Offspring growth and parental care in sexually dimorphic Nazca boobies (*Sula granti*)

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Abstract: A review of studies on nestling bird food requirements indicates that degree of sexual size dimorphism reliably predicts disparity in sex-specific food requirements, but that parents often fail to meet the excess requirement of the larger sex. We studied a population of Nazca boobies (*Sula granti* Rothschild, 1902), a sexually dimorphic pelagic seabird, to determine whether parents provide more care to daughters, the larger sex. Daughters grew to a larger size than did sons during the nestling period, but did not reach the mean size of adult females, while sons exceeded the size of adult males. Estimates of parental effort exerted for sons versus daughters indicated similar levels of effort, and that females fledged in poorer condition than males did in the study year, one of intermediate breeding conditions. Results from another study conducted during better breeding conditions indicated little limitation on growth of either sex. Together, these studies are consistent with a ceiling on parental effort in a long-lived species that allows consistent self-maintenance for parents, but causes poor performance in the costlier sex under poor breeding conditions. Complementary studies of short-lived species are needed to evaluate our suggested linkage between parental effort, self-maintenance, and sexual size dimorphism.

Résumé : Une rétrospective des besoins alimentaires des oiseaux nicheurs indique que l'importance du dimorphisme de la taille en fonction du sexe permet de prédire la disparité dans les besoins alimentaires spécifiques au sexe, mais que les parents n'arrivent souvent pas à satisfaire les besoins des oiseaux du sexe de plus grande taille. Nous avons étudié une population de fous de Nazca (*Sula granti* Rothschild, 1902), un oiseau marin pélagique à dimorphisme sexuel prononcé, afin de déterminer si les parents fournissent plus de soin à leur progéniture femelle, le sexe de plus grande taille. Les poussins femelles atteignent une taille plus importante que les poussins mâles durant la période de nidification, mais sans parvenir à la taille moyenne des femelles adultes, alors que les poussins mâles dépassent la taille des mâles adultes. Nos estimations indiquent que les parents fournissent un niveau d'effort semblable pour leurs progénitures mâle et femelle; durant l'année de notre étude, une année de conditions de reproduction moyennes, les femelles ont quitté le nid en moins bonne condition que les mâles. Les résultats d'une étude antérieure faite durant de meilleures conditions de reproduction montre peu de restriction de la croissance chez les deux sexes. Ensemble, ces deux études semblent indiquer l'existence d'un plafond à l'effort parental chez les espèces à forte longévité, qui permet le maintien des parents eux-mêmes, mais qui cause une performance réduite du sexe le plus onéreux lorsque les conditions de reproduction sont mauvaises. Des études complémentaires chez des espèces à faible longévité seraient nécessaires pour confirmer le lien que nous faisons entre l'effort parental, le maintien de soi des parents et le dimorphisme sexuel en fonction de la taille.

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Introduction

Sex-specific food requirements (SSFR) of growing birds (Anderson et al. 1993) may induce higher costs in parents raising sons versus daughters, with implications for adaptive sex allocation (Charnov 1982; Hardy 2002). SSFR may also lead to differential mortality or poor condition of the costlier sex during food shortfalls, if they lack increased access to food relative to members of the other sex (e.g., Howe 1977, 1979). The important role of SSFR in bird breeding biology has motivated a number of studies on the costs of raising sons and daughters (Table 1).

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One source of confusion in this literature has been the conflation of SSFR in offspring and the amount of care that parents actually provide to offspring of each sex. Studies of captive, growing birds show a strong positive correlation between degree of sexual size dimorphism (SSD) and ad libitum food-intake ratio (the ratio of the larger sex's intake over the smaller sex's intake; Table 1). SSD and the nestling field metabolic rate ratio also show a significant correlation (Table 1). However, SSD and the parental food delivery ratio in altricial species do not reach significance (Table 1), suggesting that parents introduce a confounding element. These data indicate that SSD predictably causes higher food requirements in the larger sex, but that parents do not always meet the needs of the larger sex as well as they do those of the smaller sex. Members of the larger sex can sometimes translate their larger size into a competitive advantage, mitigating the effect of a shortfall from the parents (Anderson et al. 1993; Hipkiss et al. 2002), or parents may work harder for offspring of the expensive sex to meet its needs (Cameron-MacMillan et al. 2007). However, often the larger sex shows higher sensitivity to food limitation as a nestling, particularly during natural or experimental food

Table 1. Published data associating the maximum sexual size dimorphism (SSD; ratio of sizes) during parental care and the ratio of food requirements (larger sex or smaller sex) in nestling birds, and annual adult survival for studies measuring parental care.

Species	Maximum SSD	Food-intake ratio	Annual adult survival	References
Captive hand-fed altricials and self-fed precocials				
Pekin duck, *Anas platyrhynchos* L., 1758	1.10	1.03		National Research Council 1977
American kestrel, *Falco sparverius* L., 1758	1.14	1.07		Anderson et al. 1993
Western marsh harrier, *Circus aeruginosus* (L., 1758)	1.20	1.23		Krijgsveld et al. 1998
Golden eagle, *Aquila chrysaetos* (L., 1758)	1.21	1.15		Collopy 1986
Broiler chicken, *Gallus domesticus* (L., 1758)	1.25	1.20		National Research Council 1977
Capercallie, *Tetrao urogallus* L., 1758	1.36	1.34		Lindén 1981
Great-tailed grackle, *Quiscalus mexicanus* (Gmelin 1788)	1.52	1.16		Teather 1987
Eurasian sparrowhawk, *Accipiter nisus* (L., 1758)	1.52	1.21		Frumpkin 1988
Wild turkey, *Meleagris gallopavo* L., 1758	1.58	1.46		National Research Council 1977
Metabolic rate in wild				
Eastern bluebird, *Sialia sialis* (L., 1758)	1.02	1.07		Droge et al. 1991
Rook, *Corvus frugilegus* L., 1758	1.14	1.14		Slagsvold et al. 1986
Western marsh harrier	1.25	1.23		Riedstra et al. 1998
Red-winged blackbird, *Agelaius phoeniceus* (L., 1766)	1.33	1.27		Fiala and Congdon 1983
Peregrine falcon, *Falco peregrinus* Tunstall, 1771	1.45	1.24		Boulet et al. 2001
Great-tailed grackle	1.52	1.20		Teather and Weatherhead 1988
Western sparrowhawk	1.62	1.44		Vedder et al. 2005
Parent-fed in wild				
Eastern bluebird	1.02	0.97	0.38–0.040	Gowaty and Droge 1991; Gowaty and Plissner 1998
Common grackle, *Quiscalus quiscula* (L., 1758)	1.08	0.87	0.52	Howe 1979; Peer and Bollinger 1997
Ural owl, *Strix uralensis* Pallas, 1771	1.15	1.13	0.62–0.89	Cramp and Simmons 1985; Brommer et al. 2003
Nazca booby, *Sula granti* Rothschild, 1902	1.16	1.11	0.921	This study; D.J. Anderson, unpublished data
Golden eagle	1.21	1.11	0.79–0.91	Collopy 1986; Kochert et al. 2002
Western marsh harrier	1.25	1.00	0.39	Cramp and Simmons 1980; Witkowski 1989
Blue-footed booby, *Sula nebouxii* Milne-Edwards, 1882	1.27	1.00	Unknown	Drummond et al. 1991; Guerra and Drummond 1995; Torres and Drummond 1999
Brown falcon, *Falco berigora* Vigors and Horsfield, 1827	1.35	1.00	0.61–0.89	McDonald et al. 2004, 2005
Peregrine falcon	1.45	1.26	0.25–0.32	Cramp and Simmons 1980; Boulet et al. 2001
Western sparrowhawk	1.52	0.97	0.57	Newton 1978; Newton and Marquiss 1979; Cramp and Simmons 1980; Newton and Moss 1986
Great-tailed grackle	1.52	1.27	Unknown	Teather and Weatherhead 1988; Johnson and Peer 2001

Note: All known estimates, including those reflecting nonsignificant differences, are included. Pearson product-moment correlation of the first two variables are significant for the hand-fed altricials and self-fed precocials (assumed to satisfy their food requirements; $r = 0.68$, $P = 0.04$, $n = 9$) and wild metabolic rate groups (assumed to reflect primarily baseline metabolic requirements; $r = 0.83$, $P = 0.02$, $n = 7$), but not for the wild parent-fed group ($r = 0.49$, $P = 0.13$, $n = 11$). Food-intake ratio may be derived from actual mass of food ingested, number of food transfers, number of parental visits, or metabolic rate. Related studies that did not provide sufficient data to calculate food-intake ratio (e.g., Fiala 1981) or maximum nestling SSD (e.g., Cameron-MacMillan et al. 2007) were not included. Note that hand-feeding of great-tailed grackles led to depressed growth relative to wild nestlings; blue-footed booby data are for first-hatched chicks only; capercaillie data reflect assimilated energy only.

shortages (Clutton-Brock et al. 1985; Røskaft and Slagsvold 1985; Griffiths 1992; Daunt et al. 2001; Velando 2002; Brommer et al. 2003; Kalmbach et al. 2005; McDonald et al. 2005), consistent with the idea that parents fail to meet their extra needs.

In contrast to most other taxa, food delivery to avian broods can be estimated accurately by observation in many species (e.g., Rodway and Montevecchi 1996) or by periodic weighing (Ricklefs 1984), providing one index of parental effort. Parental time budgets also can be measured with relative ease by various means (e.g., Cameron-MacMillan et al. 2007). Nonetheless, few data exist to evaluate the sensitivity of parental effort to offspring sex in wild birds. Available studies often used species showing SSD because body size accurately predicts daily energy requirement (Weathers 1992), and offspring sex and induced parental effort may co-vary as a result. Interpretation of these results can be complicated in cases where parental effort is measured for only minor portions of the nestling period, when only one indicator of effort is measured, and when the quality of breeding conditions (which can interact with parental breeding strategy) is not characterized. Few data exist for long-lived birds (Table 1), which are expected to operate under a lower offspring-cost ceiling than do short-lived birds, to maintain consistent allocation of somatic resources to self-maintenance (Medawar 1952; Goodman 1974). Long-lived birds might be less likely to meet the excess demands of the costlier sex under this reasoning, leading to their malnutrition and poor performance.

To address these issues, we analyzed several types of data to assess the interaction of nestling SSD and parental effort in Nazca boobies (*Sula granti* Rothschild, 1902; known until recently as a subspecies of the masked booby, *Sula dactylatra* Lesson, 1831; American Ornithologists' Union 2000), a pelagic seabird with female-larger adult SSD. Adult female mass exceeds that of males by 16% (Anderson 1993). If similar SSD exists among offspring, then food requirements should differ for sons and daughters. Obligate siblicide in this species reduces brood size to one shortly after hatching (Anderson 1989; Humphries et al. 2006), so brood size is effectively one for the purposes of studying parental effort, and sex-dependent outcomes of sibling competition (e.g., Arroyo 2002; Muller et al. 2005) are not a complicating factor. Nazca boobies are among the longest-lived birds (Anderson and Apanius 2003). We used canonical discriminant function analysis to integrate data on mass of food delivered, feeding frequency, and parental mass changes to test the null hypothesis of equal parental effort for sons and daughters, providing data for one extreme of the longevity spectrum. Finally, we compare the results with those from the same population in a different year (Apanius et al. 2007), providing a perspective incorporating environmental heterogeneity.

Materials and methods

Study site and fieldwork

We studied Nazca booby nesting biology at Punta Cevallos, Isla Española, Galápagos islands (1°23′S, 89°37′W), Ecuador, during the 2000–2001 breeding season (October 2000 – May 2001). Anderson and Ricklefs (1987) and Huy-

vaert and Anderson (2004) provide details of the study site, a colony with approximately 3500 breeding pairs (Anderson 1993). We monitored 80 nests from egg-laying until the offspring died or attained juvenile plumage at approximately 100 days to test for associations between offspring sex and parental effort. To control variation in parental quality (Clifford and Anderson 2001), we selected 80 nests with two-egg clutches in which chicks hatched over a 15 day period (between 19 December 2000 and 2 January 2001). The hatching period was restricted to 15 days to minimize variability in measurements attributable to temporal environmental heterogeneity. Sex of chicks in this cohort was determined after the field season. Because of chick mortality ($n = 19$) and failure of sex determination ($n = 16$), 45 families (19 sons and 26 daughters in single-chick broods) provided data for the subsequent analyses.

Sex determination

Blood samples were taken by puncture of the brachial vein from all nestlings in the cohort that survived to 5 days old (i.e., victims of siblicide were not studied). Later, a sample of feather pulp was taken from each chick that attained juvenile plumage. Both samples were preserved in 70% ethanol at ambient temperature until transport to our laboratory at the end of the breeding season. Genomic DNA was purified from blood and feathers by phenol–chloroform extraction (Sambrook et al. 1989). Sex of the nestlings was determined by polymerase chain reaction amplification of an intron region of the CHD gene (Fridolfsson and Ellegren 1999; Maness et al. (2007) validated the technique for this species).

Sex ratio of nestlings is expressed as proportion of males. The 95% confidence interval (CI) for the proportion of males was estimated using a normal approximation to the binomial distribution with a correction for continuity applied (Fleiss 1981).

Nestling growth

To determine whether or not the female-larger SSD is established during the nestling period, we measured mass and other morphological characters from ages 1 day (the day after hatching) to 100 days at 10 day intervals. We weighed nestlings in tared bags hung from a Pesola® spring scale (0–250 g for smaller nestlings, 0–2500 g for larger nestlings). Morphological measurements included culmen length (base to tip), ulna length, and flattened wing chord. Following the example of Massemin et al. (2002), we used a principal component analysis to develop a composite variable to describe nestling size. The composite size variable (the first principal component) explained 93.6% of the variance in the morphological measures and was calculated (based on the factor loadings) as

$$[1] \quad \text{Size} = 0.508(\text{culmen}) + 0.507(\text{ulna}) + 0.482(\text{wing}) + 0.502(\text{mass})$$

A growth curve based on the size variable was fitted using a nonlinear mixed-effect model. Mixed-effect modeling is possible because of the longitudinal nature of the data, with resulting correlations in measurements owing to inter-individual variability, enabling the partitioning of variance

attributable to systematic and random effects (Davidian and Giltinan 1995). McRoberts et al. (1998) demonstrated the superiority of the mixed-effect approach over other regression techniques for modeling growth owing to this ability to parse random-effect variances. The growth curve used in this analysis was based on a standard logistic curve (of the form $f(x) = 1/(1 + e^{-x})$) applied in a mixed-effect model:

$$[2] \qquad \text{Size}_{ij} = \frac{u_{i1} + b_1}{\left(1 + e^{\frac{-(\text{age}_{ij} - b_2)}{b_3}}\right)} + \varepsilon_{ij}$$

Table 2 gives descriptions of the growth model variables and parameters. Variance in random and fixed-effect parameters entered the model as normally distributed variables. The fixed-effect parameters were b_1, b_2, and b_3; the random-effect parameter was u_{i1}. Both were assumed to be independently and normally distributed. The residual errors ε_{ij} were assumed to be normally distributed and independent of u_{i1}. Sample-size limitation precluded the inclusion of additional random-effect parameters.

Two growth models were developed, one in which the parameters were constrained and did not vary by sex (H_0) and another in which the parameters varied by sex (H_A). The models were compared using an information-theoretic approach based on comparison of Akaike's information criterion (AIC) values and likelihood modeling.

Food delivery and intake

The method for measuring nestling food intake followed Anderson and Ricklefs (1992), capitalizing on the fact that food deliveries are infrequent and cause large nestling mass increments. We weighed nestlings at 4 h intervals for a 24 h period beginning at 0600 and continuing until 0600 the following day, at 10–12 day intervals from 13 January (median age of the chick cohort was 15 days) until 5 March (median age of the chick cohort was 66 days). Each positive mass increment over a 4 h period was adjusted to account for defecation and respiration during the period using a size-based mass loss function derived by Anderson and Ricklefs (1992), which was taken to indicate the mass of food ingested by the nestling over that period.

The method for observing food delivery was adapted from Torres and Drummond (1999). Two-hour feeding observations were conducted between 1430 and 1830 (the peak feeding time; Anderson and Ricklefs 1992; this study) almost daily from 28 January (when the median age of subject nestlings was 30 days) to 30 April (when subjects were beginning to fledge). Observations began at nestling age 30 days because feedings are concentrated in the late afternoon and early evening from this age forward (Anderson and Ricklefs 1992), allowing us to minimize the hours of the day for effective observation, and because we suspected that SSD would appear after this age. Four areas with 10–15 focal nests in each were scanned for 0.5 h daily from a distance of at least 15 m during this concentrated feeding period; the starting time and sequence of areas scanned were varied across days to minimize bias in feeding detection. Disturbance effects resulting from our presence at this distance were assumed to have no effect on the birds, given the indifference of Galápagos Nazca boobies to humans. Scans were conducted with the naked eye to detect parents

Table 2. Description of variables in the logistic growth model.

Variable or parameter	Description
Size_{ij}	The jth size measurement for the ith nestling
Age_{ij}	The jth age (in days) for the ith nestling
u_{i1}	Effect parameter for random variability in the asymptotic size, i.e., individual variability in asymptotic body size. This is modeled as the random component of variance
b_1	Fixed-effect parameter for the asymptotic size
b_2	Fixed-effect parameter for the inflection point of the growth curve, i.e., the age (in days) at which growth slows down from the exponential rate
b_3	Fixed-effect parameter for the growth rate
ε_{ij}	Effect parameter for the systematic variability, i.e., fluctuation in body size at the population level for different ages. This is modeled as the random component of variance.

returning from sea and begging nestlings, and binoculars were then used to determine if parents completed feeding (i.e., food or liquid was transferred from adult to nestling).

Parental mass, effort, and fledging success

At the beginning of the nestling period (when nestlings were 15–28 days old, January 2001), both parents at subject nests were captured by hand at the nest, weighed, and measured using the same techniques as for nestlings. Late in the breeding effort (nestling ages 83–93 days, 21 March 2001 – 31 March 2002), parents were captured again at the nest and weighed.

We used canonical discriminant function analysis to determine the extent to which parental effort differed by parent and offspring sex. In the analysis, a canonical composite variable for parental effort was calculated based on food intake, food delivery, morphological differences, and mass change of parents over the breeding season. Randomization testing was used to determine if disparity in parental effort for sons and daughters in our sample differed from cases in which parental effort was randomly re-allocated in the discriminant function analysis. Manly (1997) suggested that discriminant function analysis is particularly well suited to randomization testing. Randomization tests are powerful and robust, so small sample size and violations of statistical assumptions do not result in a loss of power (Peres-Neto and Olden 2001). In this analysis, we calculated the disparity (d) between the composite effort measures for parents of sons and of daughters. We then compared the d for our data set with a D distribution calculated from 1000 resamples (with replacement) of the data set in which offspring sex was randomly reassigned. The null hypothesis of equal effort is supported if the value calculated for disparity in parental effort does not differ appreciably for most of the values in the disparity-effort distribution, $p(d \in D) > 0.05$ and rejected if $p(d \in D) < 0.05$.

Offspring were considered to have fledged successfully (reached independence at approximately age 160 days) if they survived long enough to attain juvenile plumage (at approximately 100 days), since mortality after attaining juvenile plumage is rare (Humphries et al. 2006).

Fig. 1. Growth curves for Nazca booby (*Sula granti*) male and female nestlings developed from nonlinear mixed-effect models. The *y* axis depicts a maximum likelihood composite variable, lacking units, derived from a discriminant function analysis (see text).

Fig. 2. Daily mean food intake by age for Nazca booby male and female nestlings. The sums of the seven age-specific estimates for males and females are 1313.9 and 1459.8 g, respectively. Inset shows relative food intake (food intake divided by body mass). Error bars show 95% confidence intervals.
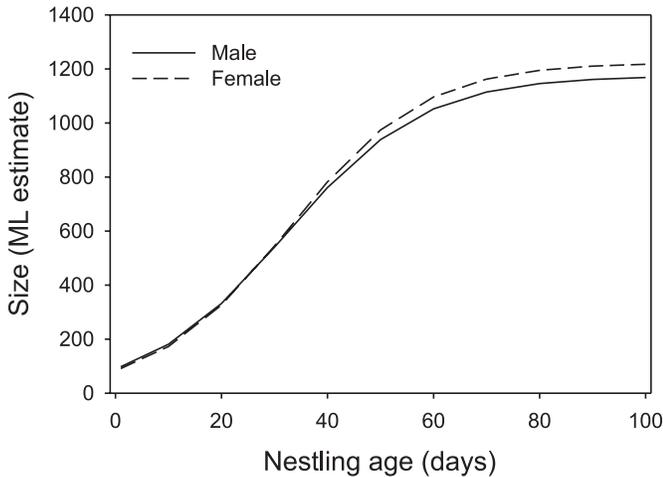
Table 3. Parameter values from the unconstrained model describing Nazca booby males and females.

Parameter	Male	Female
b_1	1 170	1 226
$\mathrm{var}(u_{i1})$	9 396	14 868
B_2	32.0	32.8
B_3	13.0	12.6
$\mathrm{var}(\varepsilon_{ij})$	6 499	6 499

Note: Note the variances for the effect parameter for random variability in the asymptotic size, $\mathrm{var}(u_{i1})$, and the effect parameter for the systematic variability, $\mathrm{var}(\varepsilon_{ij})$, are modeled, as these are the random and fixed components of variances in the size measurements.

Statistical analysis

All statistical analyses except that of annual adult survival were performed using SAS/STAT® version 8 (SAS Institute Inc. 2001). Although numerous analyses could have been conducted for several variables, we limit formal analyses to two major tests of the composite size variable: analysis of changes in size (i.e., the growth curve) and the parental effort variable. Only summaries of other variables are provided to allow the reader to examine patterns. Univariate analyses of the ancillary variables would likely reveal a statistically significant, but spurious, difference between sons and daughters for at least one of the variables, so ancillary variables were only analyzed as parts of composite variables.

Statistical analyses were performed using SAS/STAT® version 8 (SAS Institute Inc. 2001). Growth curves were fitted using Proc NLMIXED and the discriminant function analysis was performed using Proc CANDISC. The randomization resamples were performed using SAS® macros that allowed random reassignment of offspring sex and multiple applications of the discriminant function analysis.

Results

Sex determination

Sex was determined for 85 nestlings from 55 different
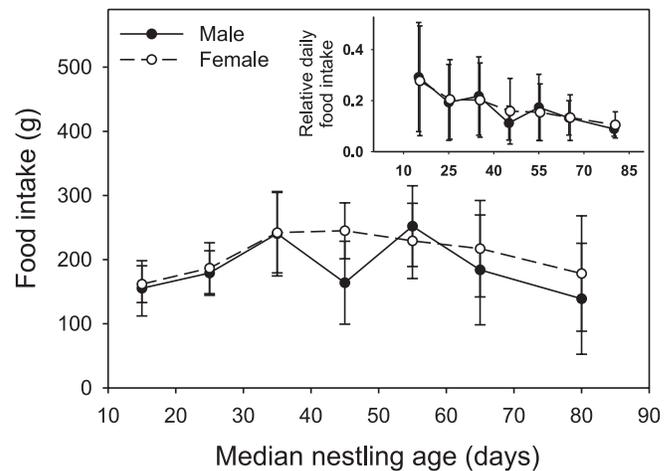
Table 4. Standardized canonical coefficients for parental effort measures, distinguishing overall parental effort required to rear Nazca booby sons and daughters.

Variable	Coefficient
Food intake sample	
1	–0.317467
2	–0.133608
3	0.032422
4	–0.512551
5	0.080070
6	–0.097967
7	–0.140631
Feedings observed	–0.061447
Female	
Culmen	–0.032149
Ulna	0.540528
Wing	0.166598
ΔMass	–0.017510
Male	
Culmen	–0.239624
Ulna	0.277964
Wing	–0.224060
ΔMass	–0.102946

Note: Sample 1 was taken at approximately chick age 25 days and sample 7 at approximately 85 days.

families. Overall, sex ratio at hatching did not differ significantly from parity (p(male) = 0.506, 95% CI = 0.394–0.618).

Nestling growth

The growth model in which parameters varied by sex (H_A) explained the data better than did the constrained model (H_0) (H_A: AIC = 5598.9; H_0: AIC = 5602.5). The AIC weight (a relative plausibility index described in Burnham and Anderson 2002) for the constrained model was 0.142, suggesting that the constrained model contributed ap-

Table 5. Parental mass and morphology measures in relation to offspring sex (mean measurement and 95% confidence intervals) of Nazca boobies.

	Father				Mother			
	Culmen (cm)	Ulna (cm)	Wing (cm)	Relative Δmass (%)	Culmen (cm)	Ulna (cm)	Wing (cm)	Relative Δmass (%)
Son	101.4±1.2	224.6±2.8	456.2±4.8	–0.18±2.7	104.4±1.0	238.3±3.4	477.4±4.0	–0.90±2.8
Daughter	102.2±1.0	223.2±2.0	459.0±5.3	–0.52±1.7	104.5±1.1	235.9±2.0	477.1±4.3	–1.22±1.9

preciable information to the explanation of the growth data. Acknowledging the contribution of the constrained model, we used model parameter averaging (following Burnham and Anderson 2002) to calculate growth curves (Fig. 1). However, to understand the effect of sex on growth we evaluated the parameters from H_A only (Table 3). Differences in growth patterns of males and females were attributable mainly to differences in asymptotic size (b_1), with older females being larger than older males; thus, the female-larger SSD in Nazca boobies is established during the latter part of the nestling period. The growth rate (b_3) was slightly higher for males than for females, but females tended to stay in the exponential phase of growth longer than males did, as indicated by the difference in inflection points (b_2). In addition, asymptotic size of females was more variable than that of males, as indicated by the variances of the effect parameter for random variability in the asymptotic size, var(u_{i1}). The asymptotic mass of male nestlings was 105.8% of the mean adult male mass found by Anderson (1993), 1721.6 vs. 1627.0 g, but the asymptotic mass of female nestlings was only 99.4% of the typical adult female mass (1870.4 vs. 1881.0 g).

Disparity in parental effort and fledging success

Standardized coefficients for the discriminant function (Table 4) indicated that none of the individual predictor variables (Table 5) had a strong role in distinguishing parental effort for offspring of different sexes. The classification score (or canonical variable) of parental effort induced by sons was 0.968 and for daughters was –0.740, resulting in $d = 1.71$ (a difference of 0.968 and –0.740, respectively) and $p(d = D) = 0.838$; thus, we detected no differential parental effort in raising sons versus daughters. Although the sign of the effort variable differs for daughters (negative, indicating higher effort) compared with that for sons (positive), the disparity in effort does not vary appreciably from the disparity in effort obtained from a randomized (or null) distribution. In the randomization of the disparity, the median effort disparity was 2.22, the 5th percentile was 1.42, and the 95th percentile was 3.43. The low level of disparity was exemplified by the results for two of the key predictor variables: daily food intake (Fig. 2) and change in parental mass over the breeding season (Table 3). The mean duration of parental care (as indicated by the nestling's age at attaining juvenile plumage) did not differ for sons (107.2 days) and daughters (110.7 days; one-tailed Student's t test, $t_{[38]} = 0.332$, $P = 0.17$).

Parental morphology measures and sex-specific differences in the measures (Table 4) were consistent with differences previously determined for this population (Anderson

1993); thus, the sample of adults in this study was not physically unusual.

Fledging success of female nestlings, p(hatched daughter fledged) = 0.808 (95% CI = 0.645–0.970), did not differ appreciably from that of male nestlings, p(hatched son fledged) = 0.894 (95% CI = 0.743–1.00).

Discussion

Our results show sex-specific growth patterns of Nazca boobies establish the female-larger SSD during the nestling stage. Despite the expectation that food requirements should also differ by nestling sex (see Introduction), our analysis indicated equal parental effort for sons and daughters during this breeding season. The length of the growth period (a proxy for duration of parental care) did not differ for sons and daughters, and daily food intake was similar for the two sexes (Fig. 2). The pattern of daily food intake in this study differed from those in a previous study (Anderson and Ricklefs 1992) in which daily food intake relative to body mass was consistently >10%. In contrast, relative food intake in this study dropped to 10% at median chick age 80 days (Fig. 2), after SSD and any attendant difference in food requirement had appeared (Fig. 1). Thus, the present study was conducted during a period of relative food stress. We should logically expect poorer performance of daughters compared with that of sons, and we found the asymptotic mass of male nestlings was 105.8% of the mean adult male mass found by Anderson (1993), but the asymptotic mass of female nestlings was only 99.4% of the typical adult female mass. This result suggests that female, but not male, nestlings were food-stressed to a degree that their growth was compromised. An alternative view of the similar food intakes of sons and daughters, that members of the smaller sex are more active in sibling competition, and so require more food than would be expected for their body size (Newton 1978) is not applicable because sibling competition is restricted to the first 1%–3% of the growth period and is decided by hatching sequence and not by sex (Anderson 1989; Westbrock 2005). Other measures of offspring performance, including survival to adulthood, may also be affected by the nutritional deficit that we have inferred for daughters, leading to an expectation of a deficit of adult females owing to post-fledging mortality (Maness et al. 2007). Townsend and Anderson (2007) concluded that the adult sex ratio was in fact male-biased at 0.589 (95% CI = 0.589–0.589). The failure of parents to meet the needs of sons and daughters equally, at least in some years, thus appears to have significant demographic consequences at the population level.

A related study (Apanius et al. 2007) on this same popu-

lation during the 2002–2003 breeding season produced results complimentary to the present study. In 2002–2003, we observed higher nestling survival (0.866) than during the present study (0.707; Yate's corrected χ^2 = 16.37, df = 1, P < 0.001), likely indicating higher food availability in 2002–2003. Apanius et al. (2007) found parents of daughters spent 8.4% and 5.5% more time at sea for daughters than for sons at offspring ages 70 and 90 days, respectively, after the appearance of SSD and while offspring were still sustaining growth with their food intake (Fig. 1). In contrast to the 2000–2001 results, asymptotic mass of daughters in that year was 5.8% greater than their mothers' mass, and that of sons and fathers did not differ, consistent with an excess food requirement of daughters that was met in that year. Supporting the idea that potentially long-lived Nazca booby parents would provide extra care to daughters if they also remained under a low-cost ceiling, data from 2002–2003 on parent mass loss and immunoglobin G showed no evidence of excess costs to self-maintenance from raising daughters (Apanius et al. 2007). Together, these studies indicate that Nazca booby daughters have greater food requirements than do sons, and parents meet those excess demands when food availability allows both satisfied daughters and uncompromised self-maintenance.

Our randomization procedure to test for disparity in parental effort significantly enhanced our ability to draw conclusions from our data. In randomization tests, a null distribution of potential values of the test statistic is created. In comparing the value of the sample test statistic (d) to the null distribution (D), the probability (or p value) is evaluated as the proportion of resample test statistics that are more extreme than the observed test statistic (Manly 1997; Peres-Neto and Olden 2001). In effect, a randomization test allows one to find support for a null hypothesis. Conversely, traditional parametric (and nonparametric) statistical tests can only fail to reject a null hypothesis. In addition, randomization tests are unencumbered by assumptions; they apply only to the sample itself and not to an underlying population, so statistical tests of assumptions are unnecessary.

Our multi-year data set provides initial support for the new hypothesis that, in effect, parents shunt (sensu Mauck and Grubb 1995) more costs of reproduction to the sex with higher food requirements during periods of food stress as a consequence of sustained self-maintenance. We suggest that potentially long-lived species should be more likely to exhibit this pattern than short-lived species, but available data are too sparse to evaluate this prediction. Estimates of parental effort (distinct from estimates of offspring food requirement) for sons and daughters exist for only a few species, and no estimate of annual adult survival is available for some of these species (Table 1). Environmental food availability is expected to influence the degree to which the food requirement of the expensive sex is satisfied and evaluation of that parameter is generally lacking. Simple comparison of sex-specific food delivery as a function of SSD and annual adult survival across species is likely to be uninformative, because breeding conditions will be difficult to standardize across species. Instead, we recommend multiyear studies of parental effort in long-lived and short-lived species showing nestling SSD to determine whether short-

lived species are more likely to satisfy the larger sex's food demand during food shortages. Of special interest would be simultaneous documentation of parental self-maintenance as a function of offspring sex.

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