Oecologia (2000) 124:107–115

Martin Wikelski · Peter H. Wrege

Niche expansion, body size, and survival in Galápagos marine iguanas

Received: 26 January 1999 / Accepted: 5 January 2000

Abstract Foraging theory predicts that dietary niche breadth should expand as resource availability decreases. However, Galápagos marine iguanas often die during algae shortages (El Niños) although land plants abound where they rest and reproduce. On Seymour Norte island, a subpopulation of iguanas exhibited unique foraging behavior: they consistently included the succulent beach plant *B. maritima* in their diet. We investigated the consequences of land-plant feeding for body size and survival. *Batis*-eaters supplemented their algae diet both before and after intertidal zone foraging, and more *Batis* was eaten during tides unfavorable for intertidal zone foraging (dawn and dusk). Larger, energy-constrained iguanas fed more on land than did smaller animals. Compared to intertidal zone algae, *Batis* was 39% lower in caloric content (1.6 vs. 2.6 kcal g^{-1} dry mass), 56% lower in protein (8.3 vs. 18.9% dry mass) and 57% lower in nitrogen (1.3 vs. 3.0% dry mass). In spite of its lower nutrient value, iguanas that supplemented their diet with this plant were able to attain nearly twice the body size of other iguanas on the island. Age estimates indicate that many *Batis*-eaters survived repeated El Niño episodes during which animals of their relative size-class experienced high mortality on other islands. The larger animals were, however, completely dependent upon this supplementary source of food to maintain condition, and all perished in the 1997–1998 El Niño when high tides inundated and killed *Batis* on Seymour Norte Island. We hypothesize that *Batis* feeding developed as a local foraging tradition, and that dietary conservatism and strong foraging site fidelity explain why the inclusion of land plants in the diet has been observed in only a single population. Ultimately, a unique algae-adapted hindgut morphology and physiology may limit a switch from marine to terrestrial diet.

Key words Niche expansion · Body size · Reptiles · Herbivory · Survival

Introduction

Foraging theory predicts that dietary niche breadth should expand as resource availability decreases (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971; Stephens and Krebs 1986; Pianka 1994). When food is scarce, consumers cannot afford to bypass inferior food items and are expected to broaden their diet to include less preferred and/or novel food items (Feinsinger and Swarm 1982; Schluter 1982; Durtsche 1992; Nogales and Hernandez 1994; Lima and Magnusson 1998). However, many animals do not follow these theoretical predictions and may die before any diet adjustment occurs (e.g. Jarman and Sinclair 1979).

This is true for Galápagos marine iguanas (*Amblyrhynchus cristatus*), which are among the most specialized of vertebrate herbivores. These 1- to 10-kg animals feed almost exclusively on intertidal zone and subtidal macrophytic algae (Darwin 1883; Dawson et al. 1977; Trillmich and Trillmich 1986; Wikelski and Trillmich 1994). This feeding niche is particularly interesting because of its ephemeral nature. Marine iguanas in all but the largest size-classes are limited to feeding during the low tide, at most about 2 h per day (Wikelski and Hau 1995). This period is further shortened because the poikilotheric iguanas lose body heat in the cold ocean waters and must move to alternate micro-habitats where they can warm up (Buttemer and Dawson 1993). The largest animals can circumvent the time-of-day limitations to feeding because they are strong enough to dive in the subtidal region, feeding underwater. However even these animals are time-limited by rapid loss of body temperature. By modeling the bio-physical constraints

M. Wikelski (✉)
University of Illinois at Urbana-Champaign, Dept. of Ecology, Ethology and Evolution, 515 Morrill Hall, 505 S. Goodwin Ave., Urbana-Champaign, IL 61820, USA
e-mail: wikelski@life.uiuc.edu
Fax: 217-244-4565

P.H. Wrege
Dept. of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

on energy uptake and assimilation, M. Wikelski and C. Carbone (unpublished work) have shown that the maximum attainable body size is well below the size predicted by digestive capacity alone. Thus each population has an island-specific maximum body size, determined by the quality of algae resources and environmental temperatures (Wikelski et al. 1993; Wikelski et al. 1997; Wikelski and Trillmich 1997; M. Wikelski and C. Carbone, unpublished work; see also Burghardt and Rand 1982).

Male marine iguanas experience strong sexual selection for large body size during the breeding season, because body size correlates with access to fertile females (Trillmich and Trillmich 1984; Wikelski et al. 1996). However, the increased reproductive success that comes with larger body size is sometimes costly, because animals close to the attainable body size maximum are particularly vulnerable to changes in the quality of the food resource (Owensmith 1993). Up to 90% of marine iguanas die when high-quality species of algae disappear during El Niño events, and the large size-classes die at disproportionate rates (Laurie 1989; Wikelski and Trillmich 1997). Thus, diet expansion to include land plants would seem to have selective potential, particularly during El Niños. Although land iguanas (*Conolophus* spp., the sister taxon of *Amblyrhynchus;* Rassmann 1997) thrive on lush green land plants during El Niño events (Snell 1987), foraging niche expansion in marine iguanas has rarely been observed. On the island of Seymour Norte, however, a single population is known to regularly supplement their diet of algae by eating a particular species of land plant, *B. maritima*, and has done so for at least 25 years (D. Day, personal communication). *Batis*, also called “saltwort” or “beachwort”, is a dioecious shrub, widely distributed along the Pacific coast of the Americas, from California south to Peru, in the Galápagos Islands, the Hawaiian Islands, and on the Atlantic coast of the Americas from Florida to Brazil (Wiggins and Porter 1971). It is most often associated with salt lagoons and inshore depressions that become periodically flooded (e.g., during storm tides).

In this paper we characterize the unique feeding behavior of the Seymour Norte population, and evaluate the consequences of diet expansion for body size and survival. We show that animals eating the succulent beach plant *Batis* attain body sizes well above what would be possible by eating only algae, and likely gain considerable reproductive advantage as a result. In addition, diet expansion increased the probability of survival during times of food shortage, but at the cost of dependence on land plants to maintain body condition. We suggest that extreme conservatism in local foraging traditions, which is characteristic of all marine iguana populations, best explains the unique occurrence of this behavior.

Materials and methods

Study site and environmental measures

Marine iguanas were studied intensively on the western side of Seymour Norte island (90°18′W, 0°24′S) from 4 June 1996 until 19 June 1996. The study site was visited on 5 January 1997, during the breeding season, to evaluate maximum body sizes of iguanas along the coast, and on 6 May 1998 and 16 May 1999, to investigate changes of body mass and iguana abundance during and after a strong El Niño event.

The study site consisted of *c*. 60 m of rocky beach coastline with intertidal zone flats, behind which lay a sandy and brushy region running about 20 m inland from the beach. At one location within the latter region, a sandy pothole, presumably a former salt lagoon, harbored patches of the succulent *Batis*, and a few clumps of saltbush (*Cryptocarpus* sp.). The entire patch of *B. maritima* (hereafter referred to as the “*Batis* patch”), on which marine iguanas were regularly observed feeding, was about 40 m long and 50 m wide and was bordered along two sides by a tourist path. There were also many other *B. maritima* bushes along the coast, though usually of higher growth than in the study site. We estimated percent cover within the *Batis* patch by scoring the substrate as “soil” or “*Batis*” at 10-cm intervals along two random transects.

The times of high and low tides were obtained from the tidal charts of the Ecuadorian navy for neighboring Santa Cruz island (distance: *c.* 10 km). The standard operative environmental temperature was recorded using a thermoprobe mounted inside a black 15-cm-diameter copper ball (Bakken 1992). Temperature data were stored every 10 min on a Hobo data logger (Onset Inc., Pocassett, Mass., USA).

Morphological and behavioral measures

At the beginning of the study we captured (by noosing) 37 marine iguanas of all size classes (29 males and 8 females) that were observed crossing the *Batis* patch *en route* to their intertidal zone feeding area or that were observed feeding on *B. maritima*. Of these individuals 33 were observed regularly throughout the rest of the study and are included in the analyses. We measured body size (snout-to-vent length, SVL, to the nearest 1 mm), body mass (to the nearest 10 g) and sex (by external morphology). Upon release, iguanas received an individual temporary paint number on their flanks to ease observation, and a cryptic but unique brand for long-term identification (Laurie 1989).

To compare maximum body sizes of iguanas feeding on *B. maritima* to those feeding mostly or entirely on intertidal zone algae, we went along the coastline to both sides of the study site on 11 June 1996 and measured the largest iguana we could find within successive 50-m stretches of coastline. This survey was conducted after the time of low tide, when most animals, especially the large ones, bask in the sun on exposed boulders. A similar survey was conducted during the mating season (5 January 1997), using the non-intrusive method of Laurie (1989) for estimating body size without capturing animals. This method is well established and with some training, an observer can accurately place iguanas into 50-mm size-classes.

In 1996, a team of four observers (4–11 June) and of two observers (12–19 June) made continuous behavioral observations on iguanas in the *Batis* patch from first activity (around 0630 hours) until the cessation of iguana activity (around 1745 hours). All four observers initially conducted observations together for 6 h in order to standardize observational protocols. Thereafter one or two observers monitored the *Batis* patch at any one time. Although a 2-week observation period is short, we feel that our data are nevertheless representative of longer-term foraging behavior in this population. At least for iguanas feeding in the intertidal zone, activity patterns during a tidal cycle are so stereotyped and conservative that one can accurately extrapolate behavior throughout the year from observations during a single tidal cycle (Wikelski and Trillmich 1994; M. Wikelski, unpublished work on three island populations).

Observations included 5-min scan samples to record the number and identity of all iguanas within the patch, and their feeding, resting, or transit status. At opportunistic intervals, focal samples were obtained on randomly selected individuals to quantify the duration of feeding bouts and bite-rates.

Table 1 Comparison of nutritional value of the land plant *Batis maritima* and species of marine algae (species names see Table 2) eaten by marine iguanas on Seymour Norte Island. Data are means (SE)

	B. maritima (*n*=3)	Algae (red and green) (*n*=4)	*t*-statistic	*P*
Caloric value (kcal g^{-1})	1.57 (0.13)	2.59 (0.12)	–5.29	<0.01
%Protein	8.31 (1.19)	18.86 (1.01)	–6.75	<0.01
%Nitrogen	1.32 (0.19)	3.00 (0.16)	–6.75	<0.01
%Carbon	19.35 (2.17)	31.63 (1.40)	–4.75	0.012

Between 5 and 11 June 1996, two observers surveyed the intertidal zone foraging areas around the time of low tide. Observations were initiated when the first iguanas moved over the boulder field that separated the land plant area from the intertidal zone area. We recorded the identity of marked iguanas and whether they were feeding, resting, or moving, thus gaining information on the duration of individual foraging bouts (for details of methods see also Wikelski and Trillmich 1994). We also stomach-flushed (Wikelski et al. 1993) five individuals (on 11 June 1996) which had foraged for different durations. This allowed us to compare algae and protein intake between *Batis* feeders and intertidal zone feeders. We also include unpublished data from a previous study (Wikelski and Trillmich 1994) on intertidal zone foraging intensity during a tidal cycle to compare mixed intertidal zone and land plant foraging (Seymour) with pure intertidal zone foraging (Santa Fe).

Detailed measures of foraging efficiency on *B. maritima* were obtained on 7 and 8 June 1996. We captured 11 marine iguanas when they first entered the *Batis* patch, weighed them to the nearest 10 g, and, after release, counted the number of bites on *B. maritima* by these individuals. The animals were recaptured and weighed again. The difference in body mass was divided by the number of bites to describe the intake of *B. maritima* in grams (wet weight) per bite.

To supplement and extend these detailed observations of the Seymour population, we have used our extensive observations of iguana foraging behavior collected over a 10-year period (M.W., total field time ~3.5 years), from numerous islands in the Galápagos Archipelago. In addition, we have incorporated observations from the literature, as well as from numerous Galápagos naturalist guides and our colleagues H. Snell, F. and K. Trillmich, T. Dellinger, A. Laurie, and P. Stone.

Nutrient/caloric analyses

Samples of *B. maritima* for chemical and nutrient analyses were obtained from both the main patch on the study site, and from a site *c.* 1 km distant, where there were no iguanas. We used algae from stomach flushings to obtain representative algae samples. All samples described above were sun-dried and exported under permission from the Galápagos National Park Service to Cornell University, where they were dried at 60°C until dry mass was stable. Thereafter, each sample was homogenized and analyzed for caloric value and nutrient content. Three subsamples were analyzed from each sample and the mean determination used in statistical analyses.

To facilitate comparison with previous work on algae quality and foraging energetics, we sampled the length of the algae turf at five locations within the intertidal zone area of the Seymour study site, as described by Wikelski et al. (1997).

Statistical methods

Data were processed with SPSS for Windows (SPSS 1991). Two-tailed test statistics were used. Residuals of regressions were inspected for normality. Logarithmic transformations were used in calculations if data were not homoscedastic, but we graph untransformed data for clarity in Fig. 1. Data are given as means±SD if not indicated otherwise except for regression equations (mean±SE). Significance for all tests was accepted at the α=0.05 level.

Results

On all of the Galápagos Islands, only the population of marine iguanas living along the west coast of Seymour Norte Island is known to eat any land plant regularly (Galápagos naturalist guides, personal communications), and only a single species of plant, *Batis*, is eaten. On Seymour, *Batis* could be found all along the western shoreline, and in isolated patches elsewhere on the island. The most extensive cover was in a single patch (the *Batis* patch) 200 m^2 in extent. Cover within this patch was 31.2%, with individual plants typically covering 1–2 m^2. Elsewhere, patches were mostly composed of two to six individual plants, covering up to 8 m^2. *Batis* usually grows as a 0.5- to 1.5-m-tall shrub, but plants at our study site were mostly lower than 5 cm above ground and nearly all branches appeared grazed or broken. Bite marks on the succulent leaves remained recognizable for several weeks. Isolated patches of *Batis* found elsewhere on the island, including within 10 m of the *Batis* patch, were tall and did not appear to be grazed, and iguanas were not observed feeding on them.

Although land-plant feeding on Seymour was apparently restricted to the *Batis* patch, we have no evidence of any nutritional difference between patch plants and plants from elsewhere on the island. Samples of *Batis* from the *Batis* patch did not differ from a sample collected approximately 1 km away, where no iguanas were observed (for the single distant location, values for all nutrients listed in Table 1 fell between values for samples from the *Batis* patch). Table 1 compares the caloric and nutrient content of *Batis* and the common algae species found in the intertidal zone of Seymour Norte. On a dry weight basis, *Batis* provides iguanas with significantly less protein, nitrogen, carbon, and calories than the red and green filamentous algae. We were not able to determine experimentally the assimilation efficiency of iguanas feeding on *Batis*. However, it is likely to be lower than for algae, both because marine iguanas have a gut morphology specialized (simplified) for feeding on algae (Iverson 1980, 1982), and because we frequently observed undigested fragments of *Batis* in the feces of individuals feeding within the *Batis* patch, suggesting some digestive difficulty.

It was mostly large individuals that exploited *Batis*. We observed no animals smaller than 1 kg regularly feeding on the land plant. There was a significant positive relationship between the mass of an iguana and the proportion of total feeding time spent foraging on land (Fig. 1; linear regression on log-transformed time data:

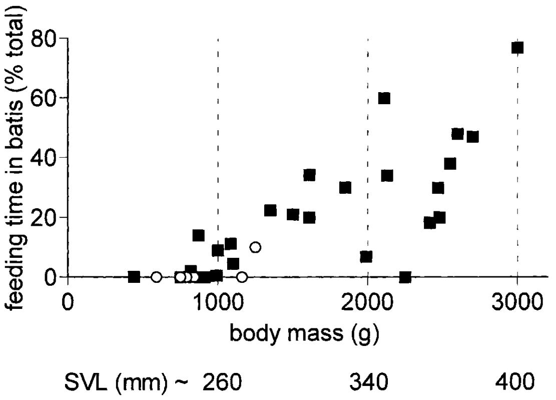

Fig. 1 Land-plant foraging on *Batis maritima* by marine iguanas on Seymour Norte Island, Galápagos Archipelago. Foraging time is expressed as the percentage of an individual's total foraging time over one tidal cycle (14 days) (*filled squares* males, *open circles* females). *Y*-axis displayed in linear units for graphical clarity; statistics were calculateded on log-transformed data. The lower labelling on the *x*-axis shows the approximate snout-vent length (SVL) of animals at the indicated body mass

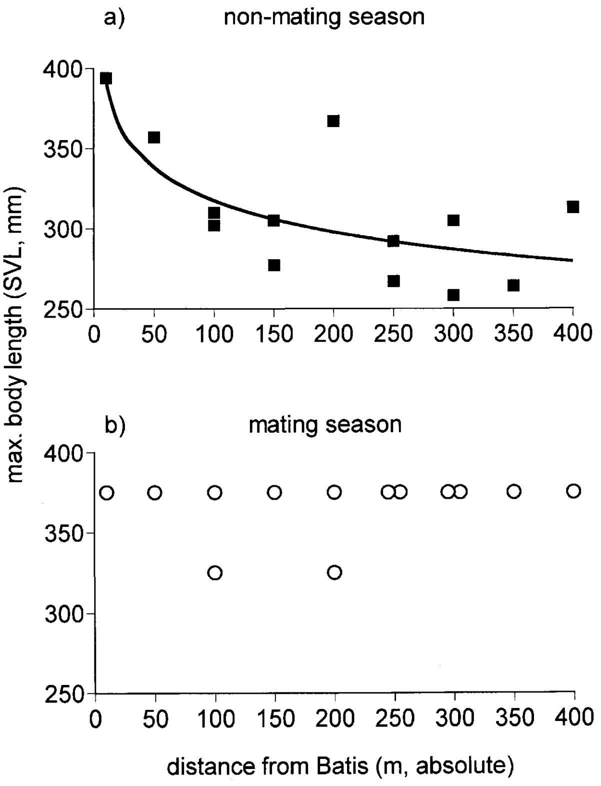

Fig. 2a,b The distribution of male body size with respect to distance from the *Batis* patch, at two times of year. *Points* represent the SVL of the largest marine iguana located along contiguous 50 m stretches of coastline, running north and south from the *Batis* patch. (Some intervals have only a single point because no animals were found at that distance in one of the directions.) **a** Measured SVL during the non-reproductive season. *Fitted curve* based on a power regression model. **b** Estimated size-class for SVL during the reproductive season

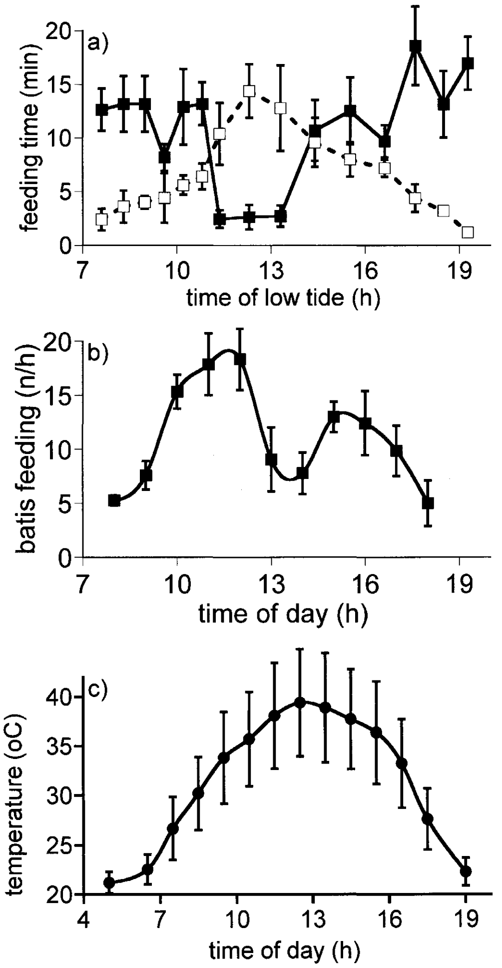

Fig. 3a-c The pattern of foraging activity in relation to tidal cycles and ambient temperature. **a** The mean (±SE) duration of foraging activity on *Batis* (*filled squares*) and on intertidal zone algae (*open squares*), plotted as a function of the tidal cycle. Only animals that fed in one or both habitats are included in the mean for a given day. **b** The mean (±SE) number of iguanas feeding on *Batis* each hour, during the 14 day study period. **c** Hourly standard operative environmental temperature (mean±SD; Bakken 1992) during the 14-day study period

$F_{1,28}=19$, $r^2=0.63$; $P<0.001$). Females of a given body size did not appear to differ from males in their tendency to exploit *Batis*, but the sample of females was small. The bias toward large body size among *Batis* feeders was not due to restricted access through social behavior. We did not observe any form of behavioral aggression by animals feeding within the *Batis* patch.

Marine iguanas living near the *Batis* patch, and potentially including *Batis* in their diets, tended to be larger than animals elsewhere on the island. Figure 2a shows that the average maximum body size decreased significantly with distance from the *Batis* patch. Individuals very close to the *Batis* patch tend to be bigger, and all others are unaffected by nearness to the patch. The observed distribution was adequately modeled as a power function with distance from *Batis* (SVL=483(±50)×distance$^{-0.09\pm0.02}$, $F_{1,12}=19$, $r^2=0.61$, $P<0.001$). In January

1997, during the reproductive season, the largest marine iguanas had spread out along the coastline and no longer showed a clumped distribution centered on the *Batis* patch (Fig. 2b; $F_{1,12}$=0.5, r^2=0.05, P=0.97, power function model as in Fig. 2a). At this time of year, large male iguanas do not feed at all, but spend their entire time defending central positions in mating clusters and courting females (Wikelski et al. 1996). Several marked animals were found to be territorial far off the study site (up to 400 m distant).

The comparatively low nutrient value of *Batis* compared to intertidal zone algae, and the skewed size distribution of individuals feeding on *Batis*, are consistent with an hypothesis that *Batis* is consumed only as a supplement to a diet based on intertidal zone foraging. This interpretation is reinforced by the foraging behavior of *Batis*-feeders through the tidal cycle. Figure 3a shows that iguanas spent more time eating *Batis* when the low tides were early in the morning or late in the afternoon – times when intertidal zone foraging is least efficient because environmental temperatures are too low for efficient movement (morning) or efficient digestion (evening) (Wikelski et al. 1993; Wikelski and Trillmich 1994). When low tides were around midday, hardly any land plants were consumed because most individuals were feeding in the intertidal zone (Fig. 3a; ANOVA $F_{1,14}$= 8.5, P<0.001). In terms of the numbers of individuals feeding on land plants, the diurnal pattern shown in Fig. 3b is very similar to that for populations feeding only on intertidal zone algae. The pattern is generated largely by individuals feeding on *Batis* on their way to and from foraging bouts in the intertidal zone. Significantly, the pattern for *Batis*-feeders differed most markedly during the midday hours. The conspicuous drop in foraging activity around 1300–1400 hours coincided with the highest standard operative temperatures measured at the study site (Fig. 3c; ANOVA $F_{1,13}$=2936, P<0.001). These temperatures exceed the preferred body temperatures of marine iguanas and thus animals feeding on land (but not those being cooled by intertidal zone wave action) have to seek shade in order not to overheat (see Bartholomew 1966).

The value of eating *Batis* depends not only on its relative nutrient value (see Table 1), but also on the efficiency with which iguanas can consume and digest the tissues. Two parameters that affect foraging efficiency are maximum intake rate (g min^{-1}) and change in intake rate as a function of time foraging. By both measures, individuals feeding on *Batis* are considerably more efficient than individuals feeding on intertidal zone algae. When feeding on *Batis*, iguanas ingested on average 0.2±0.05 g wet weight per bite. Individuals could maintain an average bite rate of 22.1±9.3 bites min^{-1} regardless of the length of the foraging bout (linear regression: bite rate=23.5(±2.2)–0.11(±0.13)×foraging time, $F_{1,45}$=0.7, r^2=0.01, P=0.4). In the intertidal zone, however, iguanas of similar body mass average only 0.04±0.02 g wet weight per bite (measured on Santa Fé Island; Wikelski et al. 1997). Because body temperature drops with time exposed to the cold intertidal zone water (Wikelski and Trillmich 1994), bite rate decreases over time from initial highs of 102±11 bites min^{-1} at 40°C body temperature to 44±3 bites min^{-1} at 25°C body temperature (Wikelski and Trillmich 1994). As a result, total intake when feeding on *Batis* increased more steeply with time than intake when feeding on algae (Fig. 4a). However, when calculated on a protein basis, there is no difference in the total intake on land (*Batis*) or in the intertidal zone (Fig. 4b). The lack of a difference in nutrient uptake is caused by the lower dietary quality of *Batis* as compared to algae (Table 1).

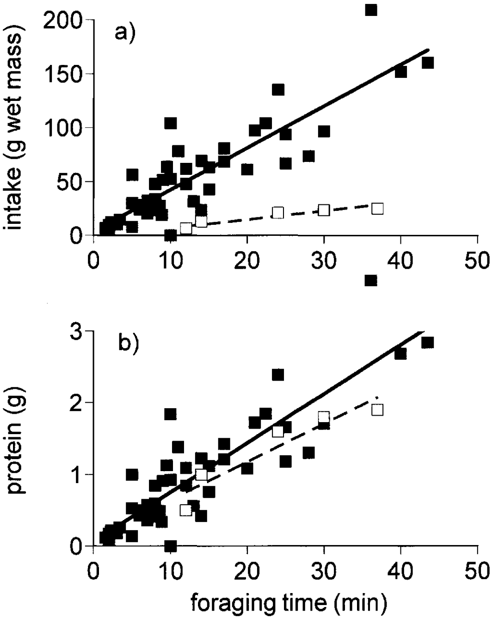

Fig. 4a,b Cumulative food intake over time for iguanas feeding on land plants and intertidal zone algae. **a** Cumulative intake of the land plant *B. maritima* (*filled squares*) increased almost uniformly over time (intake=3.78(±5.14)+3.88(±0.31)×foraging time, r^2=0.77, P<0.001), while intake of intertidal zone algae (*open squares*) increased at a much lower rate (intake=1.6(±3.7)+ 0.69(±0.14)×foraging time, r^2=0.87, P=0.01). **b** Cumulative intake of protein over time was not different, for animals feeding on *Batis* or intertidal zone algae (symbols as in **a**; protein g^{-1} (dry mass) algae, from Table 2; ANCOVA to test for differences in slopes, $F_{2,49}$=201, P<0.001; for foraging site: P=0.48)

A significant proportion of marine iguanas on Seymour Norte Island were able to attain a body size well above what would be possible from eating intertidal zone and subtidal algae alone, presumably as a consequence of diet expansion and the associated changes in foraging behavior presented above. In all populations in the Galápagos, large individuals are food-constrained in that they are usually unable to ingest sufficient amounts of algae food in the intertidal zone to completely fill their stomachs. This is because foraging time is limited by falling body temperature and a fixed period (low tide) for access to food resources (Wikelski et al. 1997). An upper limit to body size is thus determined by the quality of the algae, the time available to forage, and digestive efficiency (which is correlated with mean ambient air temperature) (M. Wikelski and C. Carbone, unpublished work). Figure 5 shows a contour plot of maximum predicted body mass

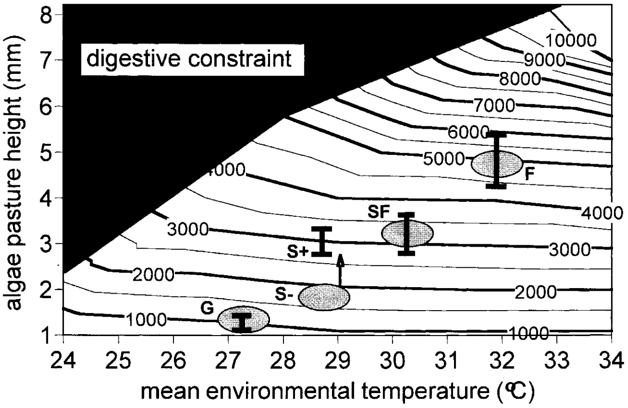

Fig. 5 Contour plot of maximum body masses of marine iguanas under a given set of environmental temperatures and algae pasture heights (redrawn from M. Wikelski and C. Carbone, unpublished work). *Lightly filled ovals* show predicted maximum body masses for largest 10% of iguanas of each island. *Black bars* depict observed maximum body mass for the largest 10% of iguanas on each island. Note that the populations on Genovesa, Santa Fe and Fernandina fit the model fairly well, but the largest Seymour iguanas are about twice as heavy as would be expected based on a diet of algae alone. None of the populations is close to the digestive constraint, i.e., there is digestive potential for the incorporation of additional food items in large adults (*G* Genovesa, *S–* Seymour, algae only, *S+* Seymour algae plus land plants, *SF* Santa Fe, *F* Fernandina)

for marine iguanas, based on a biophysical model that incorporates algae quality and environmental temperature (M. Wikelski and C. Carbone, unpublished work). In all populations that we had studied previously (on the islands of Genovesa, Santa Fé, and Fernandina; all by M.W.), observed maximum body size accorded well with the model predictions, and in all cases these animals had unused digestive potential (i.e. predicted body sizes were well below the digestive constraint boundary). The animals studied on Seymour Norte present a dramatic exception. Males that supplemented their diet with *Batis* were up to 100% larger than the maximum size predicted for animals feeding only on algae in the Seymour Norte intertidal zone (Fig. 5). Observed maximum body sizes of animals captured away from the *Batis* area on Seymour Norte (Fig. 2), and presumably eating only intertidal zone algae, also accorded well with the predictions of the biophysical model (Figs. 5, 2a).

Discussion

Only marine iguanas on Seymour Norte Island widened their feeding niche from one based entirely on marine algae to one that regularly included a land plant, saltwort

Table 2 Distribution of dietary habits and their importance for marine iguanas in the Galápagos archipelago

Food type	Species	Site of co-occurrence	Site where eaten[a]	Food habit	Importance[b]
Algae	Red (*Centrosera, Gelidium, Pterocladia*)	Islands with cold surface waters	All islands (2,9)	Ordinary	Staple of excellent quality
	Green (*Ulva*)	Islands with cold and warm surface waters	All islands (1)	Ordinary	Good quality staple
	Brown (*Giffordia*)	All islands during El Niño conditions	All islands during El Niño events (3,4) 1982/93 and 1997/1998	Emergency	Poor digestibility; only algae left in intertidal zone during El Niño events
Land plants	*B. maritima* (succulent beach plant)	Most northern shores of large islands	Seymour Norte (1); St. Cruz (1 individual in Pto. Ayora and one group in east part) (10)	Local	Additional food source, especially for large iguanas
	Sesuvium portulacastrum	All islands with beaches	Seymour Norte (7), Genovesa	Local	Testing additional food source (?)
	Portulaca oleracea	Many islands	Caamano	Local	Testing additional food source (?)
	Cryptocarpus pyriformis	Most islands with beaches	Seymour Norte (5)	Local	Testing additional food source (?)
Feces	Sea lion (*Zalophus californianus*)	Most islands	Many (most) islands (8)	Ordinary	Source of calcium (?)
	Marine iguana	All islands	Many (most) islands	Ordinary	Uptake of digestive endosymbionts (?)
Regurgitates	Boobies (*Sula* sp.)	Many islands	Seymour Norte	Local	Source of protein (?)
	Flightless cormorant (*Nannopterum harrisi*)	Fernandina Isabela	Fernandina (6) (only certain sites along the coast)	Local	Source of protein (?)
Afterbirth	Sea lion (*Z. californianus*)	Most islands	Seymour Norte, Fernandina (6), Isabela, Plaza Norte	Local	Source of protein (?)

[a] References: *1* Nagy and Shoemaker 1984, *2* Wikelski et al. 1993, *3* Cooper and Laurie 1987, *4* Laurie 1989, *5* this study, *6* F. Trillmich, personal communication, *7* P. Stone, personal communication, *8* Carpenter 1966, *9* Hobson 1965, 1969, *10* David Day, personal communication

[b] (?) indicates that the importance is hypothesized only

(*B. maritima*). Land plant foraging was restricted to a single small *Batis* patch, but had been consistent there for at least 25 years (Galápagos Natural History Guides, personal communications) Although occasional but consistent ingestion of non-algae substances has been noted in nearly all populations of iguanas that have been observed on a regular basis (Table 2), in no other case could these items be considered a significant component of the diet. On Seymour Norte, *Batis* was mainly exploited by the larger animals of the population. Animals that fed on land realized a caloric intake over and above what could be extracted from intertidal and subtidal sources of algae, and attained maximum body sizes well beyond those found elsewhere on the island. Indeed, the largest animals were nearly twice the maximum body size predicted by a biophysical model which accurately predicts body size on all other islands for which there are suitable data (n=3), and which *does* correctly predict the body size of Seymour animals away from the *Batis* foraging site (see Fig. 5; M. Wikelski and C. Carbone, unpublished work). Thus, land-plant feeding appears directly responsible for the increased body size.

We observed no tendency for individuals to monopolize access to portions of the area covered in *Batis*, although marine iguanas do defend segments of shoreline during the reproductive season in order to limit the access of other males to breeding females (Wikelski et al. 1996). We suggest that this lack of competitive exclusion is consistent with the hypothesis that *Batis* is eaten only as a supplementary, low-quality food – efficiently exploited only by animals that fall well below their digestive potential in terms of the amount of algae they can extract from the intertidal zone. We find support for this hypothesis in three aspects of our study.

First, on a dry-weight basis, *Batis* was lower in caloric content as well as protein, nitrogen, and total carbon content than a mixture of red and green algae from the Seymour intertidal zone. Lower nutrient content alone might not make *Batis* an inferior energy source, because iguanas are not constrained in the amount of time that they can forage on land, and so could compensate for low nutrient content by ingesting a greater volume (for example, Fig. 4b). However it is highly unlikely that marine iguanas eating *Batis* can match the extremely high assimilation efficiency attained when eating algae (~70%, Nagy and Shoemaker 1984; Wikelski et al. 1993). The hindgut of marine iguanas is apparently specialized for processing the simplified cell structure of the filamentous red and green algae common in the cold waters of the Galápagos Islands (Wikelski et al. 1993). They completely lack the 8–12 septa found in the hindgut of all other iguanid species, which probably function to slow down food passage (Iverson 1980, 1982). Indeed, we frequently observed undigested pieces of *Batis* in the feces of iguanas on Seymour.

Second, if foraging on *Batis* was a reasonable substitute for intertidal zone algae feeding, we would expect to see animals of all size-classes eating on land (but see Foley and Cork 1992). However, only the largest class of animals (>1 kg) regularly fed in the *Batis* area (Fig. 1), and it is exactly this size-class that should be reaching the point where there is insufficient foraging time at low tide to satisfy their digestive potential (Fig. 5). This constraint would act particularly strongly (1) on the very largest animals, and (2) when intertidal zone foraging time is further restricted by the hour of low tide (very early morning or late evening), or when ambient temperatures are particularly low. On Seymour, the largest iguanas fed most on land, the proportion of the diet represented by feeding on land plants increased with body size, and most individuals that fed on land did so more intensively on the days when the tides were early or late (Fig. 3).

Finally, our data provide little support for three alternative, non-exclusive hypotheses that might explain the observed diet expansion: medicinal use, incorporation of secondary compounds for predator defense, and harvesting of nutrients and/or minerals that are scarce in algae. If *Batis* contained either scarce nutrients, minerals, or medicinal compounds, one would expect it to be exploited by animals in most size classes (see also Billing and Sherman 1998). This, however, was not observed. Similarly, if *Batis* contained toxic chemicals that could be used as a defense against predators (basically only Galápagos hawks), the smallest and most vulnerable size classes would be expected to eat the land plant (e.g., Boppre et al. 1984).

Benefits and costs of land plant eating

For male marine iguanas, large body size confers a clear advantage in male-male competition for matings, and we suggest that it is this benefit that has ultimately selected for land-plant eating in the Seymour population. An increase in body mass from 2 kg to 2.5 kg, for example, may translate into a four-fold increase in the expected number of matings per year (Rauch 1985; Wikelski et al. 1996; Wikelski and Bäurle 1996). Such a mating advantage clearly represents a significant component of fitness, particularly when accumulated over a reproductive lifespan that may often exceed 18 years (Laurie 1989; Wikelski and Trillmich 1997).

A foraging strategy that includes land plants as a supplementary (if low-quality) source of energy may confer survival advantages in addition to reproductive benefits. Starvation in populations of marine iguanas is a common occurrence during the warm phase of the El Niño-Southern Oscillation climatic phenomenon (Laurie 1989). Ocean warming can completely remove the populations of red and green algae in the intertidal zone, which are often replaced by a less nutritious and apparently less efficiently assimilated brown algae (Laurie and Brown 1990a, 1990b). In populations that eat only intertidal algae, large marine iguanas are disproportionately prone to starvation because of their high absolute energy requirements (Wikelski et al. 1997). Following the three El Niño events of 1986–1987, 1991–1992, and 1994–1995, 100% of animals near the predicted maximum body size for a given island perished (Santa Fe, Laurie 1989; Genovesa and Santa Fe, Wikelski and Trillmich 1997; for El Niño events, see Kerr 1993; McPhaden 1994). By contrast, on Seymour Norte Island, larger iguanas clearly survived these selective events, including some males in excess of 2 kg body mass. It is highly unlikely that animals this far above the predicted maximum body size of 1.5 kg could have survived without the additional energy obtained through eating *Batis*.

However, the particularly strong El Niño of 1997/1998 demonstrated that growing large by foraging on land plants also entails a cost should the dietary supplement disappear. During this El Niño, high sea-surface level (a usual aspect of warm-phase events; Houvenaghel 1978; Fahrbach et al. 1991) caused flooding of the area where marine iguanas fed on *Batis*. In May 1998 not only was there no *Batis* available on Seymour (at least in the original patch and along the study site coastline), but none of the large iguanas had survived.

Why niche expansion occurred only on a single island

Marine iguanas of most island populations are in regular contact with terrestrial plants. For example, they pass patches of *Sesuvium portulacastrum*, saltbush (*Cryptocarpus* sp.), and *Batis* on their daily routes to foraging sites. Other marine iguana populations even sleep in or under *Opuntia* cacti, *Sesuvium* and *Croton* sp. (Wikelski et al. 1996, and personal observations). Given the apparent benefits that accrue to iguanas eating *Batis* on Seymour Norte Island, it is puzzling that the behavior is restricted to a single island, indeed to only a subset of individuals on that island. We suggest that extremely conservative foraging-site traditions by individual animals is a major component to solve this puzzle.

While significant use of alternate food resources is apparently unique to the Seymour population, the occasional “testing” of various land plant species, and limited ingestion of various “food” resources has been observed in other marine iguana populations. In Table 2 we have compiled a listing of such observations, garnered from the literature and personal communication with Galápagos researchers and naturalist guides.

Marine algae from the intertidal zone and subtidal (including both red and green species) are universally consumed by marine iguanas and represent the specialized diet of the species. In addition, the feces of both sea lions and other marine iguanas are eaten consistently, but in minute amounts, by animals in most if not all populations. These may represent sources of critical minerals (e.g., calcium, especially for females prior to laying), or of endosymbionts, respectively (Troyer 1982, 1984a,1984b,1984c). All of the other items listed in Table 2 have been observed in the diet only very rarely and/or are exploited by only a very restricted number of animals in isolated populations.

In all cases, a characteristic of these specialized feeding traditions is that they are highly local in extent. This may reflect the fact that marine iguanas are extremely conservative in how they use their foraging site. While hatchlings may spend several months searching widely along the coast for good foraging areas (Laurie 1989; Drummond and Burghardt 1982), after choosing a site, individuals can be observed year after year foraging within the same few square meters of the intertidal zone (some individuals have been consistent for at least 12 years; M. Wikelski, unpublished work). This behavioral conservatism extends also to the routes by which individuals move from resting areas into the intertidal zone for feeding. Adult males may leave traditional foraging areas to reproduce elsewhere, sometimes migrating up to 5 km. However, they do not forage during the mating season and almost always return to their traditional foraging site (Wikelski et al. 1996). Foraging site conservatism is so strict that individual iguanas have been observed starving to death during El Niño periods, in spite of resting with fat individuals that feed only meters away in tide pools (Wikelski and Trillmich 1997).

Thus, specialized foraging behavior may spread in a population through copying, and yet remain quite restricted in extent because only a small subset of individuals interacts in a given location. On Seymour, *Batis* grew in patches along the beach adjacent to the site where iguanas ate it, but no plant was grazed outside the particular land plant foraging area. Should *Batis* become re-established on Seymour, at the original location, it should prove interesting to see whether its exploitation also becomes re-established in future years. Although it appears that all of the marked “*Batis*-feeders” from this study have died, we did observe a few very small, permanently marked individuals sample *Batis*. This might allow us the unique opportunity to test whether such individuals initiate land plant feeding once they reach adult size (Galef 1995).

We suggest that foraging niche expansion in grazers may be rare because their digestive systems are adapted to a constant supply of plant matter of similar type (Lichtenbelt 1993). However, little is known about the specifics of gut physiology and endosymbionts for most vertebrates and thus further interpretations have to await additional data (Langer and Snipes 1991; McWilliams et al. 1997).

Acknowledgements We thank Alex Mendoza and Raul Carvajal Mata for help in the field, Roman Pausch and Todd Dawson for assistance and use of laboratory facilities at Cornell. We also thank David Day, Andre Machaump and Galápagos naturalist guides for help and information, and the Galápagos National Park Service, the Charles-Darwin Research Station, and TAME for enabling this work. The comments of M. Hau, P. Bednekoff, C. Carbone, T. Hayden, W. Schelsky, L. Martin, E. Tarlow, K. Nelson and James Dale improved previous versions of the manuscript. This is contribution no. 571 of the Charles-Darwin-Foundation and was supported by a Feodor-Lynen and a Smithsonian Tropical Research Institute fellowship to M.W., as well as by the Max Planck Institute Seewiesen.

References

Bakken GS (1992) Measurement and application of operative and standard operative temperatures in ecology. Am Zool 32:194–216

Bartholomew GA (1966) A field study of temperature relations in the Galápagos marine iguana. Copeia 2:241–250

Billing J, Sherman PW (1998) Antimicrobial functions of spices: why some like it hot. Q Rev Biol 73:3–49

Boppre M, Seibt U, Wickler W (1984) Pharmacophagy in grasshoppers? *Zonocerus* attracted to and ingesting pure pyrrolizidine alkaloids. Entomol Exp Appl 35: 115–118

Burghardt GM, Rand AS (1982) Iguanas of the world. Noyes, Park Ridge

Buttemer WA, Dawson WR (1993) Temporal pattern of foraging and microhabitat use by Galápagos marine iguanas, *Amblyrhynchus cristatus*. Oecologia 96:56–64

Carpenter CC (1966) The marine iguana of the Galápagos Islands, its behavior and ecology. Proc Calif Acad Sci 34:329–376

Cooper JE, Laurie WA (1987) Investigation of deaths in marine iguanas (*Amblyrhynchus cristatus*) on Galapagos. J Comp Pathol 97:129–136

Darwin C (1883) Journal of researches, new edn. Appleton, New York

Dawson WR, Bartholomew GA, Bennett AF (1977) A reappraisal of the aquatic specializations of the Galapagos marine iguana (*Amblyrhynchus cristatus*). Evolution 31:891–897

Drummond H, Burghardt GM (1982) Orientation in dispersing hatchling green iguanas, *Iguana iguana*. In: Burghardt GM, Rand AS (eds) Iguanas of the world. Noyes, Park Ridge, pp 271–291

Durtsche RD (1992) Feeding time strategies of the fringe-toed lizard, *Uma inornata*, during breeding and non-breeding seasons. Oecologia 89:85–89

Emlen JM (1966) The role of time and energy in food preference. Am Nat 100:611–617

Fahrbach E, Trillmich F, Arntz W (1991) The time sequence and magnitude of physical effects of El Niño in the eastern Pacific. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño. Springer, Berlin Heidelberg New York, pp 8–21

Feinsinger P, Swarm LA (1982) Ecological release, seasonal variation in food supply and the hummingbird *Amazilia tobaci* on Trinidad and Tobago, West Indies. Ecology 63:1574–1587

Foley WJ, Cork SJ (1992) Use of fibrous diets by small herbivores: how far can the rules be "bent"? Trends Ecol Evol 7:159–162

Galef BG (1995) Why behaviour patterns that animals learn socially are locally adaptive. Anim Behav 49:1325–1334

Hobson ES (1965) Observations on diving in the Galapagos marine iguana, *Amblyrhynchus cristatus* (Bell). Copeia 1965:249–250

Hobson ES (1969) Remarks on aquatic habits of the Galapagos marine iguana, including submergence times, cleaning symbiosis, and the shark threat. Copeia 1969:401–402

Houvenaghel GT (1978) Oceanographic conditions in the Galápagos archipelago and their relationships with life on the islands. In: Boje R, Tomczak P (eds) Upwelling ecosystems. Springer, Berlin Heidelberg New York, pp 181–200

Iverson JB (1980) Colic modifications in iguanine lizards. J Morphol 163:79–93

Iverson JB (1982) Adaptations to herbivory in iguanine lizards. In: Burghardt GM, Rand AS (eds) Iguanas of the world. Noyes, Park Ridge, pp 60–76

Jarman PJ, Sinclair ARE (1979) Feeding strategy and the pattern of resource-partitioning in ungulates. In: Sinclair ARE, Norton-Griffith M (eds) Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, pp 130–163

Kerr RA (1993) Climate – El Niño metamorphosis throws forecasters. Science 262:656–657

Langer P, Snipes RL (1991) Adaptations of gut structure to function in herbivores. In: Tsuda T, Sasaki Y, Kawashima R (eds) Physiological aspects of digestion and metabolism in ruminants. Proceedings of the Seventh International Symposium on ruminant physiology. Academic Press, London, pp 349–384

Laurie WA (1989) Effects of the 1982–83 El Niño-Southern Oscillation event on marine iguana (*Amblyrhynchus cristatus* Bell, 1825) populations in the Galapagos islands. In: Glynn P (ed) Global ecological consequences of the 1982–83 El Niño-Southern Oscillation. Elsevier, New York, pp 121–141

Laurie WA, Brown D (1990a) Population biology of marine iguanas (*Amblyrhynchus cristatus*). 2. Changes in annual survival rates and the effects of size, sex, age and fecundity in a population crash. J Anim Ecol 59:529–544

Laurie WA, Brown D (1990b) Population biology of marine iguanas (*Amblyrhynchus cristatus*). 3. Factors affecting survival. J Anim Ecol 59:545–568

Lichtenbelt WDV (1993) Optimal foraging of a herbivorous lizard, the green iguana in a seasonal environment. Oecologia 95:246–256

Lima AP, Magnusson WE (1998) Partitioning seasonal time – interactions among size, foraging activity and diet in leaf-litter frogs. Oecologia 116:259–266

MacArthur RH, Pianka, ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

McPhaden MJ (1994) Oceanography – the 11-year El Niño. Nature 370:326–327

McWilliams SR, Afik D, Secor S (1997) Pattern and processes in the vertebrate digestive system. Trends Ecol Evol 12:420–422

Nagy KA, Shoemaker VH (1984) Field energetics and food consumption of the Galapagos marine iguana, *Amblyrhynchus cristatus*. Physiol Zool 57:281–290

Nogales M, Hernandez EC (1994) Interinsular variations in the spring and summer diet of the raven *Corvus corax* in the Canary Islands. Ibis 136:441–447

Owensmith N (1993) Comparative mortality-rates of male and female kudus – the costs of sexual size dimorphism. J Anim Ecol 62:428–440

Pianka ER (1994) Evolutionary ecology. Harper Collins, New York

Rassmann K (1997) Evolutionary age of the Galápagos iguanas predates the age of the present Galápagos islands. Mol Phylogenet Evol 7:158–172

Rauch N (1985) Female habitat choice as a determinant of the reproductive success of the territorial male marine iguana (*Amblyrhynchus cristatus*). Behav Ecol Sociobiol 16:125–134

Schluter D (1982) Distributions of Galapagos (Ecuador) ground finches along an altitudinal gradient: the importance of food supply. Ecology 63:1504–1517

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404

Snell H (1987) Size of Galápagos land iguanas: episodic selection resolves a paradox. Am Zool 27:123A

SPSS (1991) SPSS statistical algorithms. SPSS, Chicago

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton

Trillmich F, Trillmich KGK (1984) The mating system of pinnipeds and marine iguanas: convergent evolution of polygyny. Biol J Linn Soc 21:209–216

Trillmich KGK, Trillmich F (1986) Foraging strategies of the marine iguana, *Amblyrhynchus cristatus*. Behav Ecol Sociobiol 18:259–266

Troyer K (1982) Transfer of fermentative microbes between generations in a herbivorous lizard. Science 216:540–542

Troyer K (1984a) Behavioural acquisition of the hindgut fermentation system by hatchling *Iguana iguana*. Behav Ecol Sociobiol 16:189–193

Troyer K (1984b) Diet selection and digestion in *Iguana iguana*: the importance of age and nutrient requirements. Oecologia 61:201–207

Troyer K (1984c) Strucutre and function of the digestive tract of a herbivorous lizard *Iguana iguana*. Physiol Zool 57:1–8

Wiggins IL, Porter DM (1971) Flora of the Galapagos islands. Stanford University Press, Stanford

Wikelski M, Bäurle S (1996) Pre-copulatory ejaculation solves time constraint during copulations in marine iguanas. Proc R Soc Lond B 263:439–444

Wikelski M, Hau M (1995) Is there an endogenous tidal foraging rhythm in marine iguanas? J Biol Rhythms 10:345–360

Wikelski M, Trillmich F (1994) Foraging strategies of the Galapagos marine iguana (*Amblyrhynchus cristatus*):adapting behavioral rules to ontogenetic size change. Behaviour 128:255–279

Wikelski M, Trillmich F (1997) Natural and sexual selection on body size fluctuates between marine iguana island populations. Evolution 51:922–936

Wikelski M, Gall B, Trillmich F (1993) Ontogenetic changes in food-intake and digestion rate of the herbivorous marine iguana (*Amblyrhynchus cristatus*, Bell). Oecologia 94:373–379

Wikelski M, Carbone C, Trillmich F (1996) Lekking in marine iguanas:female grouping and male reproductive strategies. Anim Behav 52:581–596

Wikelski M, Carrillo V, Trillmich F (1997) Energy limits to body size in a grazing reptile, the Galápagos marine iguana. Ecology 78:2204–2217