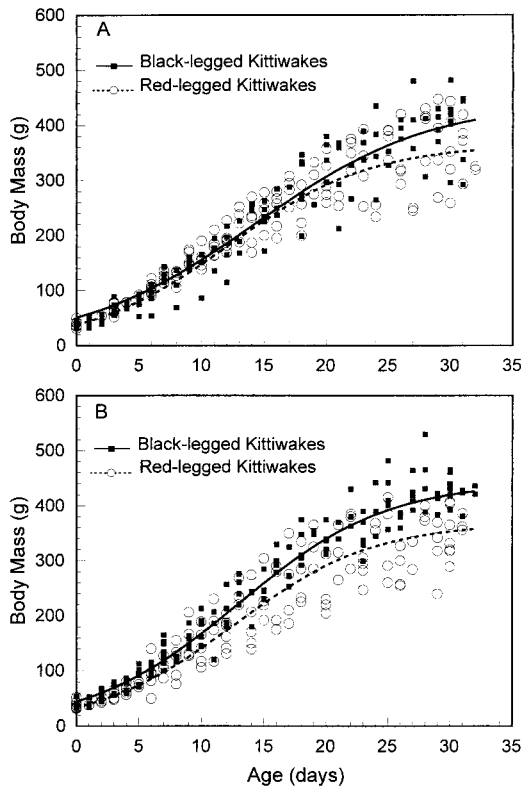
FIG. 1. Logistic model fitted to growth in body mass for (A) Red-legged and Black-legged kittiwake nestlings provisioned by Red-legged Kittiwakes and (B) Red-legged and Black-legged kittiwake nestlings provisioned by Black-legged Kittiwakes, St. George Island, Alaska.

Fitted logistic models for nestling Black-legged Kittiwakes had a higher asymptotic mass than those for nestling Red-legged Kittiwakes regardless of whether they were raised by natural or foster parents ($F = 17.36$, df = 1 and 41,

$P < 0.001$; Table 2). Growth-rate constants did not differ between species ($F = 1.82$, df = 1 and 41, $P = 0.18$) or treatments ($F = 1.47$, df = 1 and 41, $P = 0.23$; Table 2). The inflection points of the fitted curves did not differ between cross-fostered nestlings and conspecific controls for either species ($F = 0.34$, df = 1 and 41, $P = 0.56$), but the inflection point was at an earlier age (ca. 1 day) for Red-legged Kittiwake nestlings than for Black-legged Kittiwake nestlings ($F = 5.32$, df = 1 and 41, $P = 0.026$; Table 2). Maximum instantaneous rates of growth of nestling body mass were similar for the two species ($F = 2.59$, df = 1 and 41, $P = 0.12$; Table 2) and treatments ($F = 2.18$, df = 1 and 41, $P = 0.15$; Table 2).

Growth: Wing length.—Wing length of Red-legged Kittiwake control nestlings at 30 to 32 days posthatching ($\bar{x} = 200 \pm 23$ mm, $n = 13$) did not differ from that of cross-fostered nestlings ($\bar{x} = 197 \pm 21$ mm, $n = 10$). Similarly, wing length of Black-legged Kittiwake control nestlings at 30 to 32 days ($\bar{x} = 208 \pm 28$ mm, $n = 13$) did not differ from that of cross-fostered nestlings ($\bar{x} = 203 \pm 17$ mm, $n = 9$). We found no differences in wing length at 30 to 32 days posthatching between species ($F = 0.04$, df = 1 and 41, $P = 0.84$) or treatments ($F = 0.99$, df = 1 and 41, $P = 0.32$).

Logistic models of wing length for nestling Black-legged Kittiwakes had a higher mean asymptote than those of nestling Red-legged Kittiwakes regardless of whether birds were raised by natural or foster parents ($F = 7.95$, df = 1 and 41, $P = 0.007$). Growth-rate constants of fitted logistic models did not differ between species ($F = 0.35$, df = 1 and 41, $P = 0.56$) or treatments ($F = 0.35$, df = 1 and 41, $P = 0.56$). The mean inflection points of fitted curves did

TABLE 2. Parameter estimates from logistic models fitted to data on growth (body mass) of nestling Red-legged Kittiwakes and Black-legged Kittiwakes on St. George Island, Alaska, in 1993. Values are $\bar{x} \pm$ SE.

Treatment	n	K[a]	Inflection point[b]	A[c]	KA/4[d]
		Red-legged Kittiwake			
Control	13	0.177 ± 0.0104	12.17 ± 1.10	365.4 ± 24.1	15.68 ± 0.83
Cross-fostered	10	0.180 ± 0.0122	12.69 ± 0.82	368.9 ± 14.3	16.62 ± 1.35
		Black-legged Kittiwake			
Control	13	0.169 ± 0.0047	12.98 ± 0.36	443.6 ± 11.7	18.76 ± 0.79
Cross-fostered	10	0.143 ± 0.0178	14.24 ± 0.60	442.0 ± 21.8	15.68 ± 2.06

[a] Growth constant (per day).
[b] Days posthatching.
[c] Asymptotic mass (g).
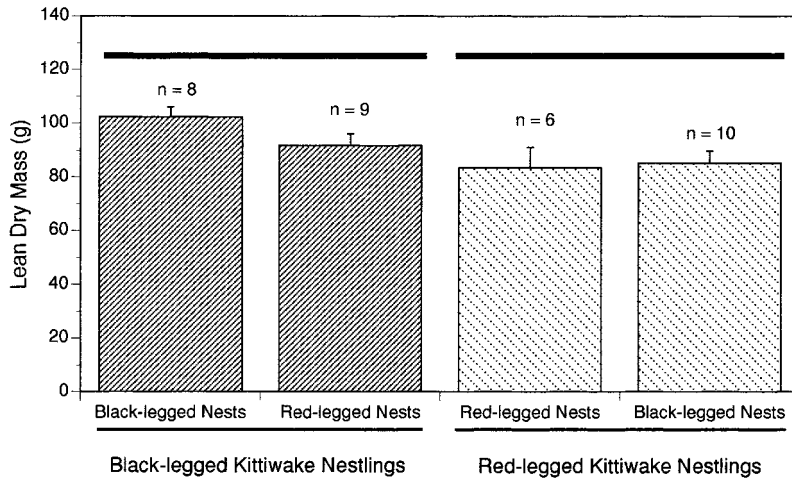[d] Maximum instantaneous rate of growth (g per day; Hussell 1972).

FIG. 2.   Lean dry mass ($\bar{x} \pm$ SE) of cross-fostered and control Red-legged and Black-legged kittiwake nestlings (30 to 32 days posthatching) at St. George Island, Alaska. Solid bar indicates no significant difference ($P > 0.05$); break in bar indicates significant difference ($P < 0.05$).

not differ between Red-legged and Black-legged kittiwakes ($F = 0.86$, df = 1 and 41, $P = 0.36$) or between cross-fostered and conspecific controls for either species ($F = 0.02$, df = 1 and 41, $P = 0.89$).

Nestling body composition.—At 30 to 32 days posthatching, lean dry mass of Black-legged Kittiwake control nestlings ($\bar{x} = 102.4 \pm 10.3$ g, $n = 8$) did not differ from that of cross-fostered Black-legged Kittiwake nestlings ($\bar{x} = 91.8 \pm 12.8$ g, $n = 9$), and lean dry mass of Red-legged Kittiwake control nestlings ($\bar{x} = 83.5 \pm 18.6$ g, $n = 6$) did not differ from that of cross-fostered conspecifics ($\bar{x} = 85.2 \pm 13.9$ g, $n = 10$; $F = 1.10$, df = 1 and 29, $P = 0.31$). Black-legged Kittiwake nestlings had higher lean dry mass than Red-legged Kittiwake nestlings whether they were raised by natural or foster parents ($F = 5.66$, df = 1 and 29, $P = 0.024$; Fig. 2).

The fat index (total body fat : lean dry mass) of control Red-legged Kittiwake nestlings at 30 to 32 days posthatching ($\bar{x} = 0.49 \pm 0.14$, $n = 6$) was higher than that of cross-fostered Red-legged Kittiwake nestlings ($\bar{x} = 0.29 \pm 0.09$, $n = 10$). Conversely, the fat index of control Black-legged Kittiwake nestlings ($\bar{x} = 0.37 \pm 0.07$, $n = 8$) was lower than that of cross-fostered Black-legged Kittiwake nestlings ($\bar{x} = 0.48 \pm 0.10$, $n = 9$). Thus, on average, nestlings of either species raised by Red-legged Kittiwake parents were 50% fatter at 30 to 32 days posthatching than were those raised by Black-

legged Kittiwake parents ($F = 19.64$, df = 1 and 29, $P < 0.001$; Fig. 3). Fat indices did not differ significantly between Red-legged and Black-legged kittiwake nestlings ($F = 1.49$, df = 1 and 29, $P = 0.23$; Fig. 3), indicating that no species effect occurred.

Estimated survival times (based on fat reserves) at 30 to 32 days posthatching were higher for nestlings provisioned by Red-legged Kittiwake parents ($\bar{x} = 4.5 \pm 1.5$ days, range 2.0 to 6.6 days, $n = 15$) than for nestlings provisioned by Black-legged Kittiwake parents ($\bar{x} = 3.2 \pm 1.1$ days, range 1.5 to 4.6 days, $n = 18$; $F = 8.83$, df = 1 and 29, $P = 0.006$).

Composition of nestling regurgitations.—Regurgitations from nestlings raised by Red-legged Kittiwake parents contained about twice as much lipid ($\bar{x} = 28.3 \pm$ SE of 1.40% of dry mass, CV = 39%) as regurgitations from nestlings raised by Black-legged Kittiwakes ($\bar{x} = 14.5 \pm 2.05\%$ of dry mass, CV = 102%; $F = 27.41$, df = 1 and 111, $P < 0.001$). The high CV in lipid content of regurgitations from nestlings raised by Black-legged Kittiwakes was mostly a consequence of regurgitations containing fish offal that was high in lipid (ca. 45% of dry mass). Water content of regurgitations from nestlings raised by Red-legged Kittiwakes ($\bar{x} = 76.1 \pm 0.59\%$) was similar to that of regurgitations from nestlings raised by Black-legged Kittiwakes ($\bar{x} = 77.2 \pm 1.09\%$; $F = 1.35$, df = 1 and 112, $P = 0.25$). Regurgitations from nestlings
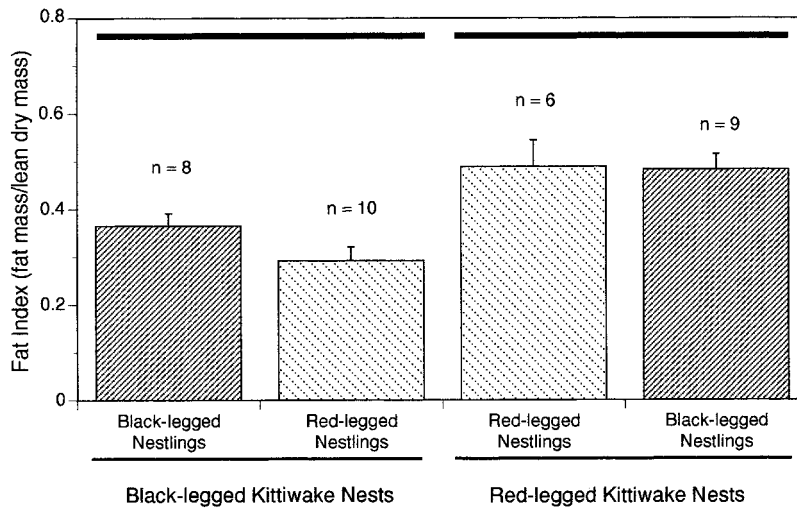
FIG. 3. Fat index ($\bar{x} \pm$ SE) of cross-fostered and control Red-legged and Black-legged kittiwake nestlings (30 to 32 days posthatching) at St. George Island, Alaska. Solid bar indicates no significant difference ($P >$ 0.05); break in bar indicates significant difference ($P <$ 0.05).

raised by Black-legged Kittiwakes contained more ash-free lean dry matter (primarily protein; $\bar{x} = 70.3 \pm 2.16\%$ of dry mass) than those from nestlings raised by Red-legged Kittiwakes ($\bar{x} = 59.2 \pm 1.41\%$ of dry mass; $F = 21.57$, df = 1 and 105, $P < 0.001$). Ash content of regurgitations from nestlings raised by Black-legged Kittiwakes ($\bar{x} = 14.8 \pm 1.12\%$) did not differ from that of regurgitations from nestlings raised by Red-legged Kittiwakes ($\bar{x} = 12.6 \pm 0.68\%$; $F = 2.38$, df = 1 and 105, $P = 0.12$).

Energy density of regurgitations (dry-mass basis) from nestlings raised by Red-legged Kittiwakes ($\bar{x} = 21.6 \pm 0.37$ kJ per g, $n = 63$) was significantly higher than that from nestlings raised by Black-legged Kittiwakes ($\bar{x} = 18.4 \pm 0.55$ kJ per g, $n = 53$; $F = 22.75$, df = 1 and 105, $P < 0.001$). Differences in energy density resulted from the higher lipid content of regurgitations from nestlings raised by Red-legged Kittiwake parents. Energy density on a wet-mass basis, however, did not differ between regurgitations from nestlings raised by Black-legged Kittiwakes and those raised by Red-legged Kittiwakes ($F = 3.59$, df = 1 and 105, $P = 0.062$).

Nestling provisioning rates.—Nestlings raised by Black-legged Kittiwakes were provisioned at nearly twice the rate ($\bar{x} = 3.03$ meals per day) as nestlings raised by Red-legged Kittiwakes ($\bar{x}$ = 1.72; $Z = 3.73$, $P < 0.001$). Provisioning rates did not differ between Red-legged Kittiwake nestlings ($\bar{x} = 1.56$) and Black-legged Kittiwake nestlings ($\bar{x} = 1.68$) raised by Red-legged Kittiwakes ($Z = 0.02$, $P = 0.98$), nor between Black-legged Kittiwake nestlings ($\bar{x} = 2.83$) and Red-legged Kittiwake nestlings ($\bar{x} = 3.33$) raised by Black-legged Kittiwakes ($Z = 1.33$, $P = 0.18$). This suggests that cross-fostering had no effect on nestling provisioning rates.

DISCUSSION

Nestling growth.—We performed a cross-fostering experiment to evaluate how differences in diet and provisioning rate affect growth, development, and survival of kittiwake nestlings. In addition, we ascertained the relative importance of species-specific genetic and dietary constraints on patterns of growth and development. For both species, the experiment revealed that growth rates of cross-fostered nestlings and conspecific controls did not differ. In addition, nestling survival rates to 30 to 32 days posthatching were similar for both species and treatments. These results suggest that nestling growth and survival were not constrained by food provisioning rate or by lipid content of the diet. Instead, growth in body mass was species specific, apparently being limited by

inherent genetic and/or physiological constraints.

Although we found no significant differences in growth patterns between cross-fostered and controls nestlings for either species, the growth-rate constant was lower, the inflection point was later, and lean dry mass at 30 to 32 days posthatching was lower in Black-legged Kittiwake nestlings provisioned by Red-legged Kittiwakes than in those provisioned by Black-legged Kittiwakes. Also, growth of cross-fostered Black-legged Kittiwakes was more like that of control Red-legged Kittiwakes (Fig. 1A) than of control Black-legged Kittiwakes (Fig. 1B). These trends suggest that Black-legged Kittiwake nestlings raised on Red-legged Kittiwake diets (less-frequent meals, high lipid intake) were constrained in their ability to assimilate and deposit protein. The inability to demonstrate a diet effect on overall growth rate may have been a consequence of low power resulting from small sample sizes.

Growth rates of Black-legged Kittiwake control nestlings were within the range of previous studies of this species in the Atlantic (Coulson and White 1958, Maunder and Threlfall 1972, Coulson and Porter 1985, Barrett and Runde 1980) and Alaska (Braun and Hunt 1983, Murphy et al. 1991). Caution is required, however, when comparing growth rates of Atlantic and Pacific kittiwakes owing to differences in adult mass and the influence that body size has on growth rate (Lance and Roby 1998).

Nestling body composition.—Comparisons of nestling development based solely on growth in body mass may obscure differences in the relative allocation of assimilated energy to lean mass versus fat deposition. Nestling Black-legged Kittiwakes had higher lean dry mass than nestling Red-legged Kittiwakes regardless of the species that raised them. This suggests that growth of lean tissue is constrained genetically and/or physiologically. Nestlings of both species raised by Red-legged Kittiwakes averaged 50% fatter than those raised by Black-legged Kittiwakes, suggesting that fat deposition is constrained by diet. Specifically, diets high in lanternfish were responsible for higher fat reserves in nestlings provisioned by Red-legged Kittiwakes. Interestingly, cross-fostered Red-legged Kittiwake nestlings accumulated smaller fat reserves than Black-legged Kittiwake controls, even though the former are smaller

(Fig. 3). This suggests that Red-legged Kittiwake nestlings raised on Black-legged Kittiwake diets (more-frequent meals, low lipid intake) were constrained in their ability to assimilate and deposit fat, which may be an adaptation of Red-legged Kittiwakes to a diet high in lipids.

Especially for seabirds, fat deposition is a significant component of nestling energy budgets (Ricklefs 1983). Nestling fat reserves generally increase over the developmental period and often exceed levels found in adults (Ricklefs 1983, O'Connor 1984, Roby 1991). Nestling fat reserves may function as (1) an energy sink for nestlings on high-lipid, low-protein diets (Ricklefs et al. 1980a); (2) insurance against poor feeding conditions during the nestling period (Lack 1968, O'Connor 1978); and (3) an energy reserve for fledglings after they leave the nest and are no longer fed by their parents (Ricklefs 1983, O'Connor 1984, Roby 1991).

Large fat reserves in developing birds may act as an energy sink to allow for assimilation of limited nutrients on a lipid-rich, protein-poor diet (Ricklefs et al. 1980a). The energy-sink hypothesis apparently does not apply to kittiwakes, because although the diet of Red-legged Kittiwakes is high in lipid, it is also high in protein (Van Pelt et al. 1997). In addition, lack of a significant difference in wing length between the two kittiwake species and treatments suggests that nutrients required for feather growth were not limited by low protein content of Red-legged Kittiwake diets.

O'Connor (1978) suggested that the level of fat reserves in nestlings is adjusted to variation in feeding frequency (food supply) during the brood-rearing period. He postulated that large fat reserves of seabird nestlings insure survival during periods when parents fail to deliver food. The larger fat reserves and lower feeding rates of nestlings raised by Red-legged Kittiwakes relative to those raised by Black-legged Kittiwakes appear to support O'Connor's (1978) hypothesis.

Fat indices provide an estimate of energy reserves available for maintenance requirements in the absence of food intake (Ricklefs 1983, O'Connor 1984). Based on fat reserves, the estimated mean survival time of nestlings 30 to 32 days posthatching that were provisioned by Red-legged Kittiwakes (4.5 days) was higher than that of nestlings provisioned by Black-leg-

ged Kittiwakes (3.2 days). Survival estimates are in accordance with higher fat indices for nestlings provisioned by Red-legged Kittiwakes (0.49) compared with those provisioned by Black-legged Kittiwakes (0.33). Ricklefs and White (1981) reported a similar relationship between 20-day-old Sooty Tern (*Sterna fuscata*) nestlings and Common Tern (*Sterna hirundo*) nestlings (3.8 days with a lipid index of 0.35 vs. 1.4 days with a lipid index of 0.24, respectively). Data on kittiwakes (this study) and terns (Ricklefs and White 1981) are consistent with the prediction of higher nestling fat reserves in species that experience a more variable food supply (O'Connor 1978) or a lower and more variable rate of energy provisioning (Ricklefs and White 1981).

Fat indices and survival times for nestling kittiwakes appear to support O'Connor's (1978) hypothesis, but it is unclear whether nestlings experience such extended periods without food (i.e. 3.2 to 4.5 days). In the Pribilof Islands, Red-legged Kittiwakes and Black-legged Kittiwakes provision nestlings daily (1.7 and 3.0 meals per day, respectively), so lipid reserves appear to exceed requirements. Relative to provisioning rates, lipid reserves in excess of nestling requirements have been noted in several seabirds (Ricklefs et al. 1985, Roby 1991), suggesting that no general relationship occurs between meal intervals and the amount of fat stored by nestlings. Instead, fat reserves of many seabirds, including kittiwakes, may be an adaptation to enhance postfledging survival.

High fat reserves may be critical during the transition from parental feeding to independence (Burger 1980), which in Black-legged Kittiwakes occurs immediately after fledging (Coulson and White 1958). Postfledging parental care has not been reported in Red-legged Kittiwakes, and for the purposes of our study we assumed that it does not occur. No data are available on the relationship between fat reserves in fledglings and postfledging survival in seabirds, but low fledgling body mass has been associated with decreased survival rates in some seabirds that receive no parental feeding during the postfledging period (Perrins et al. 1973, Jarvis 1974). Large fat reserves in other seabirds that are not fed by their parents during the postfledging period support the idea that fat reserves influence postfledging survival (Ricklefs et al. 1980b, Montevecchi et al. 1984, Roby 1991). Conversely, seabirds with extended periods of postfledging parental care exhibit comparatively small lipid reserves at fledging (Burger 1980, Shea 1985) and no relationship between fledging mass and postfledging survival (Lloyd 1979, Hedgren 1981).

Composition of nestling meals.—Analysis of regurgitations to determine the composition of nestling kittiwake diets was problematic. Lipid content and energy density of regurgitations were considerably lower than those of fresh fishes that comprised the majority of regurgitations (Van Pelt et al. 1997). Lipid content of lanternfish as determined by Van Pelt et al. (1997) was comparable to that of other studies (e.g. Nevenzel et al. 1969, Childress and Nygaard 1973, A. R. Place unpubl. data). Fresh lanternfish had a higher mean lipid content (53% dry mass; Van Pelt et al. 1997) than did nestling regurgitations composed of 100% lanternfish (ca. 35% dry mass).

Lipid content and energy density of the dominant food item for nestling Red-legged Kittiwakes was higher than that for nestling Black-legged Kittiwakes (Van Pelt et al. 1997). Specifically, lanternfish had more than three times the energy density of walleye pollock because of higher lipid and lower water content in the former (Van Pelt et al. 1997). When the proportions of the various prey types in the diet (Lance and Roby 1998) were converted to energy using the composition of fresh prey (Van Pelt et al. 1997), the estimated energy density of Red-legged Kittiwake diets was nearly twice that of Black-legged Kittiwake diets (6.8 vs. 3.7 kJ per g fresh mass, respectively). This interspecific difference in energy density of the diet is greater than that obtained from analysis of nestling regurgitations (i.e. 5.2 vs. 4.4 kJ per g fresh mass).

The discrepancy in proximate composition between fresh prey and regurgitations apparently results from events that occur between ingestion by parents and regurgitation to nestlings. Gastric secretion and differential assimilation of lipids and protein by parents and/or nestlings potentially contribute to differences in the composition of fresh prey and nestling regurgitations. Thus, the composition of nestling regurgitations is not concordant with the lipid or water content of prey, but it is unclear

whether parents or nestlings are responsible for this discrepancy.

Differences in lipid content of regurgitations between the two species undoubtedly were due to the preponderance of lanternfish in the diet of Red-legged Kittiwakes (Lance and Roby 1998). Lanternfish result in a higher energy density of nestling meals that can compensate for lower frequency of feedings. Roby (1991) suggested that seabirds enhance growth and development of their young by selectively provisioning them with high-lipid prey to meet energy requirements for nestlings without their having to catabolize dietary protein. For both kittiwake species, growth rates of lean tissue were similar between cross-fostered nestlings and conspecific controls, but nestlings provisioned by Red-legged Kittiwakes deposited more fat. This suggests that the ratio of lipid to protein in lanternfish is optimal for meeting protein requirements for growth while allowing for deposition of fat.

Diet and energetics.—The rate of provisioning energy to nestlings is a consequence of delivery rate, meal size, and energy density of the meal. Average meal sizes for the two species were similar (Lance and Roby 1998). Red-legged Kittiwakes provisioned their nestlings with meals at about half the rate of Black-legged Kittiwakes, and energy density of nestling regurgitations was similar for the two species. Thus, nestlings provisioned by Black-legged Kittiwakes received substantially more energy per day than nestlings provisioned by Red-legged Kittiwakes.

Although Red-legged Kittiwakes appeared to provision nestlings with less energy than did Black-legged Kittiwakes, growth rates were similar for cross-fostered nestlings and conspecific controls for each species, suggesting similar rates of energy provisioning for nestlings of both species. One might argue that this discrepancy resulted from undetected nocturnal feedings by Red-legged Kittiwakes. Although nocturnal observations were not part of our sampling protocol, anecdotal observations at night revealed no parental visits to nests. Furthermore, the limited data on activity patterns of adults at the nest (E. N. Flint, G. L. Hunt, and M. A. Rubega unpubl. data) do not support the hypothesis of nocturnal provisioning in Red-legged Kittiwakes.

An alternative method to estimate energy density of nestling diets was based on the proximate composition of fresh fishes and their proportions in the diets of the two kittiwake species. This method may be more appropriate than using the proximate composition of nestling regurgitations because of changes in the composition of digesta in the stomachs of nestlings. Based on the composition of fresh fishes, the energy density of nestling meals was much higher for Red-legged Kittiwakes than for Black-legged Kittiwakes, resulting in similar rates of energy provisioning to nestlings of the two species. Results of the cross-fostering experiment support the conclusion that energy provisioning rates to nestlings were similar for the two species of kittiwakes.

For Red-legged Kittiwakes, there is a clear advantage to provisioning nestlings with high-lipid meals. By specializing on prey that are high in lipids, Red-legged Kittiwake parents can reduce the frequency of meal deliveries, which lowers the time and energy costs of transporting food to the nest (Laugksch and Duffy 1986, Obst 1986). For nestlings, lipid-rich meals have high energy density and meet the nestlings' high maintenance requirements (Ricklefs et al. 1980a, Simons and Whittow 1984). The resultant high fat reserves may enhance survival of nestlings and fledglings.

Despite the apparent advantage of feeding on an energy-dense diet (e.g. lanternfish), adult Black-legged Kittiwakes concentrate their foraging efforts on a wide variety of prey that have lower energy density and are found in the relatively shallow waters near the colony. Foraging on a variety of prey close to the colony may enhance the potential for Black-legged Kittiwakes to raise a two-nestling brood, particularly when prey resources in the vicinity of the colony are high. The advantage of potentially raising two offspring may explain why Black-legged Kittiwakes have a generalist feeding strategy and do not provision their nestlings with more lanternfish. Conversely, Red-legged Kittiwakes foraging farther from the colony on energy-dense prey should produce one nestling with larger fat reserves at fledging. This strategy may enhance survival of the young, but it could preclude raising more than one nestling. The pattern of restricted foraging ranges in species that normally raise two nestlings compared with species that raise only

one nestling has been noted previously (Cody 1973, Croxall and Prince 1980).

In summary, for both species of kittiwake, survival rates, growth rates of lean tissue, and total body mass of cross-fostered nestlings did not differ from those of conspecific controls. This supports the hypothesis that growth rates are genetically constrained. Nestlings of both species raised by Red-legged Kittiwakes were on average 50% fatter at 30 to 32 days posthatching than those raised by Black-legged Kittiwakes. Regurgitations from nestlings raised by Red-legged Kittiwakes consisted primarily of lanternfish and had about twice the lipid content as those from nestlings raised by Black-legged Kittiwakes. This suggests that the rate of fat deposition was constrained by diet composition. Although a high-lipid diet was not required for normal growth in nestling Red-legged Kittiwakes, diets high in lanternfish were responsible for higher energy reserves of nestlings. We hypothesize that the advantage of lanternfish in the diets of Red-legged Kittiwakes is expressed in higher nestling survival, higher postfledgling survival, or both.

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