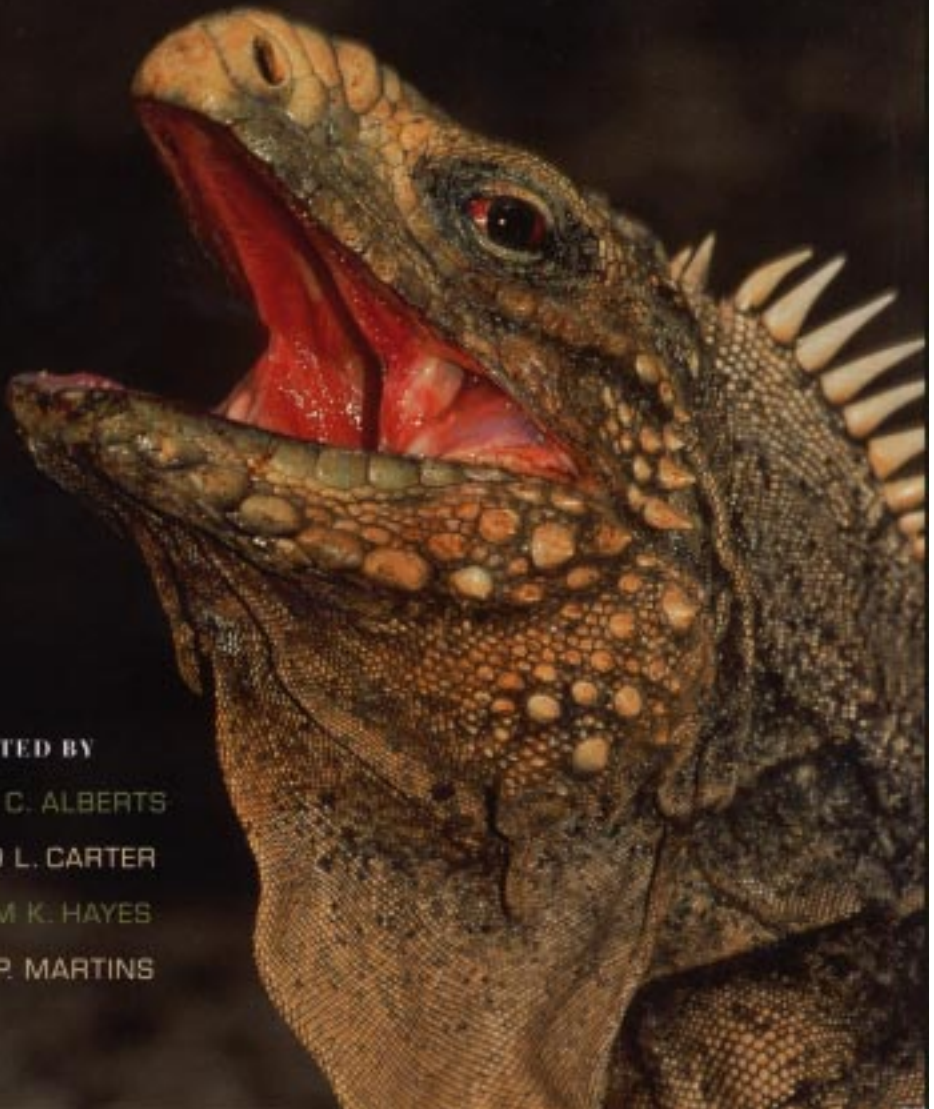


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Environmental Scaling of Body Size in Island Populations of Galápagos Marine Iguanas

Martin Wikelski and Chris Carbone

IF WE WANT TO UNDERSTAND the striking patterns in body sizes seen in populations and communities of animals, we need to understand the key factors that influence body size (Blackburn et al., 1993; Brown et al., 1993; Melton, 1993; Cates and Gittleman, 1997; Kozłowski and Weiner, 1997; West et al., 1997; Perrin, 1998; Carbone et al., 1999). This is a challenging task, however, because size is linked to many other traits and is subject to a wide variety of selection pressures (Cluttonbrock and Harvey, 1983; Schmidt-Nielsen, 1984). Several approaches have been proposed to quantify body sizes within and across species. Brown et al. (1993) and Melton (1993) assume that resource acquisition and conversion are limited and use this to predict body size. However, without a mechanistic understanding of the scaling laws involved, we cannot yet predict maximum body sizes found among species (Kozłowski and Weiner, 1997; West et al., 1997). Another approach is to examine factors that influence body size within species (Naganuma and Roughgarden, 1990). Conclusions obtained from these studies are hampered by the variety of factors influencing body size in most systems, particularly the effects of preda-

tion and interspecific competition (Dunham, 1978; Dial and Roughgarden, 1995; Petren and Case, 1997).

Marine iguanas provide an ideal species in which to examine environmental determinants of body size (Wikelski and Thom, 2000). They have no competitors and predation affects only the smallest size classes and nesting females and inhabitants on some islands. Marine iguanas have a unique foraging ecology, with daily foraging trips between warming and feeding sites spanning extreme environmental temperatures (Trillmich and Trillmich, 1986). Thus, maximizing average body temperature appears crucial to efficient energy acquisition and assimilation for this species (Wikelski et al., 1993; Wikelski and Trillmich, 1994; Wikelski and Wrege, 2000). In addition, marine iguana feeding ecology is well understood as a result of long-term projects conducted on two island populations (Wikelski and Trillmich, 1997; Wikelski et al., 1997). Each island has different environmental characteristics (Houvenaghel, 1978), allowing an unusual opportunity to examine directly the effects of environment on body size. Because marine iguanas are ectotherms, both resource acquisition

and utilization are strongly and directly influenced by environmental factors (Huey and Kingsolver, 1989).

In this chapter, we develop a mechanistic model to predict how key environmental parameters affect net rates of energy assimilation (Illius and Gordon, 1992). This analysis relies on both originally collected data and calculations based on previously published work (Wikelski et al., 1993, 1997; Wikelski and Trillmich, 1994, 1997). We mainly focus on two island populations from Santa Fé and Genovesa, but results from three additional island populations are also examined. Our analysis focuses on the large males of each island, which appear to be the most energetically constrained (Wikelski and Trillmich, 1997).

METHODS AND BACKGROUND

NATURAL HISTORY

Marine iguanas feed exclusively on macrophytic marine algae in the mostly cool waters (13–25 °C) of the Galápagos Archipelago. The foraging activities of intertidally foraging iguanas are limited to two hours around low tide (Trillmich and Trillmich, 1986; Wikelski and Hau, 1995). The time of this foraging window advances every day by approximately one hour, thus leaving little time for warming up before foraging if this window occurs in the early morning or for overnight digestion if it occurs in the late afternoon. Large-bodied animals on each island can also dive for submerged algae pastures, which they do independently of the tidal cycle (subtidal feeding; Trillmich and Trillmich, 1986; Wikelski and Trillmich, 1994). Sexual size dimorphism is pronounced, with the largest males about twice as heavy as females on a given island. Previous research on marine iguanas found that the largest size classes suffered higher mortality during periods of food shortage and severe weather and this was not simply due to age (Laurie and Brown, 1990b; Wikelski and Trillmich, 1997). The higher mortality rate is particularly interesting, because the largest individuals on Santa Fé were more than three times heavier than those

on Genovesa. This suggests that environmental conditions on each island lead to different maximum body sizes.

BASELINE DATA

Most of our data were obtained from Santa Fé (90°02' W, 0°50' S; 1988–94) and Genovesa (89°59' W, 0°19' N; 1991–94) islands, with maximum adult body sizes of 2900 g and 900 g, respectively. Additionally, we compare the results of the present study with data from North Seymour Island (90°18' W, 0°24' S; Wikelski and Wrege, 2000), Fernandina Island (91°27' W, 0°16' S; Trillmich and Trillmich, 1986), and Isabela Island (Caleta Iguana, 91°26' W, 0°48' S; M. Wikelski, pers. obs.).

Climate conditions on Genovesa and Santa Fé (wind speed, cloud cover, shaded air temperature, standard operative temperature [Bakken, 1992], and sea surface temperature) were monitored three times per day (at 0600, 1200, 1700) from November to March, 1991–92 and 1992–93 (Wikelski and Trillmich, 1994; Wikelski et al., 1996). This information was correlated with warm-up and cool-down rates of marine iguanas during the course of the study. Additionally, we collected average temperature data from Santa Fé, Genovesa, Fernandina, and Seymour islands. We refer to this temperature as (average) operative temperature. To measure this, we set out automatic temperature-recording data loggers at coastal areas where marine iguanas usually form large aggregations. Measurement devices consisted of recorders (Hobo, range –39 to 122 °C, accuracy ±0.3 °C; Onset Inc., Pocasset, Massachusetts) that were enclosed in a black hard-plastic housing (Hobo SubCase). These temperature data, collected in a standard manner on all four islands, were used to calculate differences between islands in mean ambient temperature.

Iguanas were captured, weighed, measured, and marked with synthetic paint before release (Laurie, 1989). Marked individuals were followed for up to eight weeks and observed with binoculars from prominent rocks. We implanted temperature sensitive radiotransmitters in thirty-

five marine iguanas of different body sizes on Genovesa ($n = 26$; body mass range, 140–855 g) and Santa Fé ($n = 9$; body mass range, 240–1900 g; for implantation methods, see Wikelski and Trillmich [1994]). The total number of bites made during feeding bouts was counted (Wikelski and Trillmich, 1994). Body temperature (T_b) was recorded on Santa Fé over a fourteen-day period in March 1993, and on Genovesa for a similar period in January and February 1992 and 1993. Using this data set, bite rate could be related to T_b of individual iguanas in real time. Maximum bite rate was defined as the number of bites per time interval (minimum: more than ten bites) in which an iguana could feed undisturbed (e.g., from wave action). We could not relate underwater bite rate to T_b directly, but extensive snorkeling observations indicated that underwater bite rates were indistinguishable from intertidal bite rates (unpubl. data).

Additionally, we measured T_b by inserting quick response thermoprobes deep into the cloaca of iguanas (Wikelski and Trillmich, 1994). Warm-up and cool-down rates of thirty-three iguanas on Genovesa ($n = 15$; body mass range, 150–820 g) and Santa Fé ($n = 18$; body mass range 160–3000 g) were measured. To measure T_b , the animals were held in position on the rocks or in the water until body temperature exceeded 37 °C or equalled water temperature, respectively. At the same time, we recorded the abovementioned environmental parameters. Such experimental warm-ups allowed us to measure accurately the effect of environmental conditions on body temperature.

The slopes ($\ln T_b$ change/minute) of warm-up curves were approximated with linear regressions between 23.5 and 36 °C (see Wikelski and Trillmich, 1994; r between 85 and 97%). Foraging activities of adult male marine iguanas during a fourteen-day tidal cycle were observed on Santa Fé ($n = 23$, during November, January, and March 1993) and Genovesa ($n = 15$, during December, February, and March 1993) to determine the proportion of days spent foraging in the subtidal versus the intertidal.

Our calculations of feeding performance are based on a net cumulative daily foraging time of thirty minutes in the intertidal and sixteen minutes in the subtidal; we had shown previously that one-half of the intertidal feeding time was interrupted by wave action (Wikelski and Trillmich, 1994). Algae pasture length was determined by visually estimating the length of algae blades. The accuracies achieved via this method were high (± 1 mm). The influence of algae blade length on bite size was calculated from previous results (Wikelski et al., 1997, figure 4). To calculate the total metabolizable energy intake per day, we multiplied the number of bites per day by the average food intake per bite. Bite rate was influenced by body temperature, but the relationship changed with time spent foraging in the intertidal and subtidal zone. We accounted for this change by using a bite rate function that was derived from empirical data (see the Results section). In our calculations, we used a digestive efficiency of 0.7 and a caloric content of algae based on Wikelski et al. (1993; 12.1 KJ on Santa Fé and 10.0 KJ on Genovesa). Daily intakes were summed over a fourteen-day period to determine the intake over one tidal cycle. We then related the total net energy intake to the metabolically active grams of body mass by using Nagy and Shoemaker's (1984) scaling of field metabolic rate against body mass (compare Christian et al., 1997).

Digestive efficiency was shown to be independent of gut filling (Nagy and Shoemaker, 1984; Wikelski et al., 1993). We determined digestive constraints by assuming that gut and intestine volume scale isometrically with body mass (Troyer, 1984b; Wikelski et al., unpubl. data) and that animals only foraged if there was sufficient amount of free stomach space to harbor the food intake of a day's foraging trip (Wikelski et al., 1993; Wikelski and Trillmich, 1994). Based on these assumptions, we calculated maximum achievable digestion during one tidal cycle for the three size categories on each island.

Nightly cool-down rates were based on previous estimates of T_b using T_b telemetry (Wikelski

and Trillmich, 1994). Cool-down rates were similar for adult iguanas of different body sizes and were largely dependent on the rock cooling rates where the animal was resting. Field metabolic rates of iguanas were calculated according to Nagy and Shoemaker (1984). The energy expenditure during foraging in the intertidal and the subtidal was the same for iguanas of different body sizes (Drent et al., 1999).

MODEL OUTLINE

Calculations are based on three size categories of adult male iguanas: small, medium, and large (Genovesa: 500 g, 700 g, and 900 g; Santa Fé: 1700 g, 2300 g, and 2900 g, respectively; figure 11.1). Our determination of these size classes was based on the survivorship analysis presented in Wikelski and Trillmich (1997, figures 3–7). The first size category corresponds to the smallest size identified for maximum body condition and high survival rates (Laurie and Brown, 1990b). The second and third size categories correspond to groups found to have declining and the lowest body conditions and consequently the lowest survival rates, respectively (figure 11.1).

To calculate maximally achievable T_b , we divided each day into fourteen intervals of fifty-one minutes, corresponding to the average daily advance of the time of low tide. We assumed that adult iguanas always tried to reach the highest possible T_b up to a maximum of 36 °C (after, e.g., Bartholomew and Lasiewski, 1965; Bartholomew, 1966; Wikelski and Trillmich, 1994) and were not limited by the availability of warm-up sites (Wikelski et al., 1996).

The daily cycle of an iguana was divided into four phases of T_b change: (1) warm-up before feeding, (2) cool-down during foraging, (3) warm-up after feeding, and (4) cool-down at night (figure 11.2). We based our calculation on food intake, assuming one feeding bout per day (Wikelski and Trillmich, 1994) in either the intertidal or subtidal (depending on which option provided the highest assimilated energy). Intertidal feeding was restricted to times around low

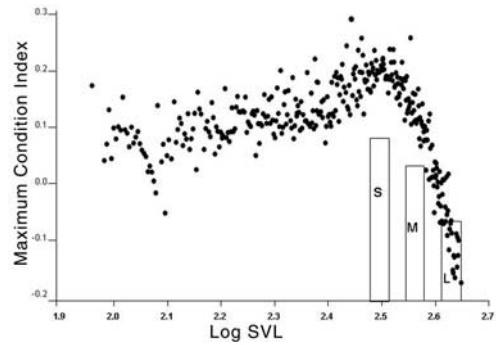


FIGURE 11.1. Maximum condition index for male marine iguanas on Santa Fé. Each point represents the maximum measured condition for each mm of snout-vent length (SVL). The condition index represents the residuals from a log-log regression of SVL against body mass for all iguanas on Santa Fé. Note that the maximum condition sharply decreases beyond $2.5 \ln(\text{SVL}) = 315 \text{ mm SVL}$. S = size category of small adult male in our analysis, M = medium, and L = large adult male category. Redrawn from Wikelski et al., 1997.

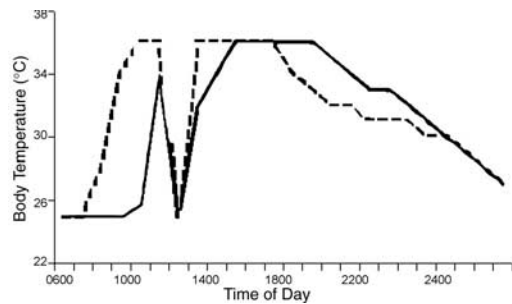


FIGURE 11.2. The temperature (T_b) profile over twenty-four hours resulting from the model analysis. T_b was low at night, increased to preferred values before foraging (here at 1130), dropped to ambient temperature during foraging (1130–1221), increased again during postforaging thermoregulation (after 1221), and finally decreased in the afternoon and during the night (after about 1600). This example is based on small (1700 g; dashed line) and large (2900 g; solid line) iguanas from Santa Fé.

tide, whereas subtidal feeding was timed to coincide with the highest rock temperatures each day; that is, shortly after midday (Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994). Iguanas of different sizes had equal access to algae pastures.

In marine iguanas, rate of digestion is related to body temperature with a metabolic quotient (Q_{10}) of 2.5, based on experimental changes of T_b of eight individuals (Wikelski et

al., 1993). Thus, an increase in mean T_b of 10 °C decreased mean gut passage time by a factor of 2.5 (see also Troyer, 1984b; Zimmermann and Tracy, 1989). We set digestion at 100% at the maximum T_b of 36 °C. For each fifty-one minute interval, we then determined the percentage of digestion (relative to maximum) following the logarithmic regression:

$$\text{Percentage maximum digestion} = 3.6933e^{(0.0916T_b)} \quad (1)$$

($r^2 = 1$; Wikelski et al., 1993).

RESULTS

Santa Fé showed greater extremes in operative temperatures than did Genovesa. The former was exposed to the cold southwestern ocean currents, but had higher maximum and minimum shaded air temperatures, as well as standard operative temperatures (table 11.1). We measured the warm-up rates of thirty-three iguanas on two islands under different environmental conditions. These data were used to calculate the overall average slope for marine iguana warm-up rates according to the following multiple regression:

$$\ln(T_b/dt) = A_0 + A_1T_R + A_2C + A_3M_B + A_4T_C \quad (2)$$

where t is in minutes, $A_0 = -0.56 \pm 0.2$, $A_1 = 0.01 \pm 0.001$, $A_2 = 0.07 \pm 0.04$, $A_3 = -0.00038 \pm 0.00002$, $A_4 = 0.16 \pm 0.05$, T_R is the rock temperature in the sun, measured to the nearest 0.5 °C, C is the estimated cloud cover (defined as 0 for 0–4 eighths [sunny]; 1 for 5–8 eighths [cloudy]), M_B is the body mass in grams; and T_C is a daytime code (defined as 1 for time intervals 0600–1000 and 1500–1800; 2 for 1000–1500), which takes into account diurnal changes in humidity and other variables ($n_{\text{total}} = 33$; $n_{\text{Santa Fé}} = 18$, $n_{\text{Genovesa}} = 15$; $F_{4,33} = 12.2$, $P < 0.001$, $r^2 = 0.63$). We did not include “island” as a variable in the multiple regression, because we aimed at a general warm-up model, to allow us to extrapolate our results to other islands.

COOL-DOWN AND INTAKE RATES

Maximum bite rate depends strongly on T_b :

$$B_{\text{max}}(T_b) = 4.02T_b - 56.82,$$

where B is the maximum bite rate ($n = 35$, $r^2 = 0.85$, $P < 0.001$; figure 11.3). To estimate the total number of bites per foraging bout, we determined how T_b decreased with foraging time (t). We used the following equation to represent the relationship between T_b and t :

$$T_b(t) = (T_0 - T_{ss})e^{ct} + T_{ss}, \quad (3)$$

where T_0 is the initial body temperature, T_{ss} is the sea surface temperature and c is a negative variable that scales the rate of heat loss to the water and is dependent on body mass in grams (M_B). We estimated values of c from the log relationship of T_b and underwater time for different sized iguanas (M_B range 150–3000 g):

$$\ln(T_b(t) - T_{ss}) = \ln(T_0 - T_{ss}) + ct. \quad (4)$$

The variable c was found to be correlated with $\ln(M_B)$:

$$c = 0.0312 \times \ln(M_B) - 0.3222$$

($r = 0.61$, $n = 33$, $P = 0.0001$). This equation was used to provide average values of c for a given body mass. Combining equations 2 and 4, we arrived at the following equation for bite rate as a function of body temperature:

$$B(T_b) = 4.02[(T_0 - T_{ss})e^{ct} + T_{ss}] - 56.82. \quad (5)$$

We integrated $B(T_b)$ with respect to time t underwater during the foraging bout to determine the total number of bites obtained:

$$B(T_b(t))dt = (4.05/c)(T_0 - T_{ss})(e^{ct} - 1) + (4.02T_{ss} - 56.82)t. \quad (6)$$

METABOLIZABLE ENERGY INTAKE

The mean fourteen-day T_b of the largest males on Santa Fé and Genovesa was 1.2 and 1.0 °C,

TABLE 11.1
Comparison of Mean Environmental Parameters on the Islands of Santa Fé and Genovesa, Galápagos

VARIABLE	SANTA FÉ		GENOVESA	
	1991/92	1992/93	1991/92	1992/93
Shaded air temperature (12 h) ¹	29.8 ± 2.3 (117)	27.8 ± 3.2 (144)	29.2 ± 3.1 (111)	27.1 ± 2.5 (95)
Cloud cover (1/8) ²	5.0 ± 2.6 (118)	4.5 ± 2.5 (146)	4.0 ± 2.4 (124)	3.8 ± 2.8 (100)
Sea surface temperature (°C) ³	25.3 ± 1.8 (119)	23.5 ± 2.1 (154)	27.3 ± 1.7 (109)	25.6 ± 1.5 (92)
Wind speed (relative values) ⁴	1.5 ± 0.6 (117)	1.5 ± 0.6 (145)	0.8 ± 0.5 (124)	1.5 ± 0.8 (98)
Minimum shaded air temperature ⁵	24.9 ± 1.5 (83)	23.3 ± 2.3 (149)	23.2 ± 1.4 (97)	—
Maximum shaded air temperature ⁶	31.1 ± 2.4 (83)	30.8 ± 4.4 (149)	29.4 ± 2.8 (96)	—
Wave activity (relative scale) ⁷	1.9 ± 0.7 (118)	2.1 ± 0.7 (145)	0.9 ± 0.6 (127)	1.2 ± 0.7 (102)

Notes: Mean values ± standard deviations are given. The number of days represented by the sample is indicated in parentheses; — indicates data not available.

¹ Results of ANCOVA comparisons between islands and years: $F = 22.3$, $P < 0.001$.

² $F = 5.0$, $P < 0.01$.

³ $F = 94.9$, $P < 0.001$.

⁴ $F = 48.1$, $P < 0.001$.

⁵ $F = 21.23$, $P < 0.001$.

⁶ $F = 6.0$, $P < 0.01$.

⁷ $F = 84.3$, $P < 0.001$.

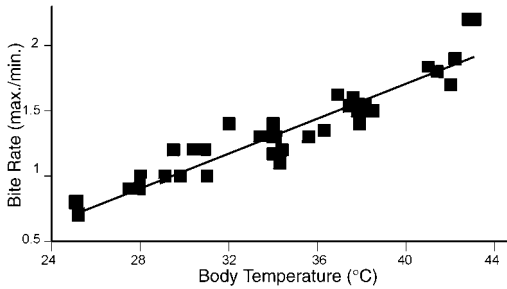


FIGURE 11.3. The maximum bite rate of marine iguanas during daily foraging trips increased linearly with increasing body temperature. Thus, foraging performance was higher at higher body temperatures.

respectively—lower than that of small adult males (table 11.2). In contrast, there were hardly any differences in body temperatures between iguanas of the same size classes between islands: the values for the mean fourteen-day T_b differed by only 0.3 and 0.02 °C for the largest and smallest males, respectively, on both islands. As a consequence of lower T_b , the intake of the large-size class (expressed as maximum energy intake per metabolic gram of body mass) was approximately 25% lower than that of the small-size class. Another consequence of a lower T_b was that the rate of digestion in the largest males was about 10% less than that of small adults. Medium-sized adult males showed intermediate values. The maximum assimilated energy for small adults in Santa Fé was 30% higher than the field metabolic rate (FMR). However, under the same conditions, the largest iguanas of Santa Fé reached maximum intake only 5% higher than FMR.

CHOICE OF FORAGE HABITAT

We assumed that the choice of foraging site (intertidal or subtidal) was determined by which site provided the highest food intake per day. The timing of intertidal foraging is set by the tides, and advances every day by about fifty minutes. Furthermore, iguanas dive for algae during the hot midday hours only (Buttemer and Dawson, 1994). This results in a food intake trade-off between intertidal and subtidal foraging: iguanas forage for less time by diving because of

the midday constraint, but can achieve high body temperatures for fast bite rates at midday. Intertidal foraging, on the other hand, allows for longer foraging times, but only permits low foraging or digestive performance when low tides are in the early morning or late afternoon, respectively (Wikelski et al., 1993).

Our results show that the largest individuals should feed exclusively in the subtidal when operative temperatures fall below about 25 °C (figure 11.4A). Above this temperature, the largest animals should employ a mixed strategy and forage both in the subtidal and the intertidal. We predict that smaller adults forage less by diving compared with the larger animals (figure 11.4B). The observed pattern in the percentage use of the subtidal (figure 11.4B) was qualitatively similar to the predicted pattern. However, at low average operative temperatures, the patterns differed somewhat between islands (approximately 50% use of subtidal on Santa Fé; 90% on Genovesa). Nevertheless, the qualitative decline in subtidal use with increase in temperature was as predicted.

MAXIMUM BODY SIZE

Our analysis enables us to examine the effects of variation in environmental parameters—average temperatures and algae sward height—to predict the maximum body mass on different islands (figure 11.5). The following three predictions can be drawn from this analysis:

1. Small animals can survive over a larger range of environmental conditions than can large animals. For example, a 2000-g iguana can survive environments with average temperatures down to 24.5 °C and 2.5 mm algae pasture height, whereas a 4000-g iguana can only survive conditions down to 26.7 °C and 4.5 mm algae pasture height before it experiences digestive constraints.
2. At high operative temperatures, the only model parameter that affected maximum permissible body size in marine iguanas was the height of the algae pasture (hori-

TABLE 11.2
Cumulative Performance over One Tidal Cycle of Marine Iguanas of Three Size Categories on Santa Fé and Genovesa

	SANTA FÉ			GENOVESA		
	SMALL	MEDIUM	LARGE	SMALL	MEDIUM	LARGE
Bites (<i>n</i>) intertidal	9880	9162	7294	20,228	13,730	6200
Bites (<i>n</i>) subtidal (diving)	3560	4580	6566	0	6910	13,960
Intake (g algae dry mass/g ^{0.8}) ¹	0.58	0.51	0.44	0.51	0.43	0.39
Intake (% of small adults)	100%	87%	75%	100%	83%	77%
<i>T_b</i> (mean) day	32.0	31.0	30.1	31.5	31.0	30.8
<i>T_b</i> (mean) night	29.3	28.9	28.7	29.3	28.4	28.0
<i>T_b</i> (mean)	30.7	29.9	29.4	30.4	29.7	29.4
Digestion (% of total)	67%	63%	60%	65.1	61.1	59.7
Digestion (% of small adults)	100%	94%	89%	100%	94%	92%
Total metabolizable energy intake (KJ)	1892	2096	2125	733	802	904
FMR (KJ)	1409 ²	1730 ²	2026 ²	458 ³	636 ³	811 ³

Notes: One tidal cycle = fourteen days. The data represent model predictions calculated for a high operative temperature (mean temperature = 33 °C). Intake (g) and FMR (KJ) were determined in prior work. Note that although mean *T_b* is only about 1–2 °C lower in large versus small animals, food intake in large animals is substantially reduced. The high temperature option shown here is a conservative estimate for differences between large and small animals.

¹Wikelski et al. (1997).

²According to Nagy and Shoemaker (1984): $KJ/d = 0.64 \times \text{body mass}^{0.68}$ for marine iguanas beyond 1000 g body mass.

³According to Nagy and Shoemaker (1984): $KJ/d = 0.079 \times \text{body mass}^{0.97}$ for marine iguanas below 1000 g body mass.

zontal contour lines in figure 11.5). However, at successively lower operative temperatures, temperature increasingly contributed to limiting the body size of an animal (i.e., the slope of the maximum body size landscape tilts upward with decreasing temperature).

3. The digestion of large animals is much more constrained than that of small animals. This is largely because large iguanas have a high thermal inertia and thus cannot rewarm quickly before and after a foraging bout.

The above quantitative predictions for maximum body size closely match the body sizes observed in different populations of marine iguanas in the Galápagos archipelago (figure 11.5). One

exception to our predictions was North Seymour Island. Most iguanas in this population have a maximum body mass of around 2000 g (Wikelski and Trillmich, 1997), which corresponds well with our prediction (figure 11.5). However, several individuals on North Seymour supplemented their energy supply with the succulent beach plant *Batis maritima*, and these individuals reached body masses of greater than 3000 g (Wikelski and Wrege, 2000).

DISCUSSION

In this chapter, we develop a mechanistic model to describe feeding performance in marine iguanas during different stages of a fourteen-day feeding cycle. This model is based both on original data and extensive previous research

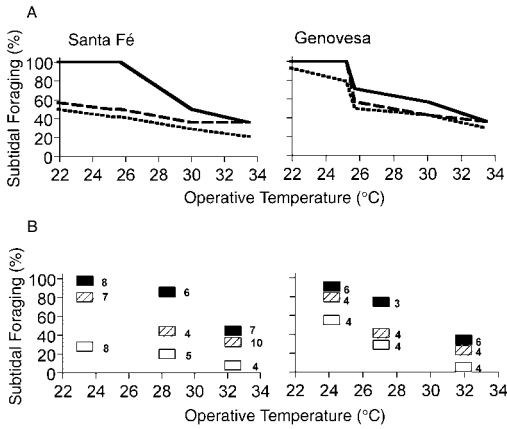


FIGURE 11.4. Percentage of subtidal foraging over the fourteen-day tidal cycle, plotted against operative temperatures on two islands. (A) Our model predicts that large animals (continuous line) forage more in the subtidal (by diving) than medium (dashed line) or small adults (dotted line). Foraging in the intertidal is facilitated by high temperatures because animals are capable of warming up sufficiently to feed before low tide. Note that predicted patterns of diving are qualitatively very similar between islands, although the body masses differ widely. (B) Observed percentage of subtidal foraging versus average operative temperature. Squares represent fourteen-day means of repeated observations for the largest (filled), medium (dashed), and smallest adult males (open). Numbers beside the squares indicate sample size of individual iguanas.

(Wikelski et al., 1993; Wikelski and Trillmich, 1994, 1997; Wikelski et al., 1997; Wikelski and Wrege, 2000). We identify warming rate as a key factor influencing foraging efficiency in this species. Marine iguanas are subject to extreme environmental temperature changes over their foraging cycle, and warming rates are key to efficient foraging and digestion.

Our results provide evidence for what we have termed the “environmental scaling” of body size in this species, wherein environmental factors, such as temperature, directly determine maximum body size of populations. We are able to use our mechanistic model to predict average feeding performance under a range of environmental conditions (Porter and Tracy, 1983; Dreisig, 1985). From this data set, we further predict the maximum achievable body mass for different algae pasture heights and operative temperatures. The predictions of the model also hold for other island populations. Based on this

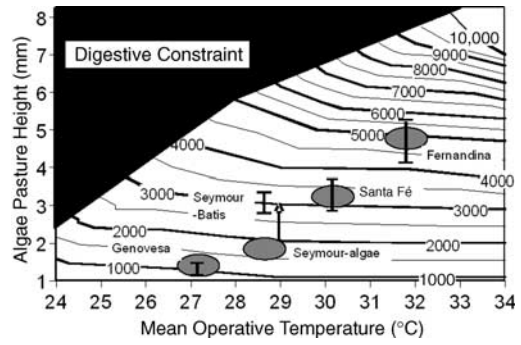


FIGURE 11.5. Maximum body mass in marine iguanas in relation to two environmental parameters—average annual operative temperature and algae pasture height. The black ovals circumscribe the predicted body sizes in grams and actual environmental conditions of the iguana populations on Genovesa, Santa Fé, Seymour Norte (“algae” = iguanas not feeding on land plants; “Batis” = iguanas that feed on land plants), Fernandina, and Isabela. The arrow depicts the situation on North Seymour, where some individuals increase their body mass by feeding additionally on land plants. Note that small animals can sustain a wider range of algae pasture heights and operative temperatures, digestive constraints are particularly strong for large animals, and temperature per se exerts a larger influence on body mass at lower temperatures (i.e., surface lines of maximum body mass tilt upward with decreasing T_b). Numbers on contour lines indicate maximum body mass (g).

analysis, we conclude that body size in Galápagos marine iguanas appears to be directly constrained by the rate of resource acquisition and resource conversion, and that these are related to a few key environmental parameters: air temperature and algae pasture height. Because predation and interspecific competition are largely absent, this study is unique: the factors of predation and competition usually confound evolutionary and ecological analyses of body sizes.

Our model produced important general predictions for environmental influences on body size. First, body size was found to influence individual tolerance to the range of environmental conditions experienced by this species (i.e., small individuals can still remain in positive energy balance under cooler air temperatures compared with large individuals). Second, different physiological or ecological processes, and combinations thereof, constrain animal body size under different environmental conditions.

Thus, the factors that directly constrain body size may be different in different environmental settings. For example, pasture height is important at high air temperatures, but not at low temperatures. This is because digestion constrains body size at low temperatures, whereas foraging efficiency constrains body size at high temperatures.

Our model also enables us to predict the range of environmental conditions over which iguanas survive (Naganuma and Roughgarden, 1990; Adolph and Porter, 1993; Sinervo and Adolph, 1994). The analysis in figure 11.5 suggests that marine iguanas would not survive at low algae pasture height or at average operative temperatures below 24 °C. This may explain why the distribution of this species is limited to the Galápagos archipelago. Other islands in the tropical Pacific are not exposed to upwellings and the nutrient-rich water that feed the algae pastures. However, nutrient-rich islands such as the Easter Islands (109°30' W, 28°10' S) (mean annual temperature, 22 °C; Fiji Times, 1995) would be too cold to allow for adequate digestion. There exist, however, areas along the coast of South America that exhibit the conditions required to support marine iguanas. However, in these areas, predation pressure would likely limit iguana distribution. This situation is similar to the present-day distribution of marine iguanas on western Isabela Island, where vertebrate predators (cats and dogs) are efficiently decimating marine iguanas to the point that their long-term persistence is in danger (Kruuk and Snell, 1981).

Our model can help us to understand general constraints on body size; it supports the

notion that energy relationships directly limit body size (Cates and Gittleman, 1997; Kozlowski and Weiner, 1997; West et al., 1997; Perrin, 1998; Carbone et al., 1999; see also Lundberg and Persson, 1993; McWilliams et al., 1997). Because our model is simple, it enables us to predict body size from environmental parameters that are easy to quantify: temperature and food availability. This allows a robust demonstration that body size is indeed constrained by both resource acquisition and conversion, and thus empirically supports the largely untested optimal body-size models (Brown et al., 1993; Melton, 1993).

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