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Validating growth and development of a seabird as an indicator of food availability: captive-reared Caspian Tern chicks fed ad libitum and restricted diets

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ABSTRACT. For seabirds raising young under conditions of limited food availability, reducing chick provisioning and chick growth rates are the primary means available to avoid abandonment of a breeding effort. For most seabirds, however, baseline data characterizing chick growth and development under known feeding conditions are unavailable, so it is difficult to evaluate chick nutritional status as it relates to foraging conditions near breeding colonies. To address this need, we examined the growth and development of young Caspian Terns (*Hydroprogne caspia*), a cosmopolitan, generalist piscivore, reared in captivity and fed ad libitum and restricted (ca. one-third lower caloric intake) diets. Ad libitum-fed chicks grew at similar rates and achieved a similar size at fledging as previously documented for chicks in the wild and had energetic demands that closely matched allometric predictions. We identified three general characteristics of food-restricted Caspian Tern chicks compared to ad libitum chicks: (1) lower age-specific body mass, (2) lower age-specific skeletal and feather size, such as wing chord length, and (3) heightened levels of corticosterone in blood, both for baseline levels and in response to acute stress. Effects of diet restriction on feather growth (10–11% slower growth in diet-restricted chicks) were less pronounced than effects on structural growth (37–52% slower growth) and body mass (24% lower at fledging age), apparently due to preferential allocation of food resources to maintain plumage growth. Our results suggest that measurements of chick body mass and feather development (e.g., wing chord or primary length) or measurement of corticosterone levels in the blood would allow useful evaluation of the nutritional status of chicks reared in the wild and of food availability in the foraging range of adults. Such evaluations could also inform demography studies (e.g., predict future recruitment) and assist in evaluating designated piscivorous waterbird conservation (colony) sites.

RESUMEN. **La validación del crecimiento y desarrollo de un ave marina como un indicador de la disponibilidad de comida: pichones de *Hydrogprogne caspia* criados en cautiverio y alimentados *ad libitum* y dietas restringidas**

Para aves marinas que crían pichones bajo condiciones de disponibilidad de comida limitada, reducir el aprovisionamiento a los pichones y las tasas de crecimiento de los pichones son la manera principal de evitar de abandonar un intento de reproducir. Sin embargo, para la mayoría de las aves marinas, los valores de referencia que caracterizan el crecimiento y desarrollo de pichones bajo condiciones conocidas de alimentación no están disponibles. Entonces, es difícil evaluar el estatus nutricional de los pichones en relación a las condiciones de forrajeo cerca de colonias de nidificacion. Para responder a esta necesidad, examinamos el crecimiento y desarrollo de pichones de *Hydroprogne caspia*, un piscívoro cosmopolita y generalista, cuales fueron criados en cautiverio y alimentados con dietas *ad libitum* y con dietas restringidas (con aproximadamente un tercio menos de las calorías). Los pichones dados a comer *ad libitum* tuvieron tasas de crecimiento similares y llegaron a un tamaño similar a pichones silvestres en la etapa de emplumamiento. También tenían una demanda energética que era muy similar a lo de predicciones alométricas. Identificamos tres características generales de pichones de *H. caspia* con dietas restringidas en comparación a pichones con dietas *ad libitum*: (1) un peso corporal más bajo específico a cada edad, (2) un tamaño del esqueleto y de plumaje más bajo por edad, como por ejemplo el largo del ala, y (3) niveles altos de corticosterona en la sangre, tanto para niveles de valores de referencia y en respuesta al estrés aguda. Los efectos de la restricción de la dieta al crecimiento de las plumas (crecimiento de 10–11% más lento en pichones con dieta restringida) fueron menos pronunciados que los efectos sobre el crecimiento estructural (crecimiento de 37–52% más lento) y peso corporal (24% más bajo a la edad de emplumamiento), aparentemente por alocar preferencialmente los recursos alimenticios para mantener el crecimiento del plumaje. Nuestros resultados sugieren que las medidas del peso corporal de pichones y el desarrollo del plumaje (ej., largo del ala o de las primarias) o las medidas de niveles de corticosterona en la sangre nos permitiría una evaluación útil del estatus nutricional de pichones silvestres y de la disponibilidad de comida en el área de forrajeo de los adultos. Estos tipos de evaluaciones

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también nos podrían proveer información para estudios demográficos (ej., el predecir la incorporacion futura de volantones) y asistir en la evaluación de áreas para la conservación de aves acuáticas piscívoras.

Key words: chick growth, corticosterone, food availability, food restriction, *Hydroprogne caspia*, indicator species, seabirds

Characteristics of avian growth and development are useful as indicators of ecological conditions (e.g., Cairns 1987) and as predictors of the future survival and performance of individual birds (Lindstrom 1999, Metcalfe and Monaghan 2001). For breeding birds, variable ecological conditions, such as a limited food supply, may induce any of several responses, including clutch size reduction, brood size reduction, reduced chick provisioning rates, or abandonment of a clutch or brood. For short-lived species with high potential reproductive output, the ability to vary clutch and brood sizes provides parents with flexibility in continuing a breeding effort (Gill 1995). For long-lived species with low reproductive output (e.g., seabirds with small or single-egg clutches), reduced chick provisioning rates and the resultant lower chick growth rates are the primary means to avoid abandonment of a breeding effort when food availability is limited (Cairns 1987). Thus, at least in some cases, chick growth rates may be a highly sensitive indicator of environmental fluctuation (Cairns 1987, Harding et al. 2003, Einoder 2009). Other physiological effects of food limitation in chicks, such as a modified corticosterone response, may also serve as an indication of ecological conditions (Nunez-de la Mora et al. 1996, Kitaysky et al. 1999, 2001, 2007, Benowitz-Fredericks et al. 2008).

Conditions during chick-rearing may have profound effects on individuals later in life, influencing postfledging survival (e.g., Magrath 1991, Gaston 1997, Sagar and Horning 1998, Stienen and Brenninkmeijer 2002), recruitment (Both et al. 1999, Perrins and McCleery 2001, Van de Pol et al. 2006), age at first breeding (Blount et al. 2006), cognitive ability (Kitaysky et al. 2003), adult size (Searcy et al. 2004), clutch sizes (Perrins and McCleery 2001), competitive ability to secure optimal nesting habitat (Perrins and McCleery 2001, Van de Pol et al. 2006), and lifetime reproductive success (Van de Pol et al. 2006). During periods or in locations where food availability is not directly monitored, measures of chick growth and condition might help predict the future success of a cohort or help explain variable recruitment rates.

Growth and development of young terns has been linked to environmental fluctuations ranging from variation in local, short-term weather to large-scale changes in climate (Robinson et al. 2002, Mauco and Favero 2005, Devney et al. 2010), with the mechanistic link between environment and growth being the ability of parents to efficiently forage and adequately provision young. Because global climate forecasts suggest that future environmental fluctuations will become increasingly frequent and intense (IPCC 2007), understanding the response of growing terns to variation in food availability may help assess their vulnerability to expected climatic changes (e.g., Devney et al. 2010). Many species of terns are also found in increasingly human-dominated landscapes where nesting habitat must often be restored and actively maintained for tern populations to persist (Kress 1983) or to minimize conflicts with other land-use or natural resource objectives (USFWS 2005). Assessing the health and condition of chicks may be a potentially useful way to evaluate the quality of these designated tern conservation sites.

For most species of terns, however, baseline data characterizing chick growth and development under known feeding conditions are unavailable, so it is difficult to quantitatively evaluate chick nutritional status as it relates to foraging conditions near breeding colonies. To address this need, we examined the growth and development of captive-reared Caspian Tern (*Hydroprogne caspia*) chicks. Caspian Terns are relatively long-lived, with moderate clutch sizes (1–3 eggs) and semiprecocial chicks that fledge about 35 d after hatch (Cuthbert and Wires 1999). They have a cosmopolitan distribution and are generalist foragers, using a variety of habitats (coastlines, estuaries, rivers, and lakes) and prey types (surface-orientated marine and freshwater fishes), and appear to use resources in proportion to availability (Cuthbert and Wires 1999). Given the current level of intensive management of this species within a portion of their range (USFWS 2005) and their cosmopolitan distribution and generalist foraging tendencies, detailed information on chick growth and development will be useful for population- and species-level studies, as well as situations where Caspian Terns would represent a suite of piscivorous waterbirds for broader ecological studies. Our specific objectives were to: (1) determine the effects of food restriction on Caspian Tern chicks and determine how chicks with limited food intake allocate energy to growth of various body components, and (2) establish baseline data sets of Caspian Tern chick growth and development in chicks fed ample and restricted diets for future comparisons to wild chicks to allow evaluation of foraging conditions near breeding colonies and assessment of potential future performance of individual chicks or cohorts.

METHODS

We collected 20 Caspian Tern chicks from a colony on East Sand Island in the Columbia River Estuary, Oregon, during the early chick-rearing period (28 May 2001). The oldest chick was selected from each of 20 nests containing either multiple chicks or 1–2 chick(s) and an egg. Using body mass at capture and body mass at age data from Schew et al. (1994), chick age at capture was estimated for all chicks and ranged from 1 to 5 d posthatch. Chicks were transported to a rearing facility on the day of capture and most chicks accepted food offerings within hours of initial capture. The rearing facility was an enclosed, unheated building in Chinook, Washington, approximately 2 km from the East Sand Island colony. We initially housed chicks in groups of 10 in plastic wading pools with a 2–5 cm layer of sand as a substrate and, at 10 d posthatch, chicks were moved to individual plastic tubs (61.0 cm × 40.6 cm and 30.5-cm tall), again with sand substrates. Wading pools were equipped with three heat lamps to simulate warmer conditions chicks would normally experience when brooded; chicks could position themselves directly under heat lamps or up to 1 m away as desired. In the individual plastic tubs, chicks experienced similar ambient temperatures to those at the East Sand Island colony, but were not exposed to precipitation or winds. Chick activity levels were constrained due to container size.

Chicks were fed Atlantic silversides (*Menidia menidia*) through day 10 postcapture, after which their diet was switched to Pacific herring (*Clupea pallasi*). Initially, all chicks were fed ad libitum, with food offered eight times daily (initial offering at 06:00 and final at 22:00, with feedings equally spaced during the day). After 5 d postcapture, when chicks were able to consume larger meals, the frequency of food offerings was reduced to six times daily (initially at 06:00 and concluding at 21:00). Between food offerings, food was always available on trays for ad libitum fed chicks (see below). Silversides were obtained from the Oregon Coast Aquarium (Newport, OR, USA) and herring from Xanadu Seafoods (Lynnwood, WA, USA). Silversides were small (ca. 5 g) and known to be of high nutritional content (B. Tarr, pers. comm.) and so were fed to young chicks adapting to our husbandry techniques. Once chicks were large enough (day 10 posthatch), the diet was switched to the larger herring (ca. 10 g). Herring are known to be an important component of the diet of Caspian Terns in western North America (Collis et al. 2002), and suitably sized fish caught off the coast of British Columbia, Canada, were readily available commercially, so this fish was selected for use during the experimental period of the study. Fish were stored frozen and partially thawed prior to feeding. In addition to this frozen-fish diet, terns received a broad spectrum vitamin supplement (Sea Tabs, Pacific Research Laboratories, San Diego, CA, USA). A vitamin tablet was inserted into the mouth of the first fish offered each tern each day. Terns did not have access to water during rearing; adequate hydration was achieved by injecting the abdominal cavities of fish with water using a syringe prior to offering fish to chicks.

Energy content of silversides and herring was determined using proximate composition analysis (Reynolds and Kunz 2001) of fish sampled throughout the rearing period. Individual fish were first weighed freshly thawed and then dried to constant mass in a convection oven to determine water content. Lipid was extracted from dried, ground fish samples using hexane—isopropyl alcohol (7:2 vol/vol) in a Soxhlet apparatus. Lean dry samples were then combusted in a muffle furnace to determine ash-free lean dry mass (94% protein, Montevecchi et al. 1984) by subtraction. The resulting energy content of both fish types was then calculated from proximate composition (water, lipid, ash-free lean dry matter, and ash content) using published (Schmidt-Nielsen 1997) energy equivalents of these fractions (lipid = 39.4 kJ/g and protein = 17.8 kJ/g).

Up to 10 d posthatch, all chicks were fed ad libitum. Diet treatments began at day 11 posthatch for each chick. Chicks were randomly assigned to one of two groups of 10 chicks each: the ad lib group was continued on the ad libitum diet for the duration of the experiment, whereas the restricted group was fed a restricted diet consisting of approximately two-thirds of the food consumed by birds in the ad lib group beginning on day 11 posthatch. The amount of food fed to restricted chicks on a given day was calculated based on the consumption by ad lib chicks on the previous day. Species and biomass of fish consumed were recorded separately for each chick throughout the rearing period.

Several morphological measurements were taken on all tern chicks during the rearing period. Mass (±1 g) and wing chord length (±1 mm) were measured daily beginning on the day of capture. Head + bill length (±0.1 mm), culmen length (±0.1 mm), tarsus length (±0.1 mm), and lengths of the 10th primary and the longest scapular feather (beginning within 3 d of emergence) were measured slightly less frequently, but on at least 5 d of every 7-d period. Growth rate curves for body mass were described for individual chicks from the day of capture until day 35 posthatch using a three-parameter logistic growth rate function, and fitted parameter values for each diet treatment group were compared using the Wilcoxon rank-sum test (due to small sample sizes, we used nonparametric tests throughout the study). Unlike body mass, bone and feather growth data were adequately fit by a linear growth model (i.e., residuals were unbiased) so, for these parameters, the Wilcoxon rank-sum test was used to compare linear growth rates for each diet treatment across the treatment period (days 10–35).

Apparent metabolizable energy coefficients (MEC) were measured for each chick at ages ranging from 27 to 30 d posthatch. The sand substrate lining in individual tubs was replaced with Dry Dek (Kendall Products, Naples, FL, USA) and all excreta were collected over a 24-h period beginning at 06:00, following the overnight fast. Excreta were frozen for storage and total energy content was later determined using bomb calorimetry on dried samples (three 1-g aliquots per chick). Apparent MEC was calculated as the energy retained in the chick (energy consumed minus energy excreted) divided by the total energy consumed during the 24-h period.

The total metabolizable energy requirement (TMER) of ad lib chicks from hatch to the nominal fledging age of 35 d posthatch (Cuthbert and Wires 1999) was calculated by multiplying daily caloric intake by the measured apparent MEC and summing across the rearing period. This TMER was then compared to an allometric prediction based on other birds (Weathers 1992), assuming a fledging body mass of 535 g. The peak daily metabolizable energy requirement (peak DMER) of ad lib chicks was compared to a similar allometric prediction (Weathers 1992).

We examined the effects of food restriction on the endocrine stress response of chicks by quantifying plasma corticosterone concentrations. Baseline corticosterone levels were measured by drawing blood five times across the rearing period, once prior to the food restriction period at 10 d posthatch and four times during the treatment period at an average age of 19, 25, 31, and 39 d posthatch (chick ages on days when bleeding occurred varied up to ± 2 d from the average age). Baseline blood draws occurred between 05:00 and 07:00 and prior to the first feeding session of the day. Each draw consisted of approximately 0.5 ml taken from either brachial vein, and blood was collected within 3 min of taking the chick from its container. The temporal response to sustained stress (initial handling followed by restraint in a cotton bag) was measured at 39 d posthatch by drawing blood within 3 min of the initial acute stress (baseline level), and again after 10, 30, and 50 min of sustained stress. Blood was refrigerated (~4° C) and stored in 0.5-ml vials until centrifuged, and plasma was drawn off into separate vials (within 4 h of blood draws). Plasma was stored frozen at approximately −20°C prior to laboratory analyses. Radioimmunoassay analyses were performed in the laboratory of A. S. Kitaysky (University of Alaska Fairbanks, Fairbanks, AK, USA) using the methods of Wingfield and Farner (1975), Wingfield et al. (1992), and Kitaysky et al. (2005). Repeated measures ANOVA was used to test for significant differences resulting from diet treatment and age on baseline corticosterone levels and from diet treatment on the stress response series. Consistent with other studies (e.g., Kitaysky et al. 1999, 2001, Sears and Hatch 2008), we assumed blood removal had a negligible effect on chick growth and development, particularly for comparisons between diet groups.

After 38 d of captive rearing, at an average age of 41 d posthatch, eight chicks were randomly selected and euthanized for body composition analysis, four from each diet treatment group. Whole carcasses were frozen for later dissection and analysis. At the time of analysis, carcasses were thawed and dissected to examine the effects of diet treatment on feather mass, body composition, and the sizes of various internal organs (primarily gastrointestinal), including the mass of the liver, gall bladder, esophagus, proventriculus, ventriculus, pancreas, small intestine, and large intestine. Additionally, the internal surface areas of the proventriculus and ventriculus were compared, as were the lengths of each small and large intestine. Following dissections, body components were dried and whole-body composition (excluding feathers) was determined using proximate composition analysis (Reynolds and Kunz 2001). The proximate composition methodology was similar to that for the fish fed to terns except that petroleum ether was used as the lipid-extraction solvent. Petroleum ether efficiently extracts storage fats (triacylglycerols), but not more polar lipids (e.g., cell membrane-associated lipids and phospholipids), so the resulting estimated lipid content is a good measure of lipid reserves that are, for example, available to buffer chicks from short-term periods of poor food availability. Tern body composition was partitioned between water, storage lipids, and lean dry matter, including polar (structural) lipids, protein, carbohydrates, and ash. Wilcoxon rank-sum tests were used for all comparisons of body composition between diet groups.

Allocation of energy to different body components was examined using the mass-specific approach of Benowitz-Fredericks et al. (2006). For external morphology measures, we regressed log-transformed mean values against log-transformed mean mass at specific ages for both diet treatment groups. We restricted data for this analysis to the period from just prior to the beginning of the treatment period (day 10) until mass growth began to depart from the linear phase of growth for the ad libitum-fed chicks (day 24). If diet treatment was a significant term in the regression (after consideration of total body mass), we interpreted this as preferential allocation of energy to the particular morphological character. Log-transformed internal anatomical measurements and whole body fat content were regressed against log-transformed mass for individuals from each treatment group. Again, if diet treatment was significant after consideration of body mass, we interpreted this as preferential allocation. If diet treatment was not significant, we then interpreted differences in morphology or body composition between treatments to be a result of differences in overall body size alone.

Values are presented as means ± SE. Statistical analyses were performed using the Statistical Analysis System (SAS Institute, Cary, NC, USA).

RESULTS

All tern chicks survived in apparent good health throughout the rearing period. Chicks fed ad libitum consumed an average of 34 g of fish at 2 d posthatch and 199 g of fish at 20 d posthatch. Daily consumption of fish varied among ad lib chicks, with an average daily coefficient of variation of 15%. Chicks fed the restricted diet consumed an average of 65% of the total biomass that ad lib fed chicks consumed during the treatment period (days 11–35 posthatch). Including the initial acclimation period up to day 10 posthatch, when all birds were fed an ad libitum diet, restricted diet birds consumed approximately 69% of the biomass that ad lib birds did during days 1–35 posthatch. Just prior to the beginning of the treatment period (day 10), the body mass of terns in the ad lib (218.3 ± 4.4 g, $N = 10$) and restricted (208.8 ± 3.0 g, $N = 10$) diet treatments did not differ ($z = 1.1$, $P = 0.27$).

Silversides had a higher energy density (5.80 ± 0.07 kJ/g wet mass, $N = 40$) than herring (4.78 ± 0.17 kJ/g, $N = 41$; $t = 5.7$, $P < 0.0001$). Herring were caught during winter when lipid reserves may have been low, resulting in a lower energy density. The TMER of ad lib chicks from hatch to the nominal fledging age of 35 d posthatch (Cuthbert and Wires 1999) was 18.8 ± 0.35 MJ ($N = 10$). This measured TMER was 6.5% greater than an allometric prediction based on other birds, assuming a fledging body mass of 535 g (17.5 MJ; Weathers 1992). The peak daily metabolizable energy requirement (peak DMER) of ad lib chicks occurred on day 20 posthatch and averaged 760 ± 31 kJ/day ($N = 10$), just 1.4% below the allometric prediction (770 kJ/day; Weathers 1992).

As expected, chicks fed ad libitum were larger at fledging age (35 d posthatch) than chicks fed a restricted diet (Table 1). The proportional difference in total body mass was 23.5%, with differences in wing chord, tarsus, and feather lengths ranging from 8 to 11% (Table 1).

Logistic model parameters for mass growth indicated significant differences in growth parameters between chicks in both diet treatment groups. The fitted asymptotic mass of ad lib chicks was greater, and growth rate inflection points occurred at a later age, than for chicks on the restricted diet (Table 2, Fig. 1). However, the exponential growth rate constant of chicks in the two diet treatment groups did not differ ($P = 0.09$). Linear growth in bone, bill, and feathers also differed significantly between diet treatments (Table 2, Fig. 2). For ad lib chicks, growth rates of feather-dominated measures were 10–12% greater, and growth rates of bone- and bill-dominated measures were 37–52% greater than for chicks on the restricted diet (Table 2).

Apparent MEC values were 0.799 ± 0.007 ($N = 10$) for chicks on the ad lib-diet treatment and 0.811 ± 0.008 ($N = 10$) for those on the restricted-diet treatment. This difference was not significant ($z = 0.9$, $P = 0.36$).

We found that chicks on the restricted diet had higher baseline plasma corticosterone concentrations ($F_{1,18} = 4.6$, $P = 0.05$; Fig. 3A). A trend toward higher baseline corticosterone with age in restricted-diet chicks was not significant ($P = 0.13$). At 39 d posthatch, restricted-diet chicks had a significantly greater corticosterone response to sustained stress ($F_{1,18} = 18.2$, $P = 0.0005$; Fig. 3B).

Feather mass was 13% greater in ad lib chicks (46.0 ± 1.3 g, $N = 4$) than those on the restricted diet (39.8 ± 1.8 g, $N = 4$) at approximately 41 d posthatch ($z = 1.9$, $P = 0.03$). For chicks euthanized for body composition analysis, total body mass was 18.4% greater in ad lib chicks (Table 3); liver mass and gall bladder mass reflected this difference (13.5%

Table 1. Mean (SE) external morphological measures of approximately fledging-aged (35 d posthatch) Caspian Tern chicks fed ad libitum (ad lib; $N = 10$) and restricted ($N = 10$) diets. Wilcoxon rank-sum tests were used to test for differences between diet treatments.

	Total body mass (g)	Wing chord (mm)	Tarsus (mm)	Head + Bill (mm)	Culmen (mm)	P10[a] (mm)	Scapular[b] (mm)
Ad lib diet	534.9 (11.9)	276.3 (2.0)	47.3 (0.5)	113 (1.1)	28.0 (0.3)	138.7 (1.8)	96.4 (2.9)
Restricted diet	409.1 (5.2)	253.9 (2.7)	43.2 (0.6)	96.4 (0.6)	20.6 (0.2)	123.8 (1.8)	87.5 (2.6)
% difference	23.5	8.1	8.5	15.1	26.2	10.7	9.2
z-value	3.7	3.8	3.3	3.7	3.7	3.4	1.9
P	0.0002	0.0002	0.0009	0.0002	0.0002	0.0002	0.06

[a] Length of the 10th primary.

[b] Length of the longest scapular feather.

Table 2. Mean (±SE) logistic (mass) and linear (bone, bill, and feather) growth model parameters for Caspian Tern chicks fed ad libitum (ad lib; $N = 10$) and restricted ($N = 10$) diets. Mass growth was characterized from the day of capture (1–5 d posthatch) until 35 d posthatch, fitting the asymptote (A), exponential growth rate constant (K), and inflection point (t_i). Bone and feather growth were fitted from the beginning of the diet treatment period (day 11 posthatch) through day 35. Wilcoxon rank-sum tests were used to test for differences between diet treatments.

	Mass growth (Logistic model)			Bone, bill, and feather growth (mm/day) (Linear model)					
	A (g)	K (day^{-1})	t_i (days)	Wing chord	Tarsus	Head + Bill	Culmen	P10[a]	Scapular[b]
Ad lib diet	548.3 (10.4)	0.190 (0.004)	12.3 (0.21)	9.01 (0.02)	0.37 (0.005)	1.57 (0.007)	0.53 (0.002)	5.60 (0.01)	3.52 (0.03)
Restricted diet	405.8 (5.1)	0.179 (0.003)	10.5 (0.18)	7.98 (0.03)	0.23 (0.004)	0.99 (0.006)	0.25 (0.002)	4.97 (0.02)	3.16 (0.03)
% difference	26.0	5.5	14.9	11.5	39.0	36.9	51.9	11.3	10.4
z-value	3.7	1.7	3.6	3.7	3.5	3.7	3.7	3.7	2.2
P	0.0002	0.09	0.0003	0.0002	0.0004	0.0002	0.0002	0.0002	0.03

[a] Length of the 10th primary.

[b] Length of the longest scapular feather.

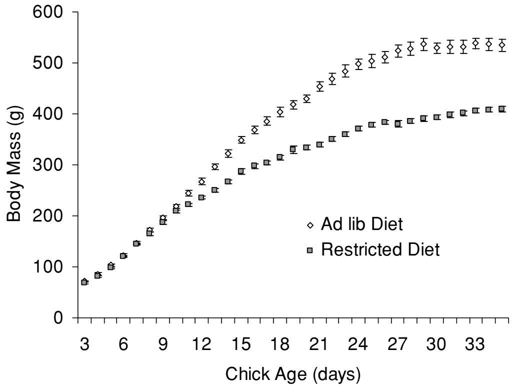

Fig. 1. Growth in total body mass (mean ± SE) as a function of age for captive-reared Caspian Tern chicks fed ad libitum (ad lib; $N = 10$) and restricted ($N = 10$) diets.

and 39.8% greater, respectively). Other internal organs, however, did not differ in size or mass between treatment groups (Table 3), indicating that other body components (i.e., structural size, muscle mass, and fat deposits) were more responsible for the differences in total body mass between chicks in the two diet treatments. Ad lib chicks had a higher ($z = 2.2$, $P = 0.03$) storage lipid content (8.9 ± 1.2% of wet mass, $N = 4$) than restricted-diet chicks (5.2 ± 0.6%, $N = 4$). The proportion of water ($z = 1.9$, $P = 0.06$) and lean dry matter ($z = 0.1$, $P = 0.99$) was similar between diet treatments. For ad lib chicks ($N = 4$), 62.3 ± 1.2% and 28.8 ± 0.7% of wet mass was water and lean dry matter, respectively, and, for restricted-diet chicks ($N = 4$), 66.5 ± 1.1% and 28.3 ± 1.3% of wet mass was water and lean dry mass, respectively.

Mass-specific allocation of energy to the various body components was similar between the two diet-treatment groups, with the exception of feathers (Fig. 4). Chicks on the restricted diet had greater feather mass and development for a given total body mass, as indicated by measurements of both flight feathers (lengths of wing chord and 10th primary) and nonflight feathers (scapular length; Fig. 4). Differences in allocation to skeletal growth (tarsus, head + bill, and culmen) between treatment groups were not significant ($P = 0.07$–0.10; Fig. 4). Differences between internal organs ($P = 0.16$–0.97) and storage lipid content ($P = 0.80$) were apparently a function of differences in body size alone.

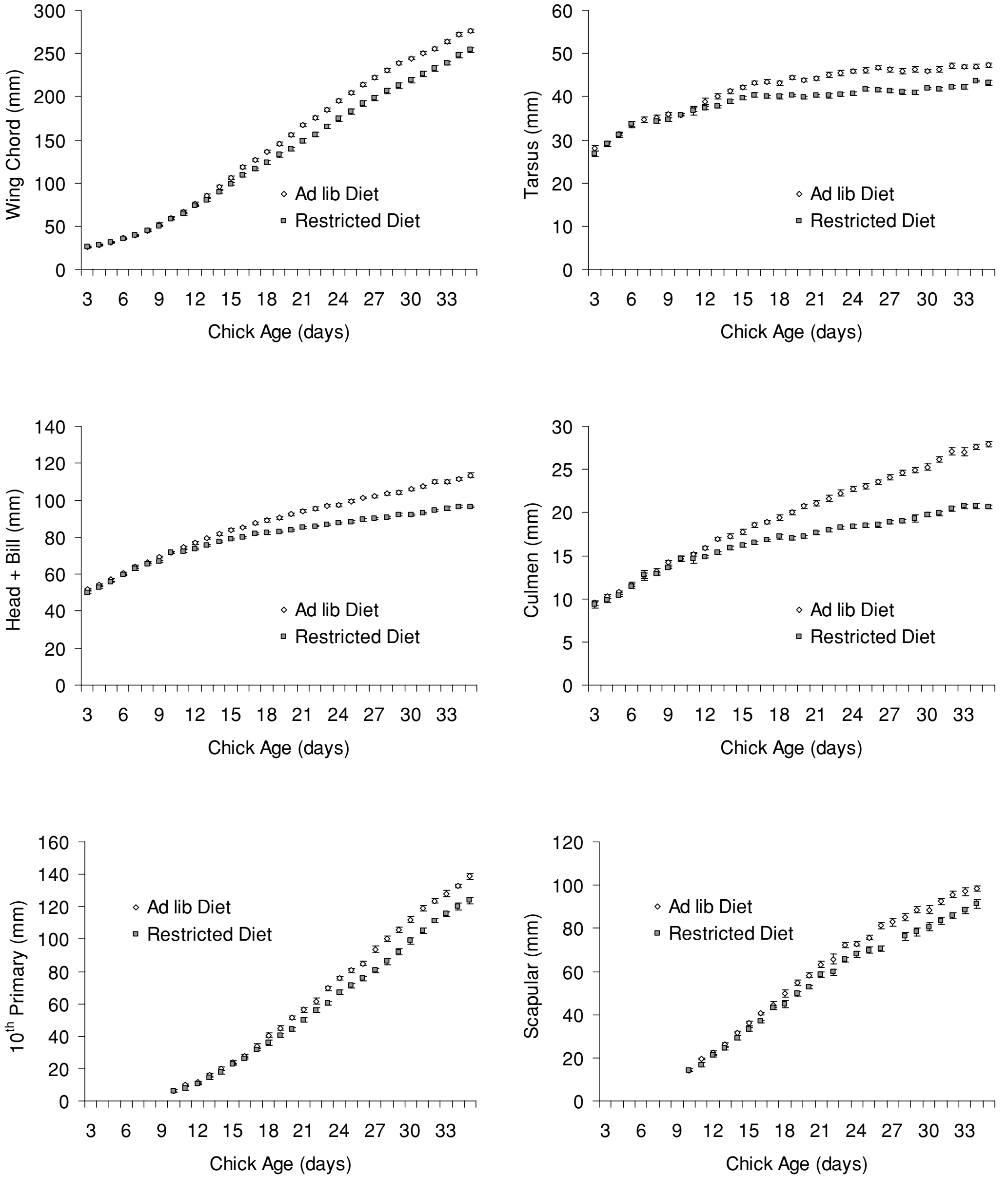

Fig. 2. Growth in length of wing chord, tarsus, head + bill, culmen, 10th primary, and scapular feathers (mean ± SE) as a function of age in captive-reared Caspian Tern chicks fed ad libitum (ad lib; $N = 10$) and restricted ($N = 10$) diets.

DISCUSSION

We found that the energy demands of captive-reared, ad libitum-fed Caspian Tern chicks were similar to estimates derived from allometric equations generated using the asymptotic body mass and fledging age of other species of birds (Weathers 1992). Because growth parameters of these captive-reared ad lib chicks were within the reported range for wild Caspian Tern chicks (Schew et al. 1994, Barlow and Dowding 2002), we assume their energy demands were similar to those of wild chicks. Among terns (subfamily

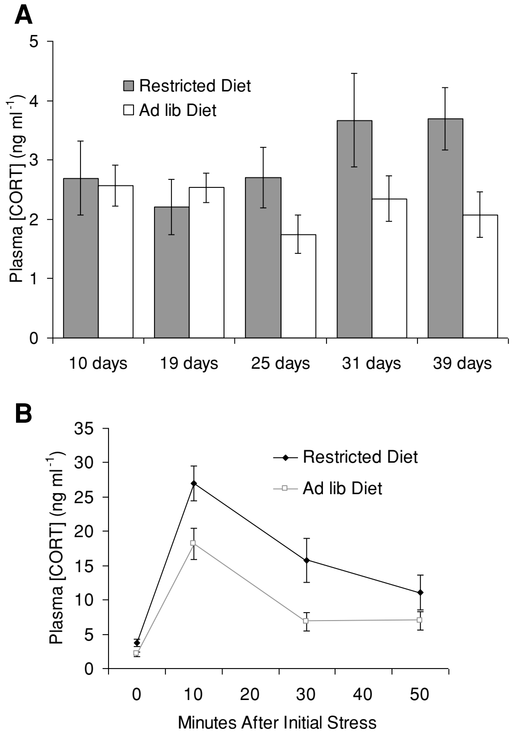

Fig. 3. Plasma corticosterone (CORT) concentrations (mean ± SE) of captive-reared Caspian Tern chicks fed ad libitum (ad lib; $N = 10$) and restricted ($N = 10$) diets. (A) baseline levels across the chick-rearing period, and (B) a temporal response to sustained stress at 39 d posthatch.

Sterninae), Caspian Terns, with a peak daily metabolizable energy requirement just 1.4% below the allometric prediction, appear to represent an intermediate developmental strategy, approximately mid-way between a quickly developing species, such as high-latitude Arctic Terns (*Sterna paradisaea*, peak DMER 65% greater than allometric prediction; Klaassen et al. 1989), and a slowly developing tropical species, such as Sooty Terns (*S. fuscata*; peak DMER 45% lower than prediction, Ricklefs and White 1981). Presumably, this developmental strategy reflects the ecological conditions faced by Caspian Terns, lacking the particularly short, but intense, seasonal burst of productivity at high latitudes, but with greater and more seasonal productivity than in the tropics.

Table 3. Mean (±SE) internal anatomical measurements of Caspian Tern chicks at ~41 d posthatching that were fed ad libitum (ad lib, $N = 4$) and restricted ($N = 4$) diets. Wilcoxon rank-sum tests were used to test for differences between diet treatments.

	Mass (g) measures									Area (mm^2) measures		Length (cm) measures	
	Total body mass	Liver	Gall bladder	Esophagus	Proventriculus	Ventriculus	Pancreas	Small intestine	Large intestine	Proventriculus	Ventriculus	Small intestine	Large intestine
Ad lib diet	505.2	16.4	0.81	4.97	1.54	5.50	1.42	11.1	0.93	617.0	1498.5	70.2	63.2
	(26.7)	(1.4)	(0.12)	(0.40)	(0.07)	(0.52)	(0.08)	(0.70)	(0.14)	(46.8)	(111.8)	(1.5)	(4.1)
Restricted diet	412.2	12.6	0.49	4.61	1.35	5.47	1.19	10.3	0.81	652.7	1649.8	68.4	53.7
	(9.6)	(0.7)	(0.09)	(0.22)	(0.18)	(0.44)	(0.28)	(0.49)	(0.09)	(30.4)	(66.86)	(2.2)	(3.0)
% difference	18.4	13.5	39.8	7.3	12.6	0.6	16.7	6.6	12.6	−5.8	−10.1	2.5	15.0
z-value	2.2	1.9	1.8	0.4	0.4	0.1	0.1	1.0	0.7	0.6	1.0	0.5	1.5
P	0.02	0.03	0.04	0.33	0.33	0.56	0.44	0.31	0.23	0.56	0.31	0.30	0.07

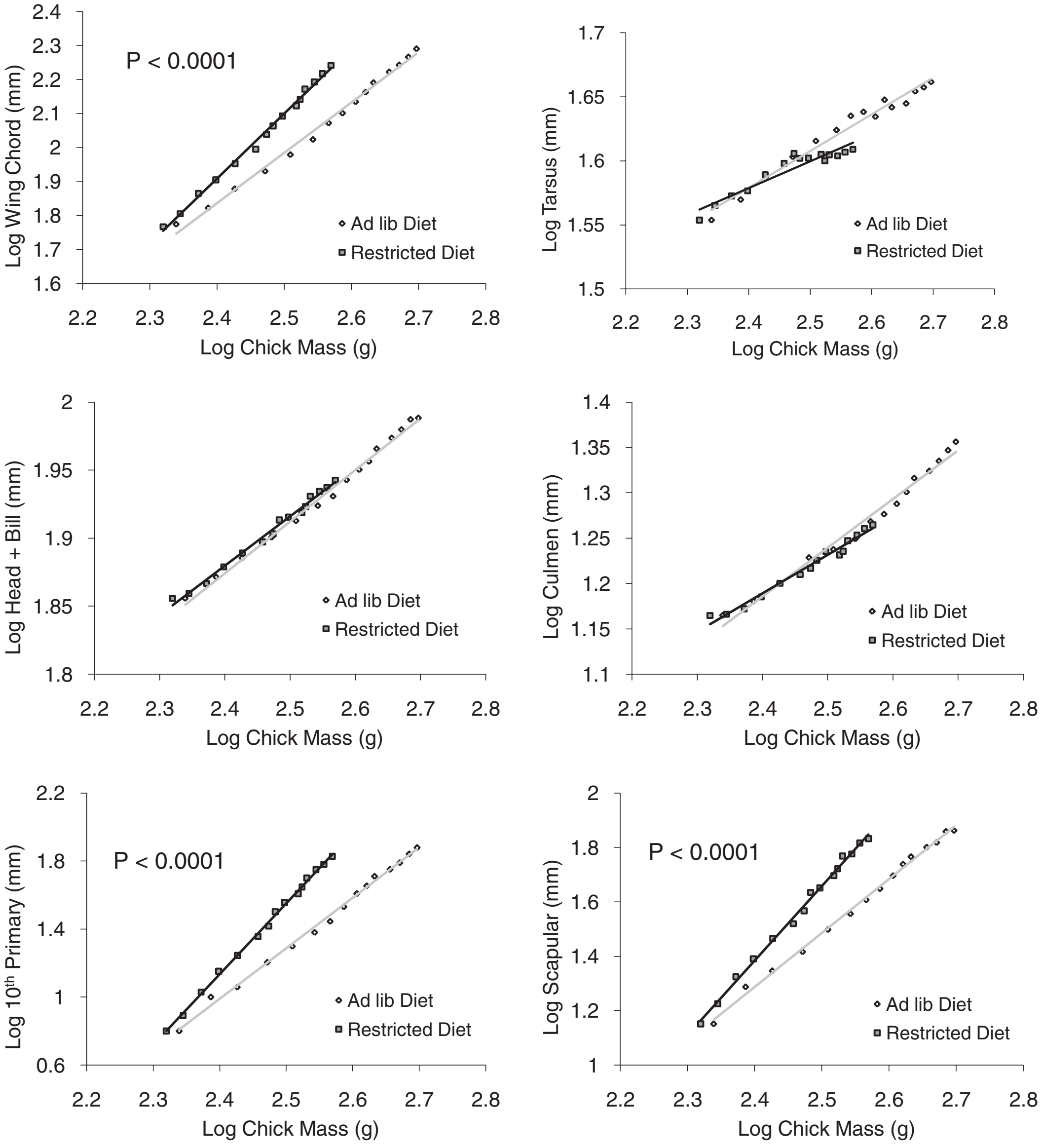

Fig. 4. Growth in length of wing chord, tarsus, head + bill, culmen, 10th primary, and scapular feathers (mean ± SE) as a function of body mass in captive-reared Caspian Tern chicks raised on either an ad libitum (ad lib; $N = 10$) diet or a restricted-intake ($N = 10$) diet. Each data point represents the mean length at a given age. Steeper slopes for restricted diet chicks indicate preferential allocation of resources to a given body component for a given body mass. For significant differences in size as a function of total body mass between diet treatment groups, P values are indicated.

When faced with nutritional challenge, Caspian Tern chicks in our study displayed differing degrees of developmental plasticity depending on tissue type. Of the linear external morphology measurements, feather-based characters differed less between diet treatment groups and the mass-specific growth rate of feathers was greater for chicks on the restricted diet. These results indicate that developing Caspian Terns can shift their energy allocation under conditions of food-energy limitation to preferentially promote feather growth. Similar preferential feather growth has been reported in other bird species and presumably reflects the short-term survival benefit of early flight capability (Lack 1968, Starck and Ricklefs 1998). Interestingly, growth of nonflight feathers (scapulars) was also preferentially maintained, suggesting that independent control of growth in distinct feather groups is beyond the physiological capability of terns.

Previous studies have demonstrated preferential allocation to skeletal growth in some seabirds (e.g., Moe et al. 2004, Benowitz-Fredericks et al. 2006, Sears and Hatch 2008), but that was not the case for Caspian Terns in our study. Given that flightless tern chicks sometimes escape predators by running or swimming (Cuthbert and Wires 1999), preferential allocation to maintain tarsal growth might have been expected and has been reported in at least one other species of tern, that is, 25% food restriction had no impact on tarsus length of Elegant Terns (*S. elegans*, Dahdul and Horn 2003). One possible explanation for our result is that most tarsal growth in Caspian Terns may occur during embryonic development and early chick rearing; the tarsi of chicks in our study grew to 75% of adult size by day 10 posthatch, prior to the onset of food restriction. In Caspian Terns, the development of leg bones and musculature may be sufficient by day 10 posthatch to support an adequate level of mobility such that subsequent preferential allocation to leg growth is not particularly advantageous.

Preferential allocation for skull growth has been observed in young Atlantic Puffins (*Fratercula arctica*) and interpreted to indicate the importance of development of the brain and central nervous system (Oyan and Anker-Nilssen 1996). We did not measure skull size directly, but the mass-specific growth of an approximate measure of skull size, head-bill length minus culmen length (Oyan and Anker-Nilssen 1996), did suggest a small, but significant, difference in allocation between our ad lib and restricted-diet groups (~6% difference in slope of the regression between nontransformed values, $P < 0.0001$). Further study of skeletal growth of terns under different feeding regimes might clarify some of these suggested effects.

Effects of prey type on the development of digestive organs have been demonstrated in other seabirds, but the effects of food quantity alone had not been examined prior to our study. For example, Elegant Tern chicks fed a less energy-dense prey type than their preferred prey developed heavier digestive organs and faster gut passage rates (Dahdul and Horn 2003). The internal organ characteristics of ad lib and restricted-diet Caspian Terns in our study were similar, with the exception of liver and gall bladder masses. Mass-specific analysis indicated that most differences between internal organs in the fledging-aged chicks (41 d posthatch) in our study were a function of differences in body mass alone and did not reflect differential allocation. It is possible either that caloric restriction alone is not sufficient to induce major developmental differences or that Elegant Terns are specialized to prey on fish with a high-lipid content and consequently need to adjust their digestive physiology if feeding on prey of lower caloric value, whereas Caspian Terns are more generalist feeders and have less need to adjust their gut anatomy for particular diets.

For Caspian Terns in our study, as in some other larids (Kitaysky et al. 1999, 2001), nutritional stress induced both a heightened baseline corticosterone level and an amplified acute corticosterone stress response. This heightened hypothalamus—pituitary—adrenal activity in response to chronic food restriction in terns is consistent with Kitaysky et al.'s (2003) ecological hypothesis to explain interspecific differences in stress response among seabirds. This hypothesis predicts that, for seabird species that frequently provision young (multiple times/day) or for species with multiple-chick broods, a heightened stress response in nutritionally challenged chicks could improve short-term survival, either by inducing greater begging from parents (to potentially increase provisioning rates) or more aggressive competition with siblings (to obtain a greater portion of the food brought to the nest). Conversely, for species with fixed, low provisioning rates (once/day or less) or for species with a maximum brood (clutch) size of one, a heightened corticosterone response in chicks would offer little advantage (e.g., Kitaysky et al. 2005). Adult Caspian Terns provision chicks with single fish multiple times per day and typically have multichick broods for at least a portion of the chick-rearing period. The heightened corticosterone response of food-restricted chicks in our study thus supports the ecological hypothesis (Kitaysky et al. 2003).

In sum, we identified three general characteristics of food-restricted Caspian Tern chicks compared to well-fed chicks: (1) lower structural growth rates, lower body mass, and smaller skeletal size for chicks at a particular age, (2) greater relative size of feather measurements, such as wing chord, for chicks of the same body mass, and (3) increased baseline and stress series corticosterone levels. Field studies comparing wild chicks to our captive-reared chicks using measures within any of these three categories would allow useful evaluation of the nutritional status of those wild chicks and serve as an indicator of the food availability to the adult terns. Measuring mass and wing chord, and sampling blood to measure corticosterone levels (i.e., quantifying characteristics 2 or 3 above) would allow such an evaluation even if a breeding colony is visited only once late in the chick-rearing period and when the age of chicks is imprecisely known. Such evaluations of chick condition could also inform tern demography studies (e.g., predict future recruitment) and assist in the evaluation of designated piscivorous waterbird conservation (colony) sites. Additional studies would be needed to confirm the applicability of our results on Caspian Terns to other tern species with similar developmental patterns or to investigate possible variation (e.g., latitudinal variation) in growth across the cosmopolitan distribution of Caspian Terns.

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