RESEARCH ARTICLE

Fast and efficient: Postnatal growth and energy expenditure in an Arctic-breeding waterbird, the Red-throated Loon (*Gavia stellata*)

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ABSTRACT
Environmental conditions can exert a strong influence on the growth and energy demands of chicks. We hypothesized that postnatal growth in a cold, aquatic environment would require a high level of energy metabolism in semiprecocial Red-throated Loon (*Gavia stellata*) chicks. We measured body-mass growth and daily energy expenditure (DEE) of free-ranging chicks in the Arctic. We used daily gains in body mass and DEE to estimate daily metabolizable energy (DME, kJ day^{-1}) and total metabolizable energy (TME, kJ chick^{-1}). Chicks gained body mass quickly, with a logistic growth rate constant 57% greater than the allometric prediction, yet were at only 60% of adult body mass at fledging. Males grew at a rate similar to that of females but for a slightly longer duration and so reached an asymptotic body mass 23% greater, and tarsus length 8% longer, than that of females. Chick growth performance was similar between first- and second-hatched chicks within broods of 2, which suggests that food availability was not limited. DEE increased in proportion to body mass, and DME peaked at 1,214 kJ day^{-1} on day 25 posthatching. Over the average 49-day postnatal period, TME was 49.0 MJ, which is within the range of error of the allometric prediction. Parents provided 58.6 MJ as food to meet this energy requirement. Given this chick energy requirement and the range of energy content of prey observed in the chick diet, selecting prey with higher energy content would greatly reduce adult provisioning effort. Red-throated Loon chicks did not have a high postnatal energy requirement, but rather grew quickly and fledged at a small size—with the effect of reducing the length of the postnatal period and, consequently, parental energy investment in chicks.

Keywords: diver, energy allocation, growth rate, postnatal development

Rápido y eficiente: Crecimiento postnatal y gasto de energía en *Gavia stellata*, un ave acuática que cría en el Ártico

RESUMEN
Las condiciones ambientales pueden tener una fuerte influencia en el crecimiento y la demanda energética de los polluelos. Nuestra hipótesis es que el crecimiento postnatal en un ambiente acuático frío podría requerir un alto nivel de energía metabólica en los polluelos semi precoces de *Gavia stellata*. Medimos el crecimiento de la masa corporal y del gasto energético diario (GED) de polluelos silvestres en el Ártico. Empleamos los aumentos diarios en masa corporal y en GED para estimar la energía metabolizable diaria (EMD, kJ d^{-1}) y la energía metabolizable total (EMT, kJ polluelo^{-1}). Los polluelos aumentaron la masa corporal rápidamente con una tasa de crecimiento logístico constante 57% más grande que la predicción alométrica, aunque representaron solo 60% de la masa corporal del adulto al momento del emplumamiento. Los machos crecieron a una tasa similar a la de las hembras, pero por un periodo un poco más largo y por ende alcanzaron una masa corporal asintótica 23% más pesada, y una longitud del tarso 8% más larga, que las hembras. El desempeño del crecimiento de los pichones fue similar entre polluelos eclosionados en primer y segundo lugar dentro de nidadas de dos individuos, sugiriendo que no hubo un límite en la disponibilidad de alimentos. El aumento de GED fue proporcional a la masa corporal y EMD tuvo un pico a 1214 kJ d^{-1} en el día 25 luego de la eclosión. A lo largo de los 49 días promedio del período postnatal, EMT fue 49.0 MJ, lo que está adentro del rango de error de la predicción alométrica. Los padres proveyeron 58.6 MJ como alimentos para alcanzar este requerimiento energético. Dado este requerimiento energético del polluelo y el rango del contenido de energía de las presas observado en la dieta de los polluelos, la selección de presas con mayor contenido energético reduciría enormemente el esfuerzo de aprovisionamiento del adulto. Los polluelos de *G. stellata* no tienen un requerimiento energético postnatal alto, sino que crecen rápido y dejan el nido con un tamaño pequeño, lo que reduce la duración del periodo posnatal, y consecuentemente, la inversión parental de energía en los polluelos.

INTRODUCTION

Growing chicks must ingest sufficient energy to support the costs of tissue synthesis, tissue maintenance, dietary thermogenesis, activity, and thermoregulation (Weathers 1996). The sum of these energetic costs over the postnatal period, from hatching until fledging, represents the total expense of producing a fledgling. In species with chicks that self-feed, the chicks must acquire sufficient food to meet this requirement; otherwise, parents must acquire the food and provision it to their chicks (Nice 1962). Chick energy requirement is most related to body mass because metabolic rate, which scales positively with body mass, is a dominant pathway of energy expenditure (Drent et al. 1992, Klaassen 1994). However, each pathway of energy expenditure may vary in relation to life history traits and the environment (Weathers 1992). Accordingly, some species are more energetically expensive to produce than others, even after accounting for body mass (Schekkerman and Visser 2001, Hodum and Weathers 2003). Species with high chick energy demands require high food intake to maintain energy balance (Klaassen et al. 1992, Benowitz-Fredericks and Kitaysky 2005). Under conditions of restricted food intake, growing birds must allocate limited energy among competing metabolic demands (Dunn and Brisbin 1980, Konarzewski 1995). Consequently, if energy intake is limited, growth may be compromised, with potential effects on chick survival and recruitment into the breeding population (Lindén et al. 1992, Schmutz 1993, Sedinger et al. 1995).

How chick energy allocation is related to mode of development and the environment is unclear. Weathers (1992) showed that most variation in the total energy metabolism of chicks in a diverse group of 30 species was explained by body mass and length of the postnatal period. Drent et al. (1992) showed that the combined energy costs of thermoregulation and activity made up ~30% of a chick's total energy budget in a small but diverse group of 14 species. However, most species examined in these reviews were either altricial or semiprecocial and remained at or near the nest until fledging. By contrast, the total energy requirements of some precocial, self-feeding shorebird chicks exceeded allometric predictions by 29–39% at a middle-latitude breeding site (Schekkerman and Visser 2001). Total energy requirements were even higher (up to 107% greater than predicted) at high-latitude breeding sites for both precocial (Schekkerman et al. 2003, Tjørve et al. 2007) and semiprecocial chicks (Hodum and Weathers 2003). High energy requirements in chicks that experience cold operative temperatures, or that leave the nest site after hatching to follow parents or feed, suggest that the mode of development can interact with the environment to create energy-demanding chick life histories.

FIGURE 1. A parent Red-throated Loon with its chick. Photo credit: Gerrit Vyn

Loons (family Gaviidae) are waterbirds whose semi-precocial young enter aquatic habitat shortly after hatching. The thermoregulatory demands of residing on water may be particularly important for loon chicks. Common Loon (*Gavia immer*) chicks had similar rates of energy expenditure at 10 days and 21 days posthatching, which suggests that the cost of thermoregulation may have been exceptionally high in young chicks (Fournier et al. 2002). Of all species in the Gaviidae, the Red-throated Loon (*G. stellata*; Figure 1) has the northernmost breeding distribution, up to 83°N (Barr et al. 2000), and is unique among its congeners in that chicks, in broods of 2, rely exclusively on parental provisioning for energy intake during the entirety of the postnatal period (Reimchen and Douglas 1984, Eberl and Picman 1993). Breeding Red-throated Loons do not capture prey from within their breeding lakes, which are often small and devoid of fish, but instead fly to foraging sites in coastal marine habitat or larger lakes (Johnson and Johnson 1935, Eriksson et al. 1990) up to 20 km from the breeding lake (Davis 1972). Because chicks do not self-feed, parental provisioning effort must be sufficient to meet the energy requirements of both chicks in the brood; otherwise chicks may grow at reduced rates, and brood size may be reduced by starvation (Okill and Wanless 1990, Eberl and Picman 1993, Ball 2004). Their reliance on adult provisioning for energy intake and use of aquatic habitat make the Red-throated Loon an interesting model species for examining postnatal growth and energy requirement.

We quantified growth in free-ranging Red-throated Loon chicks from the Arctic Coastal Plain of Alaska. To determine whether parents were able to meet the energy requirement of their brood, we examined differences in growth performance associated with sex and chick status

(first-hatched senior chicks, second-hatched junior chicks, or solitary singleton chicks). We used the doubly labeled water (DLW) method to quantify postnatal daily energy expenditure (DEE, kJ day^{-1}) and examined DEE for differences in sex and chick status independent of body mass. We used daily gains in body mass and DEE to estimate daily metabolizable energy (DME, kJ day^{-1}) and total metabolizable energy (TME, MJ chick^{-1}) and examined how easily parents were able to meet chick energy requirements, given prey species observed in the chick diet. We hypothesized that, given their use of aquatic habitat and the climate of their high-latitude breeding site, Red-throated Loon chicks would metabolize more energy than predicted from their body mass at fledging.

METHODS

Study Site

We conducted the study at a site on the Chukchi Sea coast of the Arctic Coastal Plain of Alaska, near the village of Point Lay (69°44′N, 163°00′W) during 2 consecutive summers (June–September) in 2009 and 2010. The habitat at the study site is dominated by thermokarst with abundant ice-wedge polygons and thaw lakes ranging in size from 0.02 to 50.00 ha. Small (0.02–0.80 ha) thaw lakes are numerous and occur in association with river deltas and dry lakebeds (Jorgenson and Shur 2007). The main vegetative communities at the site are tussock-sedge, dwarf-shrub, and moss (Gallant et al. 1995). The Arctic Coastal Plain has a polar climate characterized by monthly average temperatures <10°C throughout the year. Average daily (± SD) air temperature at the study site during the brood-rearing period (July and August) was 7.9 ± 3.7°C in 2009 and 7.8 ± 3.3°C in 2010 (NOAA 2014). In a sample of lakes used by brood-rearing loons ($n = 16$), average water temperature was 7.4 ± 2.0°C.

Chick Growth

We used aerial photography to identify areas of suitable breeding habitat and systematically searched these areas on foot for active nests. Upon discovering an active nest, we recorded its coordinates using hand-held global positioning systems and floated eggs in water to determine the extent of embryo development (Rizzolo and Schmutz 2007). We used estimated embryo age (i.e. number of days of incubation) to calculate a predicted hatching date for each nest, assuming a 26-day incubation period and 48-hr hatching interval for eggs within a typical 2-egg clutch (Barr et al. 2000). We began capturing chicks using mist nets floated horizontally on the surface of the breeding lake (Okill 1981) 10 days after hatching, when chicks were able to effectively dive to avoid predators. To collect morphometric data, we attempted to capture all active chicks at approximately weekly intervals until fledging

(Dzubin and Cooch 1992). We marked each chick with a uniquely numbered metal tag attached to the webbing of its foot. Morphometric data included body mass (±1 g), length of exposed culmen (±0.5 mm), length of diagonal tarsus (±0.5 mm), folded–flattened wing length (±1 mm), and length of the outermost primary feather (±1 mm). We determined fledging dates by visiting most brood lakes every 2 days, late in the brood-rearing period, to count the chicks present on the lake. Absent any sign of depredation at the brood lake (e.g., carcass or feathers), we considered a chick to have fledged if it disappeared from the brood lake after the earliest documented age of fledging (38 days; Barr et al. 2000).

Daily Energy Expenditure

We measured DEE in each of the 2 yr using the DLW technique (Lifson and McClintock 1966, Nagy 1980, Butler et al. 2004). In each year, we selected broods for inclusion in the DLW study using random selection stratified by brood size (1 or 2 chicks). We attempted to measure the DEE of each chick on 3 occasions during the postnatal period, at approximately 10 days, 28 days, and 38 days posthatching, to capture nonlinearities in the association between DEE and body mass; however, we were not able to sample all chicks at these exact ages. We dosed chicks in the pectoralis muscle with a solution of DLW containing 65.2 atom percent excess (APE) oxygen-18 (^{18}O) and 35.4 APE Deuterium (^{2}H). Dose volumes varied in relation to chick body mass and ranged from 0.2 mL to 1.5 mL DLW. We measured doses on an electronic balance (±0.002 g) and weighed the syringe used to inject the DLW immediately before and after the injection to correct for any residual solution remaining in the syringe. Prior to administering the dose, we collected a background blood sample to determine naturally occurring levels of ^{18}O and ^{2}H in the blood of each chick ("method A" in Speakman and Racey 1987). After DLW dosing, we held chicks for 1 hr for equilibration of the isotopes into the body-water pool (Król and Speakman 1999, Visser et al. 2000), after which we collected an initial blood sample and returned chicks to their brood lake. We recaptured chicks 48 hr after the initial blood sample to collect the final blood sample for calculating rates of change in ^{18}O and ^{2}H concentrations. Samples were collected as close as possible to 48 hr after the initial sample to minimize circadian effects (Speakman and Racey 1988). Measurements were made across 2 days to minimize the potential day-to-day variability in DEE (Speakman et al. 1994, Berteaux et al. 1996). We collected blood samples from the medial metatarsal vein by venipuncture into 6–10 untreated microhematocrit tubes, each filled with 10–15 μL of blood and immediately flamed-sealed, and stored the tubes at 5°C. In addition, we collected ~20 μL of blood from each chick into an Eppendorf tube containing Longmire buffer

for genetic determination of sex (Guzzetti et al. 2008). We collected morphometric data during each DLW capture and at age ~21 days.

Concentrations of ^{18}O and ^2H in blood samples were determined by isotope ratio mass spectrometry (IRMS) using methods described by Speakman and Król (2005). Blood samples were vacuum distilled into glass Pasteur pipettes (Nagy 1983), and the water obtained was used for determination of $^2H:^1H$ and $^{18}O:^{16}O$ ratios. The enrichment of ^2H was determined from hydrogen gas produced by online chromium reduction of water (Morrison et al. 2001). For analysis of the ^{18}O enrichment in blood samples, water distilled from blood was equilibrated with CO_2 gas using the small sample technique (Speakman et al. 1990). IRMS determination of $^2H:^1H$ and $^{18}O:^{16}O$ ratios was done using isotopically characterized gases of H_2 and CO_2 in the reference channels of the IRMS. Four subsamples of each blood sample were analyzed, and average values of enrichments were used for calculations. Injectate enrichment was determined by serial dilution with tap water and IRMS analysis of 5 subsamples of each DLW solution used (Speakman 1997). All isotope enrichments were measured (per mil, δ) in relation to working standards and converted to parts per million using the established ratios for these reference materials.

We calculated DEE using Speakman's equation 7.17 (Speakman 1997), which assumes that ^2H and ^{18}O dilute into a single dilution space and a fixed evaporation of 25% of the water flux. This equation has been validated in precocial chicks (Visser and Schekkerman 1999). We estimated percent body-water pool (i.e. total body water, %TBW) using the dilution space of ^{18}O and the plateau technique (Speakman 1997, Mata et al. 2006). We converted rates of CO_2 production (mol day^{-1}) to DEE (kJ day^{-1}) by assuming an energy equivalent of 27.33 J mL^{-1} for a diet composed primarily of fat and protein (Gessaman and Nagy 1988), as is the piscivorous diet of Red-throated Loons (Barr et al. 2000).

Data Analysis

Growth. To quantify the growth of each morphometric, we limited the analysis to chicks captured on ≥4 occasions for measurements. We selected the growth model that best fit the data for each morphometric. Candidate growth models for each morphometric included the Gompertz, the logistic, the von Bertalanffy (Ricklefs 1967), and the Janoschek (Gille and Salomon 1995) models, which all express a sigmoidally shaped relationship between the morphometric and chick age.

The Gompertz, logistic, and von Bertalanffy models differ with regard to the placement of the inflection point of the curve, which corresponds to the day of maximum growth rate, in relation to the asymptote (Ricklefs 1967). Other parameters in these models include asymptotic size

(A, g) and growth rate constant (K, day^{-1}), which is the rate at which the slope of the curve changes with age and therefore is positively associated with growth rate. For both the Gompertz and logistic models, the parameter T estimates the age corresponding to the inflection point; in the von Bertalanffy model, T corresponds to the size at hatching. The Janoschek model includes 4 parameters: size at hatching (W_0), asymptotic size (A), age at which 50% of asymptotic size is reached (t_{50}), and a shape parameter (p; Gille and Salomon 1995). We fit the Janoschek model to data from each morphometric with W_0 set to the hatchling measurements of Davis (1972; hatchlings: body mass = 55 g, tarsus length = 26.1 mm, culmen length = 9.9 mm; n = 11), or from 2 hatchlings opportunistically measured at our study site (wing length = 23.9 mm, outermost primary length = 0 mm). For body mass, we compare our estimate of growth rate constant to that predicted using Ricklefs's (1979) equation based on 190 species representing all modes of development.

For each morphometric, we selected the growth model with the lowest Bayesian Information Criterion (BIC; Schwarz 1978) value and compared the strength of support for candidate models from the data on the basis of posterior model weights (Link and Barker 2006). We used multilevel, nonlinear, mixed-effects models (Sockman et al. 2008) fitted in the NLMIXED procedure of Program SAS (SAS Institute 2009) to examine the association between growth curve parameters and sex and chick brood status: first-hatched "senior," second-hatched "junior," or solitary "singleton" chicks. Singleton chicks either hatched from clutches with a single egg or resulted from partial depredation during incubation or chick rearing. Multilevel models estimate nonlinear model parameters and examine variation in these parameters in relation to explanatory variables. We examined variation in growth parameters of the nonlinear growth models (e.g., model parameters A, K, and T) that were most supported by the data for each morphometric. For each morphometric, we included a model that permitted each parameter to vary with "sex," a model that allowed each parameter to vary with "status," and a model that allowed each parameter to vary with both "sex" and "status" as additive effects; we included a random "individual" effect on A in all models to account for repeated measurements on chicks. We used BIC posterior model weights to select the model that best described sources of variation in growth curve parameters for each morphometric.

Daily Energy Expenditure. We estimated the power curve relating DEE to body mass using a linear mixed-effects model. We log$_{10}$ transformed both DEE and body mass and included "individual" as a random effect in all models to account for repeated measurements on chicks. We examined how the relationship between DEE and body mass varied with sex and chick status by including "sex"

and "status" in models as interactions with "mass." We did not include "sex" and "status" main effects because we assumed that all chicks share a common intercept value but may differ in the slope of the relationship between DEE and body mass. We fitted models that included "sex" and "status" independently and in combination, as well as a model that included only "mass," and based model selection on BIC posterior model weights.

Energy Requirement. We determined the average metabolizable energy requirement of a Red-throated Loon chick on the basis of the logistic growth model relating body mass to chick age and the power model relating DEE to chick body mass. We calculated daily metabolizable energy (DME: ingested food energy minus excretory energy, kJ day^{-1}; Weathers 1992) as the daily sum of DEE (kJ day^{-1}) at age-specific body masses and retained energy (RE, kJ g^{-1} day^{-1}) deposited as daily gains in body mass. We estimated body tissue energy (TE, kJ g^{-1}) using measurements of %TBW of chicks using dilution of ^{18}O and the plateau method (Speakman 1997, Mata et al. 2006). We did not collect chicks to measure whole body composition in the laboratory and instead assumed that the water fraction of lean tissue (w, %) changed during postnatal growth according to the equation $w = 79.86 - 9.55 \times$ proportion of adult body mass attained (Schekkerman and Visser 2001). For adult body mass, we used average adult body mass adjusted for sex differences (1,614 g), average male adult body mass (1,741 g), and average female body mass (1,424 g; body masses from $n = 40$ adults captured from the study population). We calculated percent lean body mass as the quotient of %TBW and w, and percent fat mass as 100 − percent lean body mass. We used lean and fat fractions to calculate the energy content of tissue, assuming energy equivalents of 5 kJ g^{-1} fresh mass for lean tissue and 38 kJ g^{-1} fresh mass for fat (Weathers 1996).

We determined the relationship between the mass-specific tissue energy content of chicks and chick body mass using a linear mixed-effects model that included "individual" as a random effect. We summed DME from hatching to the average age at fledging (49 days) to determine total metabolizable energy (TME, MJ chick^{-1}) for the postnatal period. We compared our estimate to that predicted by the equation of Weathers (1992: equation 8) to examine the hypothesis that Red-throated Loon chick TME was higher than predicted given their body mass and the length of their postnatal period.

We determined the amount of energy a chick needed to ingest to meet its DME given the inefficiencies of energy assimilation (i.e. daily energy intake [DEI], kJ day^{-1} chick^{-1}) using estimates of assimilation efficiency (AE, proportion of ingested energy assimilated) from Common Loon chicks fed trout (*Oncorhynchus mykiss*; Fournier et al. 2007). Estimated assimilation efficiency of Common

Loon chicks at 32% and 53% of the age of asymptotic body mass increased from 0.64 to 0.83 (Fournier et al. 2007). We applied these AE estimates to Red-throated Loon chicks by assuming an incremental increase in AE from 0.64 to 0.83 between ages 10 and 17 days (32% and 53% of the age of asymptotic body mass for Red-throated Loons, respectively). We summed estimates of DEI over the postnatal period to determine the total amount of energy a chick ingested to meet its TME demand (gross energy intake [GEI], MJ chick^{-1}). We made these calculations at the average values of DEE and body mass as well as at their lower and upper confidence limits to set a range of plausible values given the data (we report these as the "plausible range" of DME, TME, and GEI). We calculated the portion of the energy budget required for growth of tissue as the sum of RE and the energy used for biosynthesis divided by TME, assuming that the cost of biosynthesis was 33% of RE (Ricklefs 1974).

As a heuristic exercise, we examined the influence of diet energy content on parental foraging effort given the energy requirement we quantified for a Red-throated Loon chick. We calculated the number of fish required to meet chick DEI given a diet at either limit of the range of prey energy content we observed in chick diets. We observed both rainbow smelt (*Osmerus mordax*) and least cisco (*Coregonus sardinella*) provisioned to chicks by their parents in the study population (D. J. Rizzolo personal observation); these species also were fed to chicks on the Bering Sea coast of Alaska (Ball 2004). Least cisco is a relatively energy-rich species with an average energy density of 5.2 kJ g^{-1} wet mass, whereas rainbow smelt has a lower average energy density of 3.1 kJ g^{-1} wet mass (Ball et al. 2007).

The size of prey that a chick is able to ingest changes with age as chick body size increases; further, the energy content of fish also varies with fish body length. To account for these factors, we used chick age-specific fish sizes (mm wk^{-1}; Ball 2004) and fish length-specific estimates of energy content (kJ mm^{-1} length; Ball et al. 2007) to calculate the energy content of least cisco and rainbow smelt ingested by a chick between weeks 1 and 7 of the postnatal period. We assumed that once a chick reached the age when it consumed the maximum fish size observed (145 mm fish length at chick age 3 wk; Ball 2004), the parents continued to provision fish of this size for the remainder of the postnatal period. We then calculated the number of least cisco or rainbow smelt at chick-age specific fish sizes that would be required to meet the DEI of a chick for each day of the postnatal period. Given that each fish eaten by a chick represents an individual foraging trip that 1 parent must make, this exercise demonstrates the potential range of effect that diet energy content can have on adult provisioning effort, given chick energy demands.

TABLE 1. Best-fitting nonlinear models and associated parameter estimates (95% confidence intervals) describing growth of body mass (g), tarsus length (mm), culmen length (mm), wing length (mm), and primary feather length (mm) of Red-throated Loons from Point Lay, Alaska, in 2009 and 2010. Bayesian Information Criterion posterior model weights (BICw$_i$) indicate strength of support for the model from the data in relation to the other models considered, with values closer to 1.0 indicating stronger support. Model parameters include asymptote (A), growth rate constant (K, day^{-1}), and inflection point (T, days; for all models other than the von Bertalanffy model, in which T is size at hatching, in millimeters).

Morphometric	Model	BIC w_i	A	K	T
Mass	Logistic	0.81	1,071 (1,025–1,118)	0.161 (0.148–0.173)	16.3 (15.8–16.8)
Tarsus	Logistic	0.85	74.8 (73.5–76.1)	0.105 (0.098–0.111)	7.6 (7.2–7.9)
Culmen	von Bertalanffy	0.57	45.4 (43.4–47.5)	0.049 (0.044–0.054)	16.9 (14.5–19.3)
Wing	Logistic	0.63	247.5 (241.9–253.2)	0.121 (0.117–0.126)	21.2 (20.8–21.7)
Primary	von Bertalanffy	0.99	186.4 (171.3–201.4)	0.044 (0.041–0.048)	−2.9 (−3.9 to −1.9)

RESULTS

Growth

We measured 36 chicks (20 female, 16 male) from 25 broods (12 pairs of siblings, 13 singletons). We knew with certainty the hatching date of 22% of the chicks we measured and calculated the hatching date of 16% based on the observed hatch date of their sibling, assuming a 48-hr hatching interval; we estimated hatching date using egg flotation for the remaining 62% of chicks. We captured chicks an average of 6 times during the postnatal period (range: 4–9 times), for 228 measurements that occurred 7–50 days posthatching. Average length of the postnatal period, from hatching to fledging, was 49 days (range: 42–55 days, n = 17). All chicks included in the analysis survived to fledging or were still active when last checked (minimum age of 40 days when last observed). The average interval for a chick between the last capture occasion and fledging was 6 days (range: 1–14 days).

The nonlinear growth model most supported by the data varied by morphometric (Table 1). Body mass, tarsus length, and wing length grew at the fastest rates and were best described by the logistic model, whereas slower growth of the culmen and primary feather were best described by the von Bertalanffy model (Figure 2). The estimated logistic growth rate constant for body mass (K = 0.16, 95% CI: 0.15–0.17) was 57% greater than the allometric prediction (0.10; Ricklefs 1979). Lengths of the culmen, wing, and primary feather at fledging were all below model-predicted asymptotic size, and all morphometrics other than tarsus length were less than adult size at fledging (Figure 2). Variation in growth of body mass and tarsus length was associated with sex of the chick (posterior model weights for models including "sex" = 1.0; Table 2); chick status was unrelated to growth for any morphometric (posterior model weights for all models including "status" = 0.0; Table 2). Male asymptotic body mass was 23% heavier and tarsus length was 8% longer than female measurements; this was due to males growing at a similar rate to that of females but for a slightly longer duration (Table 3).

Daily Energy Expenditure

We measured DEE of 25 chicks (10 male, 15 female) from 18 broods (7 pairs of siblings, 11 singletons). Average (± SD) duration of the DEE interval was 48.3 ± 3.9 hr. We were able to measure DEE on 3 occasions within the postnatal period for 16 chicks, on 2 occasions for 7 chicks, and on 1 occasion for 2 chicks. Chicks not sampled on all 3 occasions either were depredated, entered the study late to replace depredated chicks, had failed DLW injections, or could not be located at the time of recapture during a given sampling occasion. The average age of chicks was 12 days (range: 8–19 days) at the early sampling occasion, 30 days (range: 23–34 days) at the middle sampling occasion, and 40 days (range: 33–47 days) at the late sampling occasion. We did not sample chicks <7 days old and instead extrapolate outside of the data from age of the youngest chick sampled for DEE to age 1 day. Of the 25 chicks sampled for DEE, 22 successfully fledged, 2 were depredated, and 1 was still alive when last checked. The average age at fledging for sampled chicks was 49 days (range: 43–55 days).

Average (± SD) levels of ^{2}H and ^{18}O in background blood samples were 152.3 ± 2.1 ppm (n = 25) and 1,987.1 ± 6.1 ppm (n = 25), respectively. Estimates of %TBW based on ^{18}O dilution space declined with chick body mass (g) as described by the linear equation with estimated parameters (± SE): %TBW = 76.8 (± 1.17) − 0.0097 (± 0.0014) × body mass. DEE varied with chick body mass (g) according to the equation DEE = 11.89 (± 3.6) × M$^{0.65 (± 0.05)}$ (Figure 3). Variation in DEE was not explained by "sex" or "status." The model that included only "mass" was most supported by the data (posterior model weight = 0.98) and had much more support from the data than the next best model that included "status" (posterior model weight < 0.02). Thus, we found no evidence that sex or chick status had effects on DEE independent of body mass.

Energy Requirement

Estimated energy content of chick tissue based on %TBW measurements increased with chick body mass (g) according to the linear equation estimated with parameters
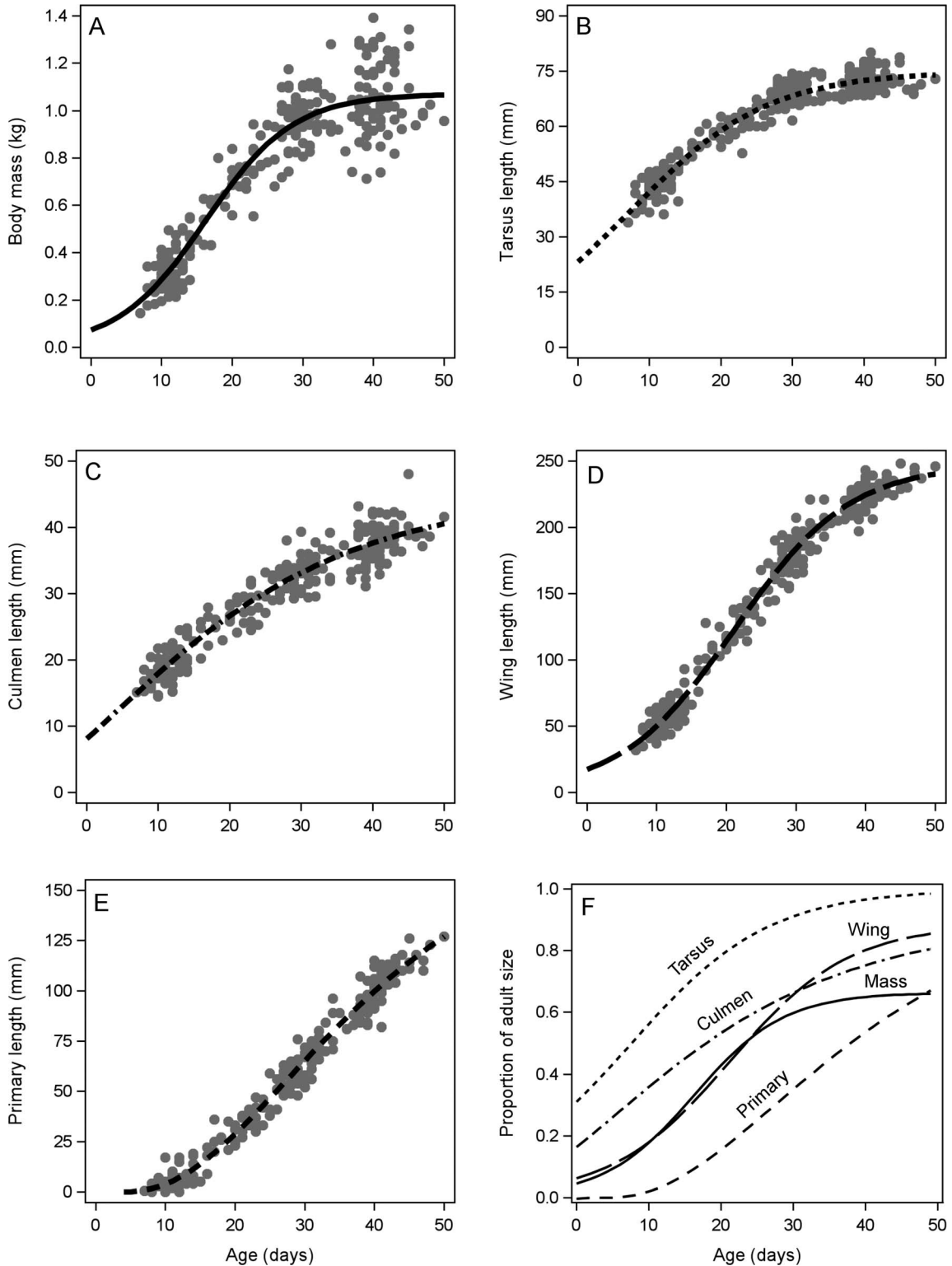
FIGURE 2. Measurements of (**A**) body mass, (**B**) tarsus length, (**C**) culmen length, (**D**) wing length, (**E**) outermost primary feather length, and (**F**) all morphometrics as proportion of adult size in relation to age of Red-throated Loon chicks from Point Lay, Alaska, in 2009 and 2010. Lines are estimates from the best-fitting growth model for each morphometric. Measurements are from 36 chicks from 25 broods.

TABLE 2. Ranking of multilevel nonlinear mixed-effects models used to examine variation in parameters describing growth in Red-throated Loons from Point Lay, Alaska, in 2009 and 2010. Models with Bayesian Information Criterion (BIC) posterior model weights (BICw$_i$) close or equal to 1.0 were more strongly supported by the data.
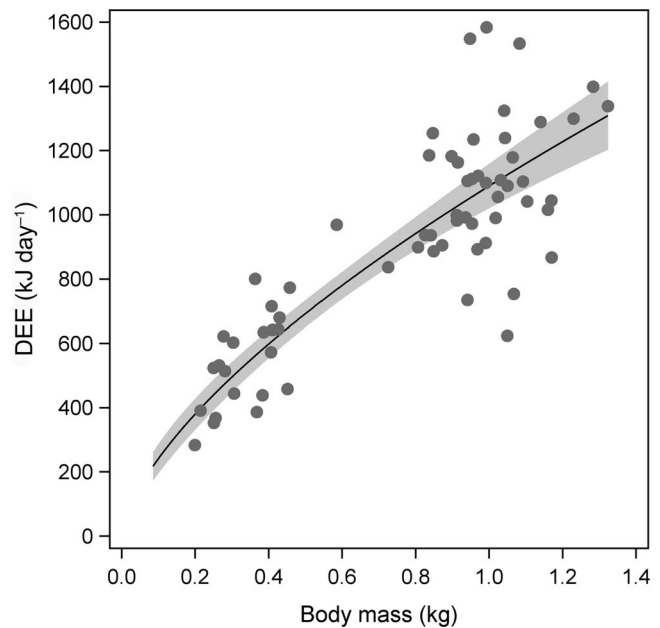
Morphometric	Model	k	Deviance	BIC	BICw$_i$
Mass	Sex	8	2,620.3	2,663.7	1.00
	Null	5	2,657.8	2,684.9	0.00
	Sex + status	14	2,621.0	2,697.0	0.00
	Status	11	2,655.2	2,714.9	0.00
Tarsus	Sex	8	990.5	1,033.9	1.00
	Null	5	1,023.5	1,050.7	0.00
	Sex + status	14	981.2	1,057.2	0.00
	Status	11	1,017.3	1,077.0	0.00
Culmen	Null	5	836.2	863.4	0.98
	Sex	8	827.8	871.2	0.02
	Status	11	824.3	884.0	0.00
	Sex + status	14	808.7	884.7	0.00
Wing	Null	5	1,611.1	1,638.3	0.99
	Sex	8	1,604.5	1,648.0	0.01
	Status	11	1,607.1	1,666.9	0.00
	Sex + status	14	1,599.9	1,675.9	0.00
Primary	Null	5	1,349.8	1,376.9	0.99
	Sex	8	1,342.3	1,385.7	0.01
	Status	11	1,339.9	1,399.7	0.00
	Sex + status	14	1,334.5	1,410.5	0.00

($\pm$ SE): tissue energy (kJ g^{-1}) = 6.6 ($\pm$ 0.46) + 0.0015 ($\pm$ 0.0005) $\times$ body mass. DME peaked at 1,214 kJ (plausible range: 1,094–1,339 kJ) at 25 days (Figure 4). This value represents the maximum DME per chick that parents had to meet through their combined provisioning effort. DME values over an average postnatal-period length (49 days) summed to a TME of 48.9 MJ (plausible range: 44.8–52.9 MJ). This empirical estimate based on DEE and RE measurements is 22% greater than TME estimated on the basis of fledging body mass and length of the postnatal period (40.2 MJ; Weathers 1992: equation 8) but is within the range of error of the predictive equation. DME values adjusted for age-specific assimilation efficiency summed to a GEI of 58.6 MJ (plausible range: 53.8–63.4 MJ), which is the amount of energy parents provisioned as food over the course of the postnatal period to meet a chick's TME requirement. When calculated on the basis of sex-specific

body-mass growth curves and estimates of RE, the TME of males was 12% greater than that of females (male: 52.0 MJ; female: 46.4 MJ). Based on average DEE and body mass, chicks allocated 20% of TME for the synthesis and accumulation of tissue during growth and used the

FIGURE 3. Daily energy expenditure (DEE) in relation to body mass during postnatal growth in Red-throated Loon chicks from Point Lay, Alaska, in 2009 and 2010. Points are DEE measurements (66 measurements from n = 25 chicks) with the fitted mean (line) and 95% confidence interval (shaded area).
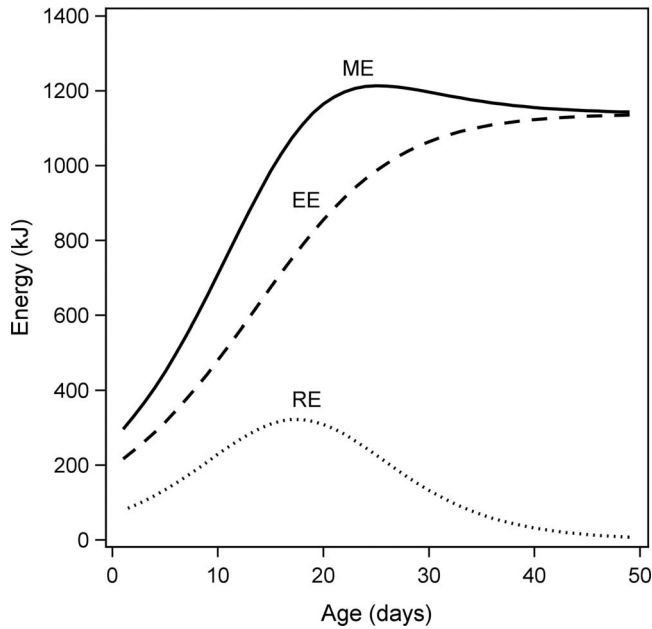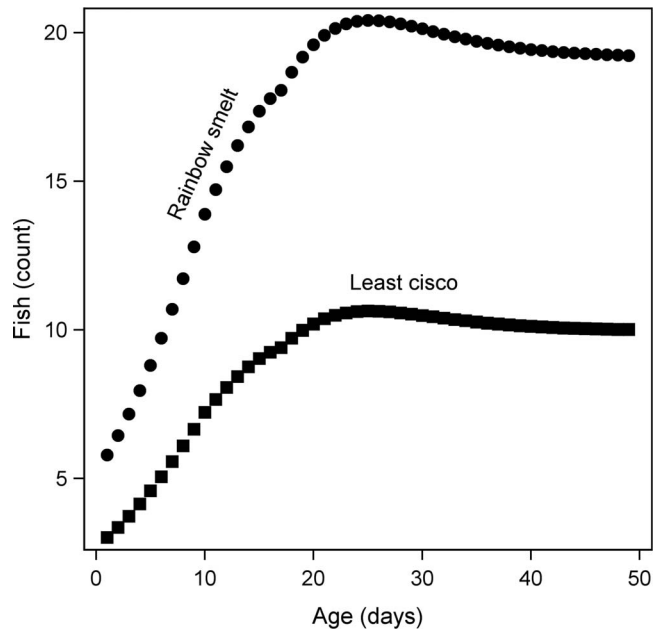
TABLE 3. Logistic model parameter estimates (with 95% confidence intervals) for body-mass and tarsus-length growth in male and female Red-throated Loon chicks from Point Lay, Alaska, in 2009 and 2010. Parameters are defined in Table 1.

Morphometric	Parameter	Estimates	
		Male	Female
Body mass	A	1,202 (1,143–1,260)	975 (928–1,022)
	K	0.15 (0.14–0.17)	0.17 (0.15–0.19)
	T	17.3 (16.6–18.1)	15.4 (14.8–16.0)
Tarsus	A	78.5 (76.5–80.2)	72.3 (71.0–73.7)
	K	0.10 (0.09–0.11)	0.11 (0.10–0.12)
	T	8.2 (7.7–8.6)	7.1 (6.7–7.6)

FIGURE 4. Energy budgets of Red-throated Loon chicks from Point Lay, Alaska, in 2009 and 2010, growing at the average growth rate for body mass, from hatching to the average age of fledging. Estimates of metabolizable energy (ME, kJ day^{-1}, solid line), shown partitioned into its components: energy expenditure (dashed line; EE, kJ day^{-1}) and retained energy of new tissue (dotted line; RE, kJ day^{-1}) for each day of the postnatal period.

FIGURE 5. Daily intake of a high-energy-content forage fish species (squares: least cisco) and a lower-energy-content species (circles: rainbow smelt) required to meet the daily metabolizable energy requirement of a Red-throated Loon chick during the postnatal period.

remaining 80% to meet the combined costs of resting metabolism, dietary thermogenesis during digestion, thermoregulation, and activity (Figure 4).

Assuming that the chick diet was composed entirely of energy-rich least cisco, adults would need to provision an average of 8.9 fish day^{-1} (range: 3.0–10.6 fish day^{-1}) to meet the daily energy requirement of 1 chick, or a total of 438 fish over the entire postnatal period (Figure 5). By contrast, assuming that chick diet was composed entirely of lower-energy-content rainbow smelt, parents would need to provision an average of 17 fish day^{-1} (range: 5.8–20.4 fish day^{-1}), or a total of 842 fish over the postnatal period. The average difference in the number of fish required to meet chick daily energy requirement between these fish species was 8.2 fish day^{-1} (range: 2.7–9.8 fish day^{-1}). Every extra fish represents 1 additional foraging trip parents would be required to make.

DISCUSSION

During the postnatal period, Red-throated Loon chicks gained body mass at a rate that was higher than predicted given their asymptotic body mass, and metabolized an amount of energy similar to that predicted given their asymptotic body mass and the length of their postnatal period. High growth rate and near-average energy

requirement were unexpected given the semiprecocial mode of development and use of aquatic habitat of this species, as well as the high-latitude climate of the study site. Although growth rate for body mass was high, asymptotic body mass and sizes of all morphometrics, other than tarsus length, were less than those of adults. Thus, chicks had not completed growth before fledging. Rapid growth to a size at fledging that was less than adult size reduced the length of the postnatal period.

Variation in growth of Red-throated Loon chicks was most related to the sex of the chick, but not related to chick status. The effect of sex on chick growth was apparent in the asymptotic size of both body mass and tarsus length. Sexually dimorphic body mass consequently raised the TME of males by 12% compared to females. A difference in energy requirement between male and female chicks may affect parental provisioning effort (Harding et al. 2009) and chick growth performance (Daunt et al. 2001, Laaksonen et al. 2004), particularly when energy intake is limited.

The absence of an effect of chick status on growth or DEE indicates that parents provisioned both chicks in their brood with adequate energy to support equivalent patterns of growth and energy expenditure. By contrast, Ball (2004) found that growth in Red-throated Loon body mass, culmen length, and tarsus length was less in junior chicks than in senior and singleton chicks at a site on the Bering Sea coast in years when the availability of energy-rich prey

was low (Ball et al. 2007). Compared to our results, average body mass at fledging was 17% lower and sizes at fledging of all other morphometrics were 4–10% smaller in the Bering Sea study (Ball 2004). The availability of energy-rich prey may underlie this difference in growth performance. During the Bering Sea study, chicks were provisioned with low- to moderate-energy species of fish and no junior chicks survived to fledging (Ball 2004). In the present study, relatively high-energy least cisco were frequently fed to chicks and more than half of broods that survived to fledging included 2 chicks (D. J. Rizzolo personal observation).

Red-throated Loon chicks gained body mass at a rapid rate. Common Loon chicks also gain body mass rapidly, with a logistic growth rate constant (0.09 day^{-1}) that was 27% greater than predicted by the Ricklefs (1979) equation (0.07 day^{-1}; Fournier et al. 2007). In Red-throated Loons, the logistic growth rate constant for body-mass gain was even higher: 57% greater than predicted. Thus, although Red-throated Loons are semiprecocial with a high degree of functional maturity at hatching, their body-mass growth rate was similar to that of an altricial species of similar size.

The rate of postnatal growth in Red-throated Loons raises the question: Why grow so fast? Rapid growth as a mechanism to reduce predation risk during the postnatal period (Lack 1968, Case 1978, Remeš and Martin 2002) seems unlikely given that chick survival in Red-throated Loons is high after the first week posthatching, when chicks are most vulnerable (Ball 2004). A limited ice-free season on breeding lakes is another potential explanation; however, the duration of the ice-free summer throughout most of its range is substantially longer than the total time required for incubation and chick rearing (Walsh et al. 1998). Furthermore, in portions of their range above 70°N latitude, Red-throated Loons nest sympatrically with Yellow-billed Loons (*Gavia adamsii*), which need >100 days to hatch and fledge their young (North 1994); this suggests that a seasonal constraint on fledging time was unlikely even prior to the current pattern of climate warming in the Arctic (Hinzman et al. 2005).

An important consequence of rapid growth is the reduction in chick TME that results both from decreasing the length of the postnatal period and having a low body mass at fledging (Weathers 1992). Rapid growth reduces chick TME because growth rate and postnatal period length are positively correlated (Ricklefs 1968). Most energy expenditure late in the postnatal period is related to maintenance, activity, and thermoregulation; thus, shortening the postnatal period reduces the sum of these costs (Weathers 1992). Further, fledging at a body mass that is less than that of adults reduces TME because resting metabolic rate increases with body mass (Drent et al. 1992, Klaassen and Bech 1992). The trade-off to reducing TME by increasing growth rate is an increased peak daily energy requirement; however, peak daily energy demand increases with growth rate at a lesser rate than TME decreases (Weathers 1992). Thus, growing fast and fledging small makes a fledgling energetically less expensive to produce but requires a high daily energy intake to achieve.

The Red-throated Loon is the only species of loon that provisions chicks exclusively by flying between brood-rearing habitat and separate foraging habitat (McIntyre 1994). Consequently, brood-rearing adults incur the cost of flight during provisioning, which is likely high given their high wing loading (Lovvorn and Jones 1994). In addition to reducing chick TME, a low postnatal asymptotic body mass may enable chicks to optimize their wing loading for flight (Wright et al. 2006) and fledge before flight-feather growth is completed. After chicks fledge from natal habitat to the sea, parents no longer incur provisioning-flight costs. In this respect, Red-throated Loons are similar to seabirds that also must leave their chicks to forage in the marine environment. The chicks of high-latitude breeding seabirds, specifically species in the family Alcidae, fledge across a broad range of body sizes (15–100% of adult size) and ages (25–60 days; Sealy 1973, Ydenberg 1989). Reaching postnatal asymptotic body mass relatively quickly, and at a size less than that of adults, is likely an adaptation to reduce adult provisioning effort.

The costs of thermoregulation in the chicks of some species breeding at high latitudes are substantial and evident in high rates of energy metabolism. Semiprecocial fulmarine petrel (family Procellaridae) chicks at 68°S latitude had TME values 33–73% greater than predicted (Hodum and Weathers 2003). TME in precocial, self-feeding shorebird chicks at 73–75°N latitude was elevated 89–107% above predicted values (Schekkerman et al. 2003, Tjørve et al. 2007). These species grew rapidly but, contrary to the inverse relationship between the length of the postnatal period and TME shown by Weathers (1992), had exceptionally high rates of energy metabolism, in part due to the high costs of thermoregulation. We predicted that Red-throated Loon chicks would have a similarly high postnatal TME; however, we found that TME was not substantially elevated given their adult body mass and the length of their postnatal period. Thus, despite residing in cold-water lakes and experiencing low operative temperatures, Red-throated Loon chick TME was near its predicted value.

To achieve energy efficiency during the postnatal period, Red-throated Loon chicks may limit their energy expenditure behaviorally. Parents brood young chicks frequently for the first several days after hatching (Barr et al. 2000). Brooding reduced the energy requirement of chicks by 26% during the first 10–11 days of the postnatal period in Arctic Terns (*Sterna paradisaea*; Klaassen et al. 1989) and by 19% during the first 16 days in Black-legged Kittiwakes

(*Rissa tridactyla*; Gabrielsen et al. 1992). Throughout the postnatal period, loon chicks regularly rest onshore with 1 parent (Barr et al. 2000), thus reducing the time spent on water. As chicks grow, they gain the thermoregulatory benefits of increased body mass (Calder 1974, Visser and Ricklefs 1993, Williams et al. 2007) and complete juvenal plumage. Further, because Red-throated Loon chicks do not forage for themselves, they can reduce their activity in response to periods of low energy intake. Thus, in Red-throated Loons, adaptations to growth in an aquatic, high-latitude environment do not include a high TME. Instead, chicks apparently have the flexibility to moderate energy demand behaviorally because they are parent-fed and benefit from reduced thermoregulatory costs of rapidly increased body mass.

In Red-throated Loons, parents provision the energy required to meet chick DME over the postnatal period; thus, provisioning effort is closely coupled with chick DME and the energy density of prey. The energy content of food is less important when chick daily energy requirements are low and thus more easily met (Degen et al. 1992). However, a high growth rate for body mass increases peak daily energy requirements (Weathers 1992). Breeding success of piscivorous marine birds is often correlated with prey quality and availability (Springer et al. 1986, Litzow et al. 2002, Wanless et al. 2005, Piatt et al. 2007). Our provisioning-rate estimates correspond with observed provisioning rates (9–23 trips day^{-1} across studies, average 13.9 trips day^{-1}; Davis 1972, Reimchen and Douglas 1984, Eberl and Picman 1993) and demonstrate that the number of fish per day that a chick required to meet its daily energy demand differed greatly between fish species at opposite ends of the spectrum of prey energy content. At the peak DME, parents provisioning lower-energy-content rainbow smelt would be required to make twice as many foraging trips per chick as parents provisioning higher-energy-content least cisco. If the upper limit on fish required per chick at peak DME corresponds with a ceiling on adult provisioning effort (Drent and Daan 1980), then provisioning higher-energy-content least cisco would permit successfully fledging both chicks in the brood, whereas access to only lower-energy-content rainbow smelt would result in brood reduction. We found that the combined DME of both chicks in a 2-chick brood exceeds the DME of a single chick at 10 days posthatching, given the observed difference in growth rate of the junior and senior chicks through the first 14 days of growth (–63%; Ball 2004). Consistent with this, brood reduction in Red-throated Loons is typically observed at 10–14 days posthatching and is often attributed to the starvation of the junior chick (Gomersall 1986, Okill and Wanless 1990, Eberl and Picman 1993, Ball 2004).

Hypotheses explaining patterns of growth in chicks include energy limitation (Ashmole 1963, Lack 1968, Case 1978), diet composition (Roby 1991), tissue-level constraints (Ricklefs 1983, Ricklefs et al. 1994), and seasonal peaks in energy availability (Sedinger and Raveling 1986, Lepage et al. 1998, Schekkerman et al. 2003). Here, we describe a pattern in growth that is best explained in relation to parental investment in chicks. In Red-throated Loons, which are a high-wing-loading species, rapid growth and low fledgling body mass reduce the adult provisioning period by reducing the total energy requirement of the chick and thus the total number of provisioning trips required of parents. Total energy demands of chicks are reduced at the expense of increased daily energy demands. Our results show that given chick diet composition, chick daily energy requirements are more easily met when adults select prey with high energy content. Under these circumstances, variation in the availability of high-energy prey should exert a strong influence on reproductive success. Accordingly, Red-throated Loon productivity is highly variable and often low (Rizzolo et al. 2014). However, the life history strategy of the Gaviidae emphasizes high adult survival over fecundity (Nilsson 1977, Evers 2004, Grear et al. 2009, Schmutz 2014) and can accommodate years of low productivity without causing population decline. Thus, natural selection should favor patterns of chick growth and energy allocation that increase adult survival even at the expense of chick survival.

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