

ENERGY LIMITS TO BODY SIZE IN A GRAZING REPTILE, THE GALAPAGOS MARINE IGUANA

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Abstract. Galapagos marine iguana (*Amblyrhynchus cristatus*) populations show considerable differences in body size. Adult body mass varies by more than 10-fold, and body length (snout–vent length, SVL) varies by ≈ 2.2 -fold. Predation and interspecific food competition are largely absent and can be excluded as potential forces explaining differences in body size among populations. This provides an ideal system in which to determine how proximate environmental factors affect adult body size. We compared the small iguanas from Genovesa Island (mean adult male SVL 250 mm) to the larger Santa Fe iguanas (mean adult male SVL 400 mm). Marine iguanas forage on intertidal algae pastures in scramble competition. Energy availability was lower on Genovesa than on Santa Fe, because of lower marine productivity on Genovesa. The length of grazable algal turf decreased with increasing sea surface temperature (SST). SST was $\approx 2^\circ\text{C}$ lower on Santa Fe than on Genovesa, implying ≈ 1.5 mm lower algae pastures on the latter. Genovesa showed a fivefold lower standing algal biomass and a twofold lower productivity of algae pastures than did Santa Fe. The smallest iguanas of each island had ≈ 1.5 -fold higher bite rates during foraging, and their absolute food intake per day was 35% that of the largest iguanas. However, food intake per bite per gram of body mass was about twice as high for small iguanas as for large iguanas. Large iguanas of both islands showed a marked decline in body mass during the two study years, whereas small iguanas (SVL < 170 mm on Genovesa and < 320 mm on Santa Fe) increased in mass. Growth rates of SVL reflected these findings. A comparison of measured metabolizable energy with published field metabolic rates (FMR) suggested that iguanas above a threshold size were in negative energy balance, because energy intake scaled to body mass with a lower exponent (0.3) than FMR (0.97). Threshold body size was lower on Genovesa than on Santa Fe and differed between years: In the lean El Niño year (1991/1992), iguanas >200 mm SVL on Genovesa and >310 mm SVL on Santa Fe significantly lost mass; in the more productive year (1992/1993), thresholds were 230 mm and 350 mm SVL, respectively. Thus, food abundance (length and turnover of algal swards) explained differences in adult body length and mass between islands as a result of energetic limitation. On a given island, foraging efficiency (intake/bite) explained the negative energy balance of large compared to small iguanas. This also explained why, on both islands, the largest animals suffered higher mortality rates than did medium-sized ones when food was scarce. The finding that small animals outcompeted larger ones because of their higher foraging efficiency resembles the grazing succession in ungulate herbivores.

Key words: algae; body size; energy limitation; foraging; Galapagos; grazing succession; herbivores; island populations; marine iguanas; primary productivity; reptiles; ungulates.

INTRODUCTION

Why do animals have certain body sizes, and how is the actual body size of an animal determined? In answering these questions, one can gain insight into the action of selective pressures that form the life history of animals (Peters 1983) and also into the proximate constraints that finally set limits to body sizes (e.g., Van Valen 1973, Schmidt-Nielsen 1984, Maurer et al. 1992, Brown et al. 1993). In explaining body sizes of animals, one usually has to deal with a wide

array of selectional forces and mechanisms for which the influence on body size is difficult to quantify (Dunham et al. 1978, Gaston and Lawton 1988), such as predation pressure (Owen-Smith 1993) or interspecific competition for food (Illius and Gordon 1987, 1992). By studying two island populations of Galapagos marine iguanas (*Amblyrhynchus cristatus*), a herbivorous reptile, one can exclude some of these factors from the outset. Predation is absent there for animals larger than hatchling size. Genovesa Island has no terrestrial predators; hawks and owls occur on Santa Fe, but, only the former prey on marine iguanas, and only on hatchlings and egg-laying females. Such predation pressure is low, as only a few females fall prey to the Galapagos Hawk every year (Curio 1965, Laurie and Brown 1990b),

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There is no interspecific food competition (Trillmich and Trillmich 1986), food abundance is quantifiable by height and degree of cover of the algal pasture (Wikelski and Trillmich 1994), and food patches are not defendable (Trillmich and Trillmich 1984, 1986). Marine iguanas occur on all islands of the Galapagos archipelago. The island populations show pronounced differences in adult body mass, ranging from island maxima of 1 kg to 12 kg body mass (Laurie 1989; W. A. Laurie, *personal communication*). Similar phenomena have been observed in lizards (see Schoener 1969, Case 1976, Pregill 1986, Case and Schwaner 1993). Strictly herbivorous throughout life, marine iguanas feed on macrophytic marine algae in the intertidal zone or by diving (Darwin 1883, Trillmich and Trillmich 1986, Wikelski et al. 1993, Wikelski and Trillmich 1994, Wikelski and Hau 1995). Large size confers a mating advantage to males (Trillmich 1983, Wikelski et al. 1996) and a fertility increase to females (Laurie 1990, Dellinger 1991). We wanted to explore why body size differs so widely among islands and which factors influence growth and final size of marine iguanas on Santa Fe and Genovesa. Santa Fe lies in the center of the Galapagos archipelago and was chosen because, building on the initial work of Laurie (1989), we had already followed that population for 10 years at the beginning of this study. Genovesa was chosen for comparison because it is home to the population of smallest marine iguanas on the Galapagos. In addition, this island is more tropical than the central islands of the archipelago and, therefore, is more frequently exposed to warm, equatorial waters that move in around the island whenever the intertropical convergence zone moves slightly south (Houvenaghel 1978).

Our analysis focuses on proximate mechanisms that may cause different selection regimes and, hence, differences in adult body sizes between islands. We approach this problem by quantifying foraging efficiencies for different-sized iguanas, using mass-specific food intake as unit of measurement (Wikelski et al. 1993). We then compare this with an independently derived measure of physiological performance of different-sized iguanas (growth and change in body mass). Finally, we scale our findings against published data on energy expenditure in this species (Nagy and Shoemaker 1984), and explain why larger animals (but also hatchlings) of each island suffer higher mortality rates than do smaller ones (Laurie and Brown 1990a, Wikelski 1994, Wikelski and Trillmich 1997).

METHODS

Physical setting and study animals

Marine iguana foraging ecology was studied intensively on the two islands, Genovesa and Santa Fe, at the study sites "Salvaje de Corazon" (89°59' W, 0°19' N) and "Miedo" (90°02' W, 0°50' S), respectively, from 1991 to 1994. These islands differ in their position

relative to the intertropical convergence zone (ITC). Genovesa is much more affected by warm waters from the Panama area, which seasonally influence the Galapagos (Houvenaghel 1978, Feldman 1986), and is less exposed to cold, upwelled waters from the Humboldt and Cromwell currents (Fahrbach et al. 1991). Upwelled waters are important for the nutrient supply of algae (Houvenaghel 1978).

Both study sites initially possessed high-density iguana populations (>2000 iguanas/km of coastline). The total population size on the Genovesa study site decreased from ≈2500 iguanas in spring 1991 to 250 in spring 1995; on Santa Fe, it fluctuated around 7000 individuals. About one-third of the animals of both populations were marked individually by branding (details of methods in Laurie 1989, 1990). Both sites held extensive intertidal feeding grounds, which consisted of mostly steep cliffs in Santa Fe, but rock flats in Genovesa.

Methods used were identical on both islands, and all of us had previously worked together to standardize techniques. Marine iguanas were studied intensively from October 1991 until April 1992, and from November 1992 until April 1993. We define each of these study periods as "year" and refer to them as the "El Niño" (1991/1992) and the "normal" (1992/1993) year, respectively. During both years, we witnessed the transition from the cold "Garua" season (June–November) to the warm season (December–May). However, both years of the study were unusually warm, and oceanographers often describe the whole period from 1990 to 1994 as a continuous, weak El Niño (Kerr 1993, McPhaden 1994).

Daily at noon, sea surface temperature (SST) was measured with a standard mercury thermometer ($\pm 0.1^\circ\text{C}$). Marine iguanas were captured during three weeks in November. They were individually identified, measured, weighed, and painted with synthetic paint to facilitate observation. Animals were recaptured in March and April (see details in Laurie 1989). Snout-vent length (SVL), rather than body mass, was used as a reference measure of size, because in both years some iguanas dramatically lost mass (some >5 g/d). Growth was measured as the increase in SVL from November 1991 to March 1993. For the determination of food intake, iguanas were assigned to six body length classes for each island. These classes divided the whole range of SVL observed on Santa Fe into 50-mm units (starting from 100 mm SVL), and on Genovesa into 30-mm units (starting from 110 mm SVL).

Individual rates of mass change were calculated by dividing the difference in body mass between capture and recapture by the capture–recapture interval (≈ 4 mo). This interval did not differ for different body length classes. To compare energy intake with published data on energy expenditure, we had to use body mass as unit of comparison (see Nagy and Shoemaker 1984), despite its shortcomings.

TABLE 1. Biomass (dry mass, mean \pm 1 SD) and relative productivity of dietary algae in the intertidal zone of Santa Fe and Genovesa Islands, Galapagos, during the 1992/1993 season. Productivity was calculated as $[(c - a)/a - (b - a)/a] \times 100$ to standardize for differences in grazing pressure at the times of initial sample and final harvest. $N = 5$ for each case.

Island, date of sample	Biomass (g/500 cm ²)			Productivity (%)	No. enclosure days	Daily productivity (%/d)
	Initial sample (a)	Comparison at harvest (b)	Enclosure at harvest (c)			
Santa Fe						
5 Nov–12 Nov	0.90 \pm 0.37	0.40 \pm 0.19	2.74 \pm 0.85	260	7	37
9 Dec–16 Dec	0.22 \pm 0.12	1.22 \pm 0.63	1.56 \pm 0.75	155	7	22
23 Jan–10 Feb	0.32 \pm 0.23	0.25 \pm 0.16	0.66 \pm 0.40	127	17	7
Genovesa						
16 Nov–1 Dec	0.28 \pm 0.16	0.36 \pm 0.19	1.15 \pm 0.60	279	14	20
23 Dec–7 Jan	0.17 \pm 0.13	0.09 \pm 0.08	0.26 \pm 0.12	100	14	7
22 Jan–6 Feb	0.03 \pm 0.03	0.01 \pm 0.02	0.04 \pm 0.04	83	15	6

Food abundance

The height of the algae pasture (algae blade length) was measured at three intertidal sample plots per island in 1991/1992, and at nine sample plots per island in 1992/1993, once every 14 d on both islands, wave action permitting. The plots were placed in areas representative of the feeding areas of marine iguanas, and covered the entire range of foraging habitat from the upper to the lower intertidal (see Wikelski and Trillmich 1994 for details on foraging areas). Each plot was marked by two rock screws drilled into the lava substrate. At each sample plot, a line grid over a wooden 50 \times 50 cm frame with mesh width of 10 cm was used to locate 16 subsample locations at the crossing points of the grid strings. At these locations, the length of algae blades was estimated by eye. Measurement with caliper was not possible; in the wave-washed intertidal area (especially at Santa Fe), this would have been very dangerous. Instead, at less wave-exposed areas, we trained to estimate the length of algae blades that had been measured with calipers, and thereby achieved high intra- and interpersonal accuracies of ± 1 mm. Algae coverage was defined as the percentage of the 16 subsample locations that was covered with algae (vs. bare rock). Foraging areas on Santa Fe were dominated by red algae (*Gelidium* sp. and *Centroseras* sp.; Wikelski et al. 1993), whereas green algae (*Ulva* sp.) prevailed on Genovesa (cf. Nagy and Shoemaker 1984).

Productivity of intertidal algae

To exclude iguanas from grazing on algae, we established enclosure plots at representative foraging areas in the medium intertidal (Table 1). Enclosures consisted of flexible wire mesh (wire diameter 1.4 mm, openings 10 mm) fixed to the ground with 6–8 rock screws drilled into the substrate. The ≈ 0.5 -m² mesh was supported by a 17-cm iron rod in the middle of the enclosure, giving it a tent-like appearance. Five algae samples, each scratched off the rock with a knife within a 10 \times 10 cm metal frame, were taken (1) when setting up an enclosure (diagonally from left to right

inside the enclosed area), (2) when harvesting an enclosure (diagonally from right to left inside the enclosed area), and (3) on the day of harvest, adjacent to the enclosure in a grazed area as a comparison. Samples were sun-dried in the field and exported under CITES permit; their dry mass was determined after drying at 60°C. This dry mass was taken as indicator of the standing biomass on a given day. To estimate productivity, we averaged the dry masses of the five samples and calculated the relative change in dry mass per day from the initial sample to the final harvest, in control vs. enclosure samples (see Table 1).

Foraging and bite numbers

The main intertidal foraging areas of both study populations were mapped by triangulation, and their plane surface areas were determined by weighing cut-out paper sheets of intertidal maps against standards. Every 5 min during the daily foraging period (on 21 March 1992 and 3 April 1992), the number of animals foraging on these areas and their respective body length classes were determined. Using the mean body mass per size class, we determined the mean daily biomass of foraging iguanas per square meter of the intertidal zone.

A foraging trip was defined as the time between entering the intertidal area and leaving it (see Wikelski and Trillmich 1994). The feeding time per day was the sum of all foraging trips per day. Its duration depended on the time of day when low tide occurred, wave action, sea surface temperature, and ambient temperature (Wikelski and Trillmich 1994). Feeding time per day did not change significantly between years. Therefore, we lumped all available information on foraging times per day for both years. The number of bites taken during foraging trips was counted from prominent rocks, using binoculars and telescopes, and was recorded with handheld data loggers (Psion, Bad Homburg, Germany). Data were analyzed with the "Observer" software package (Noldus, Wageningen, The Netherlands), and were only used when both the start and end of foraging trips had been observed and iguanas were visible $>85\%$

TABLE 2. Foraging performance of marine iguanas, by snout-vent length, on Santa Fe and Genovesa. Values are means \pm 1 SD (n in parentheses). Body mass and feeding time were obtained from a marked population observed foraging. Bite rate was based on focal animals (including flushed animals). Total algae intake was based on stomach-flushed iguanas.

SVL range (mm)	Body mass (g)	Feeding time [†] (min/d)	Bite rate		Dry mass of algae eaten		
			No./s [‡]	No./d [§]	Total (g/d)	Intake per bite [§] (mg)	Intake per bite per body mass [§] (mg/g)
A) Santa Fe							
101–150	137 \pm 21 (94)	21.9 \pm 11.4 (94)	0.63 \pm 0.17 (14)	827	1.37 \pm 0.36 (4)	1.66	12.1
151–200	235 \pm 19 (36)	26.1 \pm 14.6 (36)	0.47 \pm 0.29 (9)	736	2.18 \pm 0.53 (8)	2.96	12.6
201–250	539 \pm 46 (48)	23.2 \pm 11.3 (48)		682	2.84 \pm 1.6 (4)	4.16	7.73
251–300	770 \pm 159 (19)	27.5 \pm 17.2 (19)		660	4.06 \pm 2.3 (9)	6.15	7.99
301–350	1 241 \pm 326 (6)	22.2 \pm 25.9 (6)	0.40 \pm 0.18 (18)	533	4.1 \pm 1.6 (13)	7.89	6.2
351–400	2 180 \pm 299 (16)	22.7 \pm 23.0 (16)		545	4.26 \pm 3.9 (21)	7.82	3.59
B) Genovesa							
111–140	108 \pm 16 (7)	61.4 \pm 28 (7)	0.96 \pm 0.26 (6)	3 538	0.75 (1)	0.212	1.96
141–170	162 \pm 19 (24)	52.5 \pm 18 (24)	0.87 \pm 0.24 (6)	2 743	1.45 \pm 0.11 (4)	0.529	3.26
171–200	251 \pm 23 (154)	60.8 \pm 23 (154)		3 174	1.59 \pm 1.08 (11)	0.501	2.00
201–230	436 \pm 106 (239)	64.6 \pm 21 (239)		3 375	2.44 \pm 1.10 (9)	0.723	1.66
231–260	551 \pm 104 (81)	81.7 \pm 21 (81)	0.62 \pm 0.17 (25)	3 041	1.72 \pm 0.91 (8)	0.566	1.03
>260	670 \pm 117 (87)	68.5 \pm 22 (87)		2 549	1.89 \pm 2.58 (4)	0.741	1.11

[†] ANOVAs for both Santa Fe and Genovesa were not significant.

[‡] Data were split in only three classes (101–150, 151–250, and 251–400 mm on Santa Fe; 111–140, 141–200, and 201–>260 mm on Genovesa) because there was no difference in performance within those classes (see Wikelski and Trillmich 1994). ANOVAs: for Santa Fe, $F_{2,41} = 4.76$, $P = 0.01$; for Genovesa, $F_{2,37} = 9.55$, $P < 0.001$.

[§] Calculations: bite count data were not used for all stomach-flushed iguanas (see *Methods*).

of the time. The bite rate was defined as the number of bites divided by the time during which the animals' bite movements were visible during the feeding observations. We assumed that iguanas behaved in the same way when not visible (mean of 7.7% of the foraging time).

Food intake

We caught 111 iguanas (71 on Santa Fe, 40 on Genovesa) that had been observed focally during their foraging time. They were caught immediately at the end of the daily foraging, and their stomachs were flushed (methodological details in Wikelski et al. 1993). Stomach contents were sun-dried in the field. Samples were exported under CITES permissions Numbers 006 IC and 009 IC of the Ecuadorian government. Dry mass of the stomach contents was determined in the laboratory after drying the samples at 60°C to constant mass. The food intake per bite was determined as the dry mass of algae divided by the number of bites per day. To calculate the intake for different body length classes, we assumed that the focal animals were representative of their respective body length classes. We

then used mean bite rates of focal animals for each body length class, mean body masses of iguanas, and mean foraging times to calculate the mean feeding performance of iguanas of a given body length class (Table 2). In this calculation, we lumped data from the two years for each island and calculated the mean intake per bite.

To convert dry mass of stomach contents into energetic units, we prepared the samples as previously described (Wikelski et al. 1993) and analyzed them by bomb calorimetry. Conversion factors were 13.8 ± 2.1 kJ/g of algae dry mass ($n = 24$) for Santa Fe, and 10.0 ± 2.7 kJ/g ($n = 17$) for Genovesa. This difference in energetic content is explained by the differences in algae species composition (see also Nagy and Shoemaker 1984, Wikelski et al. 1993).

Statistical analysis

Data were processed with SPSS (1991) for Windows. Two-tailed test statistics were used. Residuals of regressions were inspected for normality (see Fig. 3 legend for an exception). Data are given as mean \pm 1 SD if not indicated otherwise, except for regression equa-

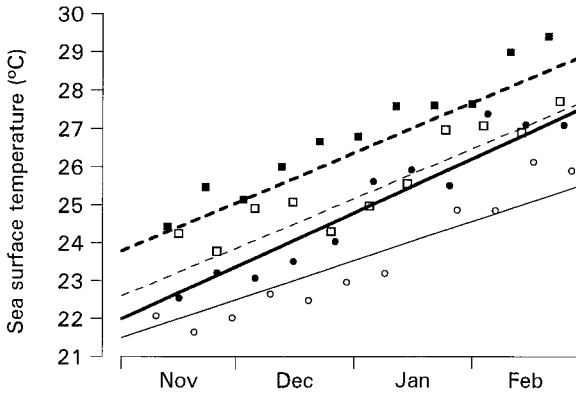


FIG. 1. Mean sea surface temperature (SST) regressions, November–February 1991/1992 (thick line) and 1992/1993 (thin line) for Genovesa (broken lines) and Santa Fe Islands (solid lines), Galapagos; 1991/1992 was an El Niño year, whereas 1992/1993 was a “normal” (i.e., cooler) year within the long-term 1991–1993 El Niño. The data points represent 10-d means for each island and year (Genovesa: ■, 1991/1992; □, 1992/1993; Santa Fe: ●, 1991/1992; ○, 1992/1993). SST increased by $\approx 4.5^\circ\text{C}$ from November to March.

tions (mean ± 1 SE). A General Linear Model was used to perform the analyses of variance whenever sample sizes were not equal. Type III sums of squares were used in tests for significance. *F* value subscripts indicate degrees of freedom of the model and error. Significance for all tests was accepted at the $\alpha = 0.05\%$ level.

RESULTS

Sea surface temperatures (SST)

Genovesa and Santa Fe differed significantly in temperature of the surrounding surface water (SST), with water temperatures at Santa Fe being about two degrees lower than at Genovesa during both years (Fig. 1; Santa Fe: 1991/1992, $25.3^\circ \pm 1.8^\circ\text{C}$ ($n = 119$), 1992/1993, $23.4^\circ \pm 2.1^\circ\text{C}$ ($n = 154$); Genovesa: 1991/1992, $27.3^\circ \pm 1.7^\circ\text{C}$ ($n = 109$), 1992/1993, $25.6^\circ \pm 1.5^\circ\text{C}$ ($n = 92$); ANCOVA factorial model: $\text{SST} = \text{island}$ ($P < 0.001$) + year ($P < 0.001$) + $\text{island} \times \text{year}$ ($P < 0.001$) + date ($P < 0.001$) + error; $F_{4,470} = 500$, $P < 0.001$; higher level interactions were not significant and were therefore dropped). Water temperatures were also markedly higher in the 1991/1992 El Niño year than in the near “normal” year 1992/1993. Water temperatures steadily increased during both years, from November until February (all linear regressions with $P < 0.001$). Such a temperature increase is expected, because this time period marks the transition from the cold season (approximately June–November) to the warm season (December–May) in the Galapagos.

Food abundance

The length of algae blades on both islands and in both years declined with increasing SST (Fig. 2, growth model regression: algae blade length = $\exp(4.03$

$(\pm 0.82) - 0.128 (\pm 0.03) \times \text{SST}$), $F_{1,58} = 15.7$, $R^2 = 0.22$, $P = 0.001$; each data point represents the mean algae blade length of 16 sampling points per intertidal plot). Since different areas of the intertidal are not uniformly represented at different points in time, the regression should only be used as an approximation. This decline did not result from declining algae cover, as algae cover did not change with increasing SST (linear regression, $F_{1,58} = 0.1$, $R^2 = 0.0$, $P = 0.87$). The mean percentage of algae coverage did not differ within an island between the two years, but was significantly lower on Santa Fe (1991/1992: $45.3 \pm 29.3\%$, $n = 5$; 1992/1993: $53.8 \pm 31.6\%$, $n = 16$) than on Genovesa (1991/1992: $69.4 \pm 20.3\%$, $n = 9$; 1992/1993: $69.9 \pm 17.8\%$, $n = 29$). The ANOVA factorial model was: coverage = island ($P < 0.01$) + year ($P = 0.58$) + island \times year ($P = 0.54$) + error ($F_{3,56} = 4.5$, $P < 0.01$). Above a SST of 28°C , there was hardly any grazable algae pasture left in the intertidal area (Fig. 2). Algae swards were longer on Santa Fe than on Genovesa, and longer in 1992/1993 (Santa Fe: 4.62 ± 2.25 mm, $n = 16$; Genovesa: 2.13 ± 1.38 mm, $n = 29$) than in 1991/1992 (Santa Fe: 3.12 ± 0.85 mm, $n = 5$; Genovesa: 1.34 ± 0.76 , $n = 9$). The ANOVA factorial model was: blade length = island ($P < 0.001$) + year ($P = 0.24$) + island \times year ($P = 0.02$) + error ($F_{3,56} = 7.5$, $P < 0.001$). The significant island \times year interaction suggests that the effect of year was proportionally stronger on Santa Fe than on Genovesa.

Productivity of intertidal algae

On both islands, the standing biomass and the estimated productivity declined as the season progressed

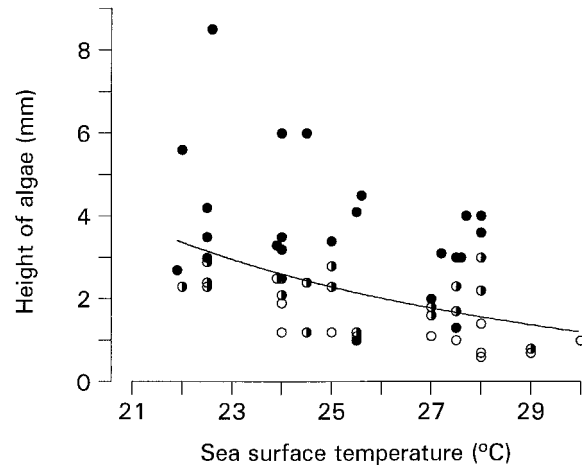


FIG. 2. Algae blade length (“pasture height”) decreases as sea surface temperature increases. An exponential regression model (line) fits better than a linear one. Each point represents the mean of 16 subsamples at one location in the intertidal area. Lower intertidal plots are indicated by solid circles, medium intertidal areas by half-solid circles, and upper intertidal by open circles. Data from Genovesa and Santa Fe Islands and from both seasons are shown together.

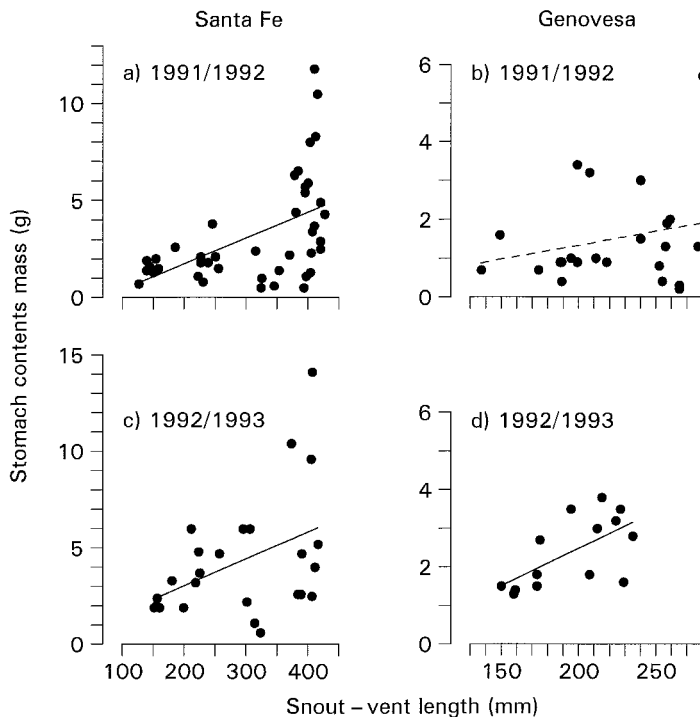


FIG. 3. Food intake of marine iguanas separated by island and year. The dry mass of stomach contents increased significantly with increasing body length of marine iguanas, except in (b). The variance in dry mass was larger for larger animals. Because log-transformation of data did not produce different results, we present the data, as measured, for clarity (despite heterogeneity of variance). Lines are linear regressions. For 1991/1992, the El Niño year, food intake at Santa Fe (a) was $-0.93 (\pm 1.0) + 0.13 (\pm 0.003) \times \text{SVL}$ ($F_{1,45} = 16.5$, $R^2 = 0.28$, $P < 0.001$); at Genovesa (b), food intake was $-0.12 (\pm 1.5) + 0.007 (\pm 0.006) \times \text{SVL}$ ($F_{1,24} = 1.2$, $R^2 = 0.05$, $P = 0.28$; the broken line indicates that the regression was not significant). For 1992/1993, the “normal” year, food intake at Santa Fe (c) was $0.23 (\pm 1.8) + 0.014 (\pm 0.006) \times \text{SVL}$ ($F_{1,25} = 5.2$, $R^2 = 0.18$, $P = 0.03$); at Genovesa (d), food intake was $-1.4 (\pm 1.3) + 0.2 (\pm 0.006) \times \text{SVL}$ ($F_{1,13} = 8.0$, $R^2 = 0.4$, $P = 0.01$).

(Table 1). The standing biomass in the intertidal foraging areas differed about fivefold, on average, between the two islands at the respective sample times (biomass ratios for Santa Fe: Genovesa were 3.2, 1.3, and 10.7 for the respective periods; Table 1). The estimated daily productivity differed about twofold (ratios of productivity per day for Santa Fe: Genovesa 1.8, 3.1, and 1.2 for the respective time periods shown in Table 1). Standing biomass inside the enclosure was always higher than at outside control areas. The factors “season” (samples taken early, mid, or late) and “island” (Genovesa or Santa Fe) showed significant influences on the biomass difference between enclosure and control plots in standing biomass (dry mass) at harvest (ANOVA two-factor paired model: difference in dry mass = island ($P = 0.01$) + season ($P < 0.001$) + island \times season ($P = 0.06$) + error; $F_{5,24} = 8.0$, $P < 0.001$).

Foraging behavior and food intake per bite

The biomass of foraging marine iguanas per square meter of the intertidal area was higher on Santa Fe (364 and 397 $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, in 1991/1992 and 1992/1993, respectively) than on Genovesa (108 and 120 $\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, in 1991/1992 and 1992/1993, respectively). On Santa Fe, marine iguanas foraged for much shorter periods (23.4 ± 13.6 min/d, $n = 219$ individual foraging days) than on Genovesa (66.0 ± 21.6 min/d, $n = 592$ individual foraging days; Mann-Whitney U test, $P < 0.001$). There were no detectable differences in foraging durations between years (Mann-Whitney U test,

$P > 0.05$); thus, we lumped data on foraging durations within each island. Within an island, iguanas of different body length classes showed no significant differences in foraging durations (ANOVA, $P > 0.05$; Table 2). The mean number of bites per second of a foraging bout differed between iguanas of different body lengths. On each island, smaller iguanas had higher bite rates (Table 2, cf. Wikelski and Trillmich 1994). In combination, this resulted in a higher total calculated number of bites per day for small vs. large iguanas (Table 2). The total number of bites per day was roughly five times higher at Genovesa than at Santa Fe, because iguanas at Genovesa foraged about three times longer per day (Table 2). On each island, the second smallest body length class had the highest food intake per bite per gram of body mass, and thus foraged most efficiently (Table 2). Foraging efficiency decreased on each island for larger animals, but also for the smallest body length class.

Daily food intake

The total food intake (dry mass of algae in stomach) per foraging day increased with body length on each island during each year (Fig. 3a–d). For the following analyses, log-transformed data of food intake and body length were used (instead of the raw data presented in Fig. 3) to make the residual variation less heteroscedastic. We found no significant heterogeneity of slopes of food intake against body length among islands (ANCOVA: body length \times island, $P = 0.33$) and among years (ANCOVA: body length \times year, $P = 0.24$; the

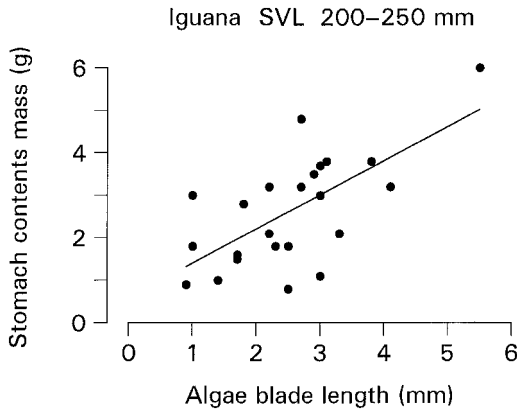


FIG. 4. The food intake (dry mass in stomach) for iguanas of a given length (200–250 mm SVL) from both study islands increased with increasing length of the algae pasture in the intertidal areas (the line represents a linear regression).

factor effect body length \times island \times year was not significant, and was discarded). Therefore, we assume that there is one common slope of food intake against body length, under different conditions. A factorial model showed that food intake was influenced by body length, and differed within islands and between islands in different years (ANCOVA factorial model: food intake = island ($P = 0.04$) + year ($P = 0.37$) + island \times year ($P < 0.001$) + body length ($P < 0.01$) + error; $F_{4,107} = 10.6$, $P < 0.001$).

On both islands, iguanas had a higher mean food intake during a “normal” year than during an El Niño year (Fig. 3). This was not attributable to differences in body length of the animals sampled in the different years (Mann-Whitney U test for Santa Fe: $n_1 = 25$, $n_2 = 46$, $P = 0.3$; for Genovesa: $n_1 = 26$, $n_2 = 14$, $P = 0.97$) but to algae blade length. To highlight this relationship, we determined the blade length of algae in the foraging areas from the data on food abundance, using the data points from both islands when algae sampling coincided closest in time with the respective stomach flushing of iguanas. We found that the food intake of iguanas of similar body length (200–250 mm SVL) was predicted from blade length of the algae in the respective foraging area (Fig. 4, linear regression: mass of stomach contents (grams) = $0.61 (\pm 0.55) + 0.80 (\pm 0.20) \times$ algae blade length; $F_{1,22} = 15.8$, $R^2 = 0.43$, $P < 0.001$).

Comparison of food intake, metabolizable energy, and field metabolic rate

To compare the mean slopes of food intake and energy expenditure as a function of body mass, we calculated the power regressions of body mass before stomach flushing against food intake. To do this, we combined data from both years, because we were first interested in the general slope of the intake function. We were allowed to do so because we had found previously that the slopes of food intake against body

length did not differ under different conditions. On both islands, food intake (dry mass of stomach contents) increased with approximately the 0.3 power of body mass, although the model was not significant for Genovesa (Santa Fe, both years combined: intake = $0.52 (\pm 0.21) \times$ body mass $^{0.26 (\pm 0.06)}$; $F_{1,70} = 16.6$, $R^2 = 0.14$, $P < 0.001$; Genovesa, both years combined: intake = $0.26 (\pm 0.40) \times$ body mass $^{0.31 (\pm 0.27)}$; $F_{1,39} = 1.3$, $R^2 = 0.05$, $P = 0.2$).

As a further step, we compared the daily metabolizable energy with published data on field metabolic rate (FMR; Nagy and Shoemaker 1984). Metabolizable energy was calculated on a daily basis by multiplying the amount of food intake by the mean energy content of stomach contents (see *Methods*). We corrected for digestive energy losses by subtracting 30% of each calculated value, thus assuming a general digestive efficiency of 70% (Nagy and Shoemaker 1984, Wikelski et al. 1993). Using these calculated data on metabolizable energy, we fitted power regressions to data sets of each island and year for a comparison with FMR in a double logarithmic plot (Fig. 5; calculations of metabolizable energy were: Santa Fe, $10.4 \times$ mass $^{0.24}$ (1991/1992) and $10.2 \times$ mass $^{0.27}$ (1992/1993); Genovesa, $8.1 \times$ mass $^{0.07}$ (1991/1992) and $1.0 \times$ mass $^{0.53}$ (1992/1993); n as before). The regression lines crossed the FMR line

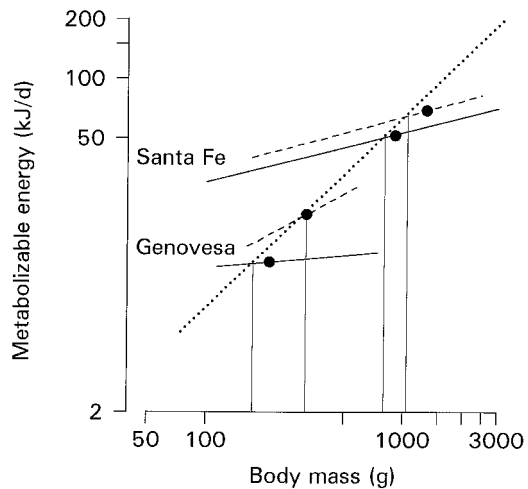


FIG. 5. A comparison between metabolizable energy and energy expenditure per day for marine iguanas on two islands and during two years (dashed line, “normal” year 1991/1992; solid line, El Niño year 1992/1993). The dotted line indicates field metabolic rate (FMR, in kJ/d) following Nagy and Shoemaker’s (1984) equation: $FMR = 0.079 \times$ (body mass) $^{0.97}$. Genovesa iguanas had a lower absolute metabolizable energy than Santa Fe iguanas at the same body mass. The predicted threshold body mass, at which the energy balance becomes negative, is indicated by thin vertical lines where metabolizable energy and FMR lines cross. This threshold mass is higher on Santa Fe than on Genovesa, and higher during “normal” than during El Niño years for each island. The solid dots on the lines represent the threshold mass above which animals actually lost body mass during the study years (calculated from Fig. 6).

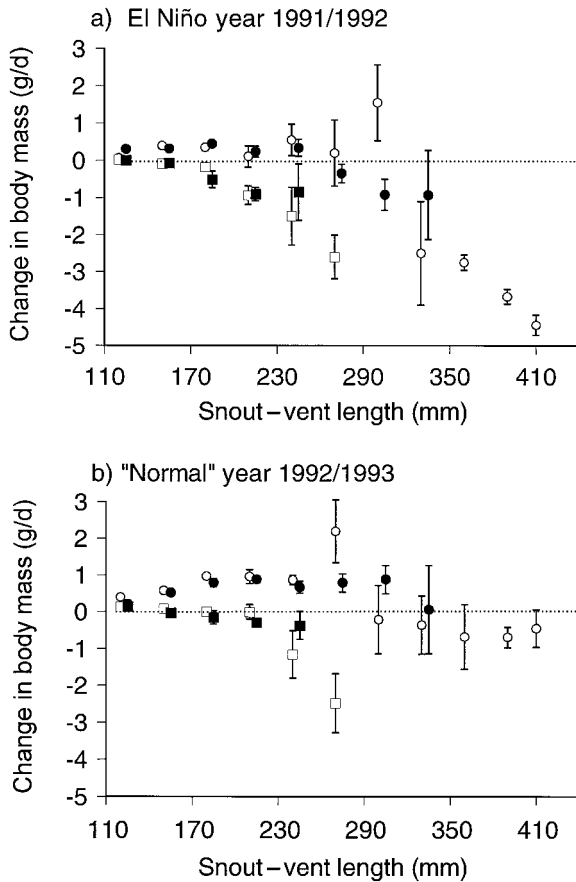


FIG. 6. Body mass changes (mean \pm 1 SE) analyzed by body length class, year, island, and sex. Large iguanas of each island lost body mass during both the El Niño year (1991/1992) and the "normal" year (1992/1993). In (a), sample sizes for increasing size classes were: \circ , Santa Fe males (1, 7, 11, 7, 6, 5, 10, 9, 39, 117, and 33 iguanas); \bullet , Santa Fe females (1, 14, 22, 8, 13, 26, 25, 4); \square , Genovesa males (11, 15, 38, 38, 21, 19); \blacksquare , Genovesa females (7, 15, 36, 41, 2). In (b), with symbols as in (a), sample sizes for Santa Fe males were 1, 3, 3, 8, 17, 11, 11, 4, 15, 44, 15; for Santa Fe females, 1, 4, 5, 7, 15, 21, 29, 7; for Genovesa males, 2, 9, 40, 52, 16, 13; for Genovesa females, 2, 22, 29, 9, and 2 iguanas.

at body masses of 172 g and 320 g on Genovesa and of 800 g and 1040 g on Santa Fe (during 1991/1992 and 1992/1993, respectively). Based on mean condition for iguanas of this length, these masses would have been equivalent to threshold SVLs of 185 mm and 230 mm on Genovesa and 298 mm and 326 mm on Santa Fe (during 1991/1992 and 1992/1993, respectively). These calculated threshold body lengths corresponded to measured threshold body lengths of 200 mm and 230 mm on Genovesa, and 310 mm and 350 mm on Santa Fe (1991/1992 and 1992/1993 in Fig. 6a and b, respectively).

Changes in body mass and body length

For the following analyses, we combined males and females, because both sexes generally showed similar

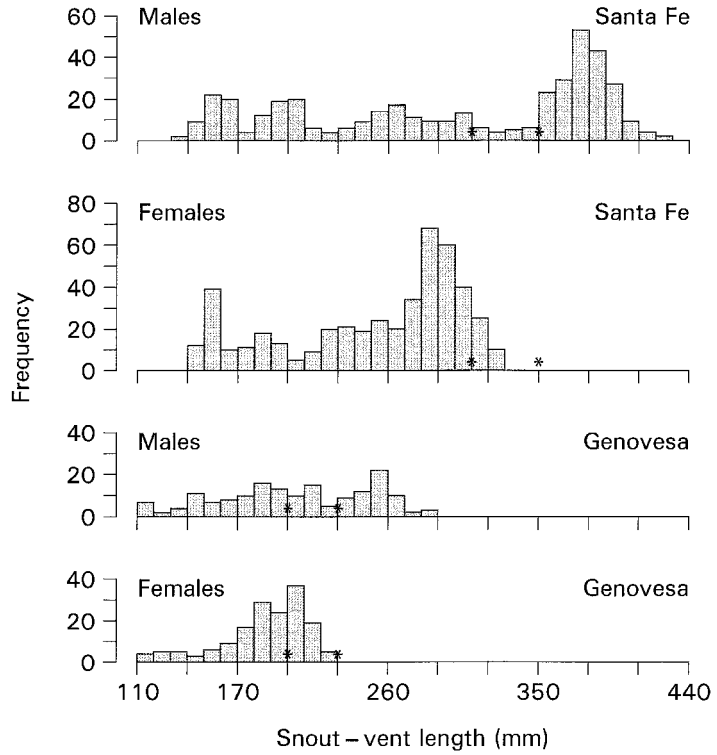
mass changes and were subject to similar selection pressures on body size (Wikelski and Trillmich 1997). During both years, large iguanas lost body mass, whereas small iguanas showed no changes or increased in body mass (Fig. 6a for the El Niño year 1991/1992, Fig. 6b for the "normal" year 1992/1993). The larger iguanas of each island showed higher mass losses than did their smaller conspecifics (Fig. 6; ANOVA for Genovesa: 1991/1992, $F_{6,237} = 12.3$, $P < 0.001$; 1992/1993, $F_{6,190} = 8.2$, $P < 0.001$; for Santa Fe: 1991/1992, $F_{11,347} = 35.4$, $P < 0.001$; 1992/1993, $F_{11,210} = 2.85$, $P = 0.002$). Genovesa iguanas had significant mass losses at a mean body length of 200 mm SVL in 1991/1992 and at 230 mm SVL in 1992/1993, whereas significant mass losses for Santa Fe iguanas occurred at mean body lengths of 310 mm SVL during 1991/1992 and at 350 mm SVL during 1992/1993. The threshold body lengths above which iguanas on a given island lost mass are shown in Fig. 7, in relation to the body length distributions of both sexes in the populations. Males were losing mass during both years, whereas females lost mass only during El Niño years (Figs. 6 and 7).

Growth in SVL was higher for a given body length on Santa Fe than on Genovesa (Fig. 8). Males had higher growth rates than females on Santa Fe, but not on Genovesa, where animals >200 mm SVL hardly grew at all during the two years. Females on Santa Fe grew faster at a given body length than did males on Genovesa (Fig. 8). Growth rates were approximated with linear regressions. For Santa Fe males, growth = $72.9 (\pm 5.5) - 0.15 (\pm 0.1) \times \text{SVL}$ ($F_{1,127} = 89$, $R^2 = 0.41$, $P < 0.001$); for females, growth = $113.4 (\pm 10.7) - 0.37 (\pm 0.04) \times \text{SVL}$ ($F_{1,65} = 77$, $R^2 = 0.54$, $P < 0.001$). For Genovesa males, growth = $29.1 (\pm 6.4) - 0.12 (\pm 0.03) \times \text{SVL}$ ($F_{1,47} = 16$, $R^2 = 0.26$, $P < 0.001$); for females, growth = $62.4 (\pm 20.3) - 0.31 (\pm 0.11) \times \text{SVL}$ ($F_{1,28} = 8$, $R^2 = 0.23$, $P = 0.008$).

DISCUSSION

Our analysis shows that body size in marine iguanas is limited by food intake, which, in turn, depends on the length of grazable algae turf. Body size differences *between* island populations of marine iguanas can be explained by differences in food availability. The energy limit of body size *within* an island population can be explained by the lower scaling of energy intake vs. energy expenditure (exponents of 0.3 and 0.97, respectively). We first discuss differences in the food supply and their implications for phenotypic differences in body size. We then compare the energy values of food intake with field metabolic rates from the literature (Nagy 1982, Nagy and Shoemaker 1984). Finally, we relate the difference in net energy gain between large and small iguanas to their mass change and growth. Knowing that predation (Curio 1965) and interspecific food competition play hardly any role, and that foraging areas cannot be monopolized (Trillmich and Trillmich 1984), we attempt to explain differences

FIG. 7. Frequency distribution of body lengths of marked marine iguanas on Santa Fe (February 1990) and Genovesa Islands (February 1991). The stars illustrate the body length at which iguanas started to lose body mass during the two study seasons (the star at the lower body length for each island represents the El Niño season, 1991/1992). This body length was determined from Fig. 6.



in body size based on food availability alone, even though we are well aware that, for example, thermal relations may also play a very important role (Huey 1991, Sinervo and Adolph 1994).

Differences in food supply between islands

Although marine iguanas of the two islands live in the same climatic zone (on the equator), the populations belong to different oceanic provinces: Santa Fe is affected by the cold southern Humboldt current and the Cromwell upwelling, whereas Genovesa is more influenced by warm waters around and north of the inter-tropical convergence zone (Houvenaghel 1978). The body size differences of marine iguanas within the archipelago are in the direction expected, based on oceanographic data on marine primary production, which is highest in western areas that are most influenced by the Cromwell upwelling system (Houvenaghel 1978, Feldman 1986). The largest iguanas (12 kg) occur in western areas, where the highest concentrations of phytoplankton pigments are detectable on satellite images. The smallest iguanas of the archipelago live on Genovesa, which is least influenced by upwelled waters (for primary production, see Houvenaghel 1978, Feldman 1986:94, Plate 5; for iguana size, see Laurie 1989; W. A. Laurie, *personal communication*; Trillmich and Rassmann, *unpublished data*).

Throughout their lives, marine iguanas feed entirely on macrophytic marine algae pastures (Wikelski et al. 1993, Wikelski and Trillmich 1994). The height of

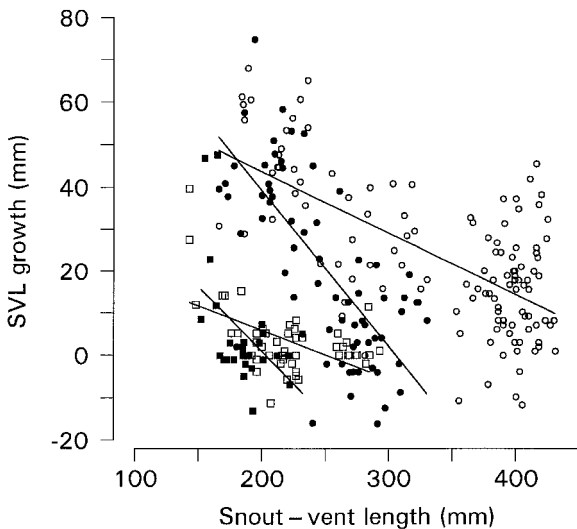


FIG. 8. The change in body length of marine iguanas from November 1991 to March 1993 for the islands Santa Fe (●, females; ○, males) and Genovesa (■, females; □, males). The lines represent linear regressions for males (right-most line for each island) and females. Growth was higher in Santa Fe than in Genovesa iguanas, and males of Santa Fe grew significantly faster than females. The loss in body length of many animals is significant, but unexplained.

these pastures was correlated to sea surface temperature (Fig. 2), which, in turn, was shown to depend on the amount of upwelling around an island (Houvenaghel 1978). The more upwelled waters that occur near an island (i.e., the colder the sea surface temperature), the more nutrients there are to promote algal regrowth between the daily foraging trips of marine iguanas. Water temperature is, of course, only an indirect measure of the amount of nutrients present. Nevertheless, it was correlated with differences in the length of algae swards between islands and years (Fig. 2). The sward length determined the amount of food gained by individual iguanas during their daily foraging trips (Fig. 4). Thus, algae sward length was the parameter that best quantified food abundance when there were no differences in algal cover. Algae length cannot, however, serve as measure of algae productivity, because the biomass of foraging iguanas per square meter of the intertidal zone was much higher on Santa Fe than on Genovesa. Thus, productivity differences between the two intertidal areas must be much larger than suggested by the linear differences in algae sward length.

Productivity of intertidal algae

Indeed, we found large differences when we compared the standing biomass and the productivity in representative, comparable intertidal foraging areas between the two islands (Table 1). The Santa Fe algae pastures showed about fivefold higher standing biomass and nearly twofold higher productivity than those on Genovesa. However, our data can only be used as a first approximation of the actual biomass and productivity, mainly because we could not control for differences in iguana grazing pressure on control areas, because we could only sample at the lowest tides of the month, and because a productivity calculation on a daily basis ignores the nonlinearity of algae growth (cf. McNaughton et al. 1996).

Constraints on food acquisition and disadvantage of large size

Both small and large marine iguanas on a given island foraged for an equal amount of time per day (Trillmich and Trillmich 1986, Wikelski and Trillmich 1994). Although small iguanas were limited in duration of continuous foraging by wave force, large iguanas were constrained by a decrease in bite rate as they cooled during foraging (Wikelski and Trillmich 1994). The differences in foraging duration between islands (Table 2) can be explained by lower wave action and higher water temperatures in Genovesa, permitting animals to stay longer in the intertidal areas (cf. Wikelski and Trillmich 1994). Small marine iguanas of each island were constrained to the upper intertidal areas, where wave action was lowest. They began foraging as soon as wave action permitted them to enter the intertidal, and grazed their way down into the lower intertidal as the tide retreated. Thereby, they kept the

upper intertidal constantly grazed down, leaving no sufficient algae pasture there for larger animals, which were then forced to feed in the lower intertidal, where wave action was much stronger (for details on foraging options, see Wikelski and Trillmich 1994).

The absolute amount of food intake (dry mass of algae per day) was lower for small than for large iguanas (Table 2). Also, the food intake per bite was less in small than in large iguanas. However, per unit body mass, large animals had lower food intake per bite than did small animals (Table 2). These results also held when we corrected for the lower mass-specific metabolic rate of small vs. large animals (we tested both the iguanid interspecific allometric exponent of 0.8 and the marine iguana intraspecific exponent of 0.97, which is ≈ 1.0 ; Nagy 1982, and Nagy and Shoemaker 1984, respectively). Higher vulnerability of larger sized individuals to decreased food abundance or quality is expected when food intake scales with body mass at a lower exponent than metabolic cost. This is because the efficiency of converting food into biomass is expected to decrease with increasing body mass during ontogeny (see Melton 1993). However, the food intake-body size relationship was not absolute; e.g., the smallest body length class of each island had a lower relative intake than the second smallest length class. One explanation is that the smallest marine iguanas were most sensitive to environmental conditions; e.g., high wave action forced them to feed in the uppermost intertidal areas that provide the lowest food supply (Wikelski and Trillmich 1994). The two islands also differed markedly in intake-per-bite per metabolic gram of body mass: Santa Fe iguanas had values about five times higher than Genovesa iguanas (Table 2), corresponding to the about fivefold higher standing algal biomass on Santa Fe.

Comparison with other grazers

Theoretical considerations (Clutton-Brock and Harvey 1983) and simulation models (Illius and Gordon 1987) have shown that, in general, sward length can determine the body size of grazing animals. Small animals within a specific guild (e.g., pasture grazers) are usually able to live on shorter swards than large animals. This comparison holds both within a species (e.g., in sheep; Allden and Wittaker 1970) and between species (e.g., among ungulates; Jarman and Sinclair 1979). In both cases, larger group members are forced to switch to less preferred habitats. In sexually dimorphic species, males are usually excluded from mutually preferred swards (Illius and Gordon 1987). In ungulates, e.g., within antelope guilds, the larger species are forced out of preferred areas, a phenomenon known as "grazing succession" (Jarman and Sinclair 1979). This parallels the situation in marine iguanas, in which large individuals were forced to forage in the cold, wave-washed lower intertidal, and the even larger males had to dive for food (Darwin 1883).

In several species of grazing mammals, individuals with high energy demands (such as lactating females) can compensate for short sward height by increasing the number of bites they take per day (>47 000 bites/d in sheep, Milne et al. 1981; >29 000 bites/d in red deer hinds, Loudon et al. 1984). This was not possible in marine iguanas, because foraging time per day was limited (for ruminants, see Hodgson 1985). In summary, marine iguanas resemble grazing ruminants in their feeding and food intake pattern, as well as in their intraspecific "grazing succession", except for their stricter time limitation.

Energy comparison between food intake and metabolism

Per metabolic gram of body mass, large animals gained less food per bite than did their small conspecifics (Table 2). To compare the mean slopes of food intake and energy expenditure (FMR; Nagy and Shoemaker 1984; Fig. 1) as a function of body mass, we calculated the power regressions of body mass (before stomach flushing) against food intake. On both islands, food intake (in dry mass of stomach contents) increased with approximately the 0.3 power of body mass (although the model was not significant for the El Niño season on Genovesa). This result followed predictions of Clutton-Brock and Harvey (1983), who argued that bite size is determined by the morphology of the mouth, which scales with an exponent of 0.33 to body mass. To estimate whether energy supply was, in fact, limited, we compared the field metabolic rate (FMR) measured by Nagy and Shoemaker (1984) with our results on energy intake (Fig. 5). This can only be an approximation, because we compared intake data from Genovesa and Santa Fe to FMR data from Fernandina island, which is more productive and where measurements were made in June, during the height of the cold season. Preliminary data (J. Drent, W. van Markenlichtentbelt, and M. Wikelski, *unpublished data*) suggest that marine iguanas show seasonal differences in energy expenditure due to seasonal differences in body temperature. This result is similar to data on *Lacerta* lizards (Rismiller and Heldmaier 1988, 1991), but contrasts with data on green iguanas (Markenlichtentbelt et al. 1993). Additionally, the largest iguanas of each population do not feed every day. Thus, our energy intake estimates for those groups will probably be too high.

Keeping these problems in mind, we found that FMR increased more steeply with body mass than did food intake (general exponent of energy expenditure is 0.8, Nagy 1982; intraspecific exponent of energy expenditure in marine iguanas is 0.97, Nagy and Shoemaker 1984; food intake exponent is 0.26 on Santa Fe and 0.30 on Genovesa). This resulted in an energy surplus in small iguanas of each island, whereas large iguanas suffered an energy deficit, at least during the time we studied them (mostly the warm season). Consequently,

at least on Genovesa, there was year-round mortality, mostly of large iguanas (Wikelski and Trillmich 1997). Furthermore, the energy balance became negative at smaller body masses (and lengths) during the El Niño year, for each island (see the crossing of metabolizable energy and FMR regressions in Fig. 5). It is very interesting to note that there was no statistically significant difference in the slopes of food intake against body length between islands and years. Consequently, the differences in metabolizable energy among islands and years are attributable to differences in y -intercepts. This result is compatible with the hypothesis that the differences in body size arose from a "Type 1 alloenergetic change" in the allometry of energy intake with size (Melton 1993). The latter could be either environmental or genetic in origin, or both, but we are presently unable to evaluate these possibilities.

The differences between measured and calculated values of energy balance are considerable, but show the relations that we expected from purely food-based considerations. Deviations are likely, due to inadequacies in the methods of measuring metabolizable energy (energy intake from stomach flushing, digestive efficiencies from Mn^{2+} determinations and feeding trials; Wikelski et al. 1993) and to the fact that FMR was measured on another island with a different temperature regime (W. D. van Markenlichtentbelt, *personal communication*). Furthermore, we have calculated energy values on the basis of body mass and not of body length (SVL). The latter might have been the more appropriate way of measuring body size under the prevailing, variable conditions, under which body masses at a given body length changed considerably. However, because SVL measures for FMR are not given in Nagy and Shoemaker (1984), this is the best comparison we can presently make.

Physiological performance: growth rates

Small iguanas can use the net surplus energy (above FMR) for growth or fattening. Laurie and Brown (1990b; Fig. 7) predicted how marine iguanas should allocate the surplus energy between growth and fattening to reach the optimal life history trajectory (compare also Naganuma and Roughgarden 1990). Large iguanas, suffering energy deficits, experience mass losses and, finally, higher mortalities than do small conspecifics of a given island (Wikelski 1994). Figures 6 and 7 demonstrate which part of the population would actually be affected by food shortages during bad conditions. The comparison of energy intake and FMR can also explain why growth is different between islands for iguanas of a given body length (Fig. 8). Animals on Genovesa had a lower net surplus energy, or "production power" (Brown et al. 1993, Melton 1993), than those of the same body length on Santa Fe (Fig. 5; Huey 1991). Thus, a Genovesa iguana has less net production energy than a Santa Fe iguana of similar size. Again, this could be a consequence of "alloenergetic"

differences between the two island populations (Melton 1993).

The lower growth rates of females compared to males could be explained by sex-specific life history tactics (Wikelski and Trillmich 1997). Females mature much earlier than males and allocate most surplus resources to egg production, rather than to growth, after reaching the threshold size for reproduction at the age of ≈ 3 –5 years (Laurie 1990; see also Reiss 1989). At that size, males continue to grow for several more years before they also begin to participate seriously in reproduction (Trillmich 1983, Wikelski and Bäurle 1996, Wikelski et al. 1996). Concentrating solely on energy intake, FMR relations oversimplify the picture; many other factors may also influence growth in reptiles, particularly temperature (Andrews 1982, Sinervo and Huey 1990). Nevertheless, the scenario presented here, based exclusively on foraging energy, apparently captures the major aspects of the situation correctly. This implies that food supply is one of the major factors selecting for body size (Wikelski and Trillmich 1997).

Phenotypic plasticity or evolution of body size?

When we find differences in body size between populations, can they be interpreted as the result of evolutionary changes, or can they be explained by phenotypic plasticity? Marine iguanas of the two study populations showed no differences in life history parameters and maturation (Laurie and Brown 1990a, Wikelski 1994), contrary to, e.g., salamander populations of different body size (Bruce and Hairston 1990). Thus, one could argue that a lower food supply sufficiently accounts for the smaller body size of Genovesa marine iguanas. We cannot exclude this possibility at present. However, both a natural and a human-induced experiment with Santa Cruz Island marine iguanas make a purely phenotypic determination of body size unlikely. Marine iguanas growing up on a rocky islet (Caamano Islet) 800 m off the coast of Santa Cruz reach a maximum mass of ≈ 2.5 kg (Trillmich 1983). Iguanas that leave the crowded Caamano islet to feed on Santa Cruz, where introduced cats keep iguana densities low and, thus, food supply high (Kruuk and Snell 1981, Cayot et al. 1994), grow to more than double the sizes they would reach on their home islet (Trillmich 1983). This size still falls twofold short of the sizes reached by iguanas from Isabela Island, where maximum body mass values of up to 12 kg have been recorded (W. A. Laurie, *personal communication*). However, at present, we cannot quantitatively compare the density of marine iguana populations or the productivity of algae between Santa Cruz and Isabela Islands.

Evidence for an upper threshold body size for Santa Cruz marine iguanas comes also from a feeding experiment by Karl Angermeyer, a German settler who fed iguanas regularly for >20 years. Even his largest animals, which are genetically identical to the Caamano iguanas previously mentioned (Patton 1984), did not

grow larger than 6 kg. His iguanas also could not be induced to grow any further, even by a 6-mo feeding pulse (huge amounts of cooked rice; M. Wikelski, *unpublished data*). Therefore, it might be argued that the different body sizes of marine iguana island populations are not sufficiently explained by pure phenotypic plasticity. However, we do not know whether the 6-mo feeding pulse was long enough to detect differences in marine iguana growth. On the other hand, migration of males among islands (Rassmann 1996) may maintain enough gene flow among populations to make local adaptations of body size impossible. Only a common garden experiment, in which hatchlings from different islands grow up under identical conditions, could distinguish whether, and to what degree, growth strategies are genetically determined. Such an experiment could resolve the question of phenotypic and genetic influences on body size of marine iguanas, but is presently not possible, due to National Park regulations.

This study has shown the importance of food for body size, building on the approach of Dunham (1978), Roughgarden and Fuentes (1977), and Congdon (1989). Galapagos marine iguanas enable us to quantify the way in which food supply determines maximum body size of island reptiles. We could not determine the relative contributions of genetic factors vs. food (and biophysical influences) on differences in body size (see Sinervo and Huey 1990, Niewiarowski and Roosenburg 1993).

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