

FORAGING STRATEGIES OF THE GALAPAGOS MARINE IGUANA (*AMBLYRHYNCHUS CRISTATUS*): ADAPTING BEHAVIORAL RULES TO ONTOGENETIC SIZE CHANGE

by

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(With 8 Figures)

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Summary

Ontogenetic development in reptiles entails major changes in size-related foraging options. We studied the changes in foraging behavior of marine iguanas. In this species, size increases about twenty- to hundredfold from hatching to full adult size. The foraging strategy of marine iguanas was studied at Miedo on Santa Fé Island in the Galapagos archipelago. During low tide, large marine iguanas (>250 mm snout vent length (SVL)) foraged more in the lower intertidal than small ones (<250 mm SVL) which preferred the upper intertidal with higher temperatures and less frequent wave washing. Animals usually returned to the same foraging site day after day and had lower food intake after changing their foraging site. Feeding accounted for 60% of the time spent in the intertidal. Smaller animals fed every day, larger ones only every other day. Smaller individuals shuttled faster between foraging and basking sites than larger ones. Total feeding time per day was, however, the same for both size classes. At neap tides (= high water level at low tide) animals had shorter foraging bouts than at spring tides with much lower water levels at peak low tide. Length of feeding bouts depended most on wave action, time of low tide (during the daylight period), and body mass of an animal. Small animals fed significantly less at higher than at lower wave activities. All animals on Santa Fé spent more time feeding

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in the intertidal than in the subtidal. Only large males additionally foraged subtidally and the more so the bigger they were. During the reproductive season, territorial males were less likely to go foraging, but when feeding, territorials fed more subtidally than non-territorials, went foraging earlier, and spent less time foraging in the IT than non-territorials. Ability to resist wave drag increased with body size but did not decrease at lower body temperature, whereas running speed did so significantly. Bite frequency during foraging also decreased with decreasing body temperature and smaller, younger animals had higher bite rates than older, bigger ones. White-painted animals rewarmed slower than naturally black ones and partially compensated for this by shortening foraging bouts but increasing their number. The observed age-related changes in foraging behavior can be explained by postulating a rule of the form 'forage while warm and warm up when getting inefficient at grazing'. Of course, animals will also stop feeding should the stomach be filled before the end of the low tide cycle. To explain age- and motivation-related differences in foraging behavior, the only change that needs to be postulated is in the thresholds of body temperature inducing switches from foraging to warming-up and back. These changes are adaptive responses to size-related changes in costs and benefits of foraging in a cool, wave-washed environment.

Introduction

Changes in foraging strategy are common during ontogenetic size development. The best examples can be found among reptiles, because independent of their parents juveniles often increase their body mass over 100-fold before reaching adult size (POUGH, 1973; POND, 1977). As most physiological properties of animals scale with body size (PETERS, 1983; SCHMIDT-NIELSEN, 1984), we would expect that early ontogenetic stages face problems which differ widely from those of adults. If so, size changes during ontogeny could lead to widely differing foraging patterns unless animals compensate by behavioral means for changing physiological capabilities and environmental constraints. In other words, animals may have to change the basis on which they decide when, where, and how much to feed as they grow. In addition, adult animals often have to decide between foraging and reproduction.

These questions are highly relevant for growing Galápagos marine iguanas (*Amblyrhynchus cristatus*). They hatch at about 50-60 g and grow to a mass of about 1 to 12 kg (LAURIE, 1989, 1990). Herbivory is relatively rare in reptiles (TROYER, 1983), and marine iguanas are unique in feeding on softbodied macrophytic marine algae (DARWIN, 1883; HOBSON, 1965, 1969; CARPENTER, 1966). Most marine iguanas obtain their algal diet from foraging in intertidal (IT) areas which are only accessible at low tide (TRILLMICH & TRILLMICH, 1986). This restricts foraging to a short time

each day. Only large marine iguanas can feed independent of the tidal cycle by foraging in subtidal (ST) areas (TRILLMICH & TRILLMICH, 1986).

Marine iguanas are adapted to foraging at the fringe of the sea by possession of long sharp claws, tough skin, blunt heads, flattened tails (TRACY & CHRISTIAN, 1985), and highly developed salt glands (SCHMIDT-NIELSEN & FANGE, 1958; DUNSON, 1969). But physiologically they did not adapt to the cold temperatures of their IT or ST foraging environment (14-25°C) by lowering preferred body temperature (BARTHOLOMEW, 1966; TRILLMICH & TRILLMICH, 1986). As it grows, foraging in a cold environment presents less and less of a challenge to an iguana preferring high body temperature around 35-40 °C. Increasing heat retention abilities resulting from higher body mass (BARTHOLOMEW & LASIEWSKI, 1965; MORGAREIDGE & WHITE, 1969) might be expected to lead to large differences in foraging behavior between large and small animals (*cf.* HERTZ *et al.*, 1988).

These ideas could not be tested so far since little was known about the foraging behavior of small marine iguanas. TRILLMICH & TRILLMICH (1986) only described the foraging behavior of animals larger than 500 g. Since such animals are already about 10 times heavier than hatchlings, it is obvious that a substantial part of the ontogeny of foraging has been missed. Here we try to fill this gap in our knowledge by: (i) documenting for the first time the foraging behavior of small marine iguanas (< 500 g); (ii) looking in more detail at the transition between IT and ST foraging; and (iii) experimentally analysing the factors influencing foraging habitat choice and foraging decisions.

We also studied the influence of male territoriality during the reproductive season on foraging decisions. We suggest a model which makes changes in foraging behavior during the animals' ontogeny understandable in terms of one common set of foraging decisions.

Background natural history.

Marine iguanas are endemic to the Galápagos archipelago. On Santa Fé, males are territorial from November until the end of December. Their territories include female resting sites. Females resting on a territory, usually copulate with the male on whose territory they rest (TRILLMICH, 1983). Marine iguanas on Santa Fé are food limited and large population

fluctuations resulting from varying food supply were observed by LAURIE (1989; LAURIE & BROWN, 1990 a, b) during his 6-year study.

Material and methods

Field work was carried out at the Miedo study site (*cf.* LAURIE, 1990), on the SE coast of Santa Fé, a 2400 ha uninhabited, arid island without introduced predators. Animals were captured by gripping their tails or by noosing. We painted numbers on the animals' sides with synthetic paint (LAURIE, 1989). Captured animals were sexed on the basis of external morphology (adults) or by measuring cloacal pouch depth with stainless steel probes (DELLINGER & VON HEGEL, 1990). Snout to vent length (SVL in mm) was measured to the nearest 1 mm using a 600 mm stainless steel rule. Body mass was determined with spring balances (Pesola). Condition was defined as mass/SVL^3 (LAURIE & BROWN, 1990 b). Marine iguanas with an SVL < 250mm (mass < approximately 600 g) were termed "small animals" and were compared to "large animals" (SVL > 250 mm).

Observations of foraging animals were made from prominent rocks or cliffs using binoculars and telescopes. In the observation area, strongly inclined cliffs and narrow IT areas prevailed. On 37 days, in November (23, 29, 30) and December 1989 (1-22, 30, 31), and January 1990 (7-13, 23-27), observations were made for approximately five hours per day covering all the time available for IT feeding at low tide. 1309 individual IT-foraging bouts (from entering to leaving the IT) of marine iguanas were recorded (1174 bouts of 178 small individuals, 135 IT-bouts of 41 large individuals), totalling 140 animal feeding hours.

Focal animals were observed from the moment they entered the foraging area until the end of a feeding bout (leaving the IT or ST area for basking or terminating foraging). Every 30 sec the locality and activity of focal animals were recorded. Feeding was recorded continuously as was the washing of waves over animals, and fleeing from approaching waves. The focal animals were individually known from previous capturing and marking. In addition, durations of individual foraging bouts of non-focal animals were recorded.

To determine bite frequency over feeding bouts, one person exclusively counted bites of focal animals. Data were discarded when the animal was not visible continuously during the entire foraging bout. Every half hour, rock temperature and wave activity were determined (*see below*).

The *total feeding time per day* is defined as the cumulative sum of all feeding bouts of one individual per day, *warm-up time* as the timespan between two feeding bouts, and *feeding bout* length as the time interval between entering and leaving the IT or ST foraging area. The times and height of low tide (in m) were taken from the tide tables of Santa Cruz island (source: Ecuadorean navy).

328 diving excursions of 40 individually known subtidally foraging marine iguanas were observed over a period of seven weeks from November 30, 1989, until January 15, 1990. This covered periods in the reproductive (November — December) and immediately post-reproductive season (January). Daily observations covered all the time the iguanas utilized for diving (08:00 to 16:00h). No animals were observed diving before 08:00 or after 16:00 (*cf.* TRILLMICH & TRILLMICH, 1986). Within a 150 m strip of coastline we could record all swimming and diving activity and the location of all marked animals.

The total number of ST feeders and their time spent feeding every day were recorded. Within one diving bout, some males performed multiple dives. The duration of each dive was recorded for ST feeders as well as total time in water. Presence or absence of territorial males on their territories was observed every day before and after foraging.

Wave activity was recorded on a standardized scale graded from 0 to 4 (0 = no waves; 1 = sea slightly moved, small waves; 2 = medium waves, amplitude about 1 m; 3 = large waves, amplitude 1-2.5 m; 4 = big breakers, amplitude > 2.5 m). Cloud cover was estimated in eighths. Ambient air (50 cm above the ground in shade) and rock temperature (sun exposed

rock surface) were determined three times a day using a mercury thermometer accurate to $\pm 0.1^\circ\text{C}$. Sea surface temperature was measured to the nearest 0.2°C every day at noon. There was a sharp difference between the upper and lower IT, with higher wave activity, higher algae abundance and lower surface temperatures in the latter (WIKELSKI *et al.*, 1993); the boundary between the two areas was quite abrupt, with barnacles covered by red algae in the lower IT, but bare in the upper IT. This cannot be attributed to grazing pressure but is rather due to higher temperatures in the more exposed upper intertidal (F. WALSH, pers. comm.).

At the transition between upper and lower IT, wooden models resembling hatchling and juvenile marine iguanas in size and shape were fixed on a pesola (scale 5 kg) equipped with a 'maximum-force-indicator'. The measured force, exerted by score 3 waves on the model during medium tide, was taken as an indicator of the gripping strength necessary to resist the drag force of waves washing over foraging animals.

Physiological measurements.

The strength of an iguana's grip on standard wire mesh (width: 10 x 10 mm) was determined at different deep-body temperatures (T_b 's; measured by inserting a temperature probe at least 2 cm deep into the cloaca) for a sample of 44 animals of different sizes and sexes. Harnesses were made for each of the size classes to distribute force equally over their bodies. After T_b measurement, animals were placed on a mesh fixed to a wooden frame on the ground. Their feet were placed in a standardized, natural position relative to the body. Spring balances (Pesola) of 2.5 kg, 5 kg, 10 kg and 25 kg with maximum force indicator were used to pull on the harness (at an angle of 45° from behind the animal). Force was increased slowly and steadily until the first toe or foot lost its grip and left the mesh. The iguanas apparently hang on to the mesh as hard as possible to avoid being pulled off. This resembles the situation encountered by a marine iguana many times a day whenever a wave washes over it in the intertidal foraging area. Measurements were performed twice and were not used for analysis if the difference between the first and second value was greater than 10% (which happened for five individuals which apparently did not properly grip the mesh).

Harnesses were then taken off and animals put into a 3.5 m long and 40 cm wide enclosure with 30 cm high plastic side walls on sandy soil. The time the animals took to run 3.5 m was measured with a digital wrist watch. Iguanas were then held in $20\text{--}23^\circ\text{C}$ seawater until T_b had reached water temperature. Strength and speed measurements were repeated. The sequence of measurement (first high or first low T_b) had no effect on the results in 5 animals tested both ways (first high and then first low T_b). Therefore, 'first high T_b ' was chosen for measurement convenience. Most marine iguanas appeared not to be scared by the experiments and many did not even try to escape after being released.

Fifty-one individuals that had first been observed entering IT areas were captured immediately after they returned from a foraging bout and their T_b 's were measured within 15 sec. They were then weighed and measured. T_b of 13 animals was also measured immediately before they entered the foraging area. For these measurements, no individual was sampled more than once.

Four different-sized focal animals were painted white on the back with synthetic paint after 9-13 consecutive days of foraging observation. Rates of heat gain of these individuals were determined before and after painting and compared to equal-sized unpainted marine iguanas. The four painted iguanas were then observed focally for the four days following painting. The white paint rubbed off soon after and all four marine iguanas were healthy in February 1992.

R_s signifies Spearman rank correlation as opposed to r which stands for Pearson product-moment correlations.

Results

Behavior during IT foraging.

a) General observations.

More animals entered the foraging area during calm moments than when the IT was washed, especially when wave activity was high (entering during low tide: 174 animals per 30 min during calm times, 44 per 30 min during wave washed times; total observation time 98 min; $\chi^2 = 13.9$, $df = 1$, $p < 0.001$). At the beginning of each foraging bout, iguanas raised their body to avoid physical contact with the cold surface, even when running to their favorite feeding spot.

Hatchlings tried to avoid wave washing by running upward either to the uppermost foraging areas or, when high waves approached, to dry land. When they were interrupted during feeding by smaller waves, they flattened their bodies against the rocks and often hid behind barnacles (the barnacles of the IT area grow to heights of 10 cm).

Site fidelity of all animals to individual foraging sites was very high: $90 \pm 4\%$ of all feeding bouts recorded for a given individual were in the same area ($N = 54$ animals). Sixteen animals that were observed for more than 10 days at one area and then changed to a foraging area which they had not used on the previous days had shorter than normal total feeding times per day on subsequent days at the new site (Wilcoxon paired rank test, $T = 26$, $N = 16$, $p < 0.05$). This suggests reduced food intake in the less familiar area since food intake is positively correlated with foraging time (see below).

b) Quantitative comparison of small and large animals.

Small animals (< 250 mm SVL) stayed in the upper IT most of the time ($90 \pm 4\%$ of IT time budget; total daily feeding time 23.8 ± 11.3 min.; $N = 47$ small marine iguanas on 178 feeding days) and only entered the lower IT at times when there were hardly any waves (score 0). Large animals ($N = 25$) preferred to feed in the lower IT areas ($60 \pm 9\%$ of time spent in IT; total daily feeding time 28.6 ± 23.4 min, $N = 41$ feeding days)(difference between distributions of small and large animals: Mann Whitney U-test, $z = 3.32$; $N_1 = 47$, $N_2 = 25$; $p < 0.01$). All animals had similar time budgets during foraging in the IT (Fig. 1; Friedman test, $\chi^2 = 1.46$, $df = 2$, $p =$

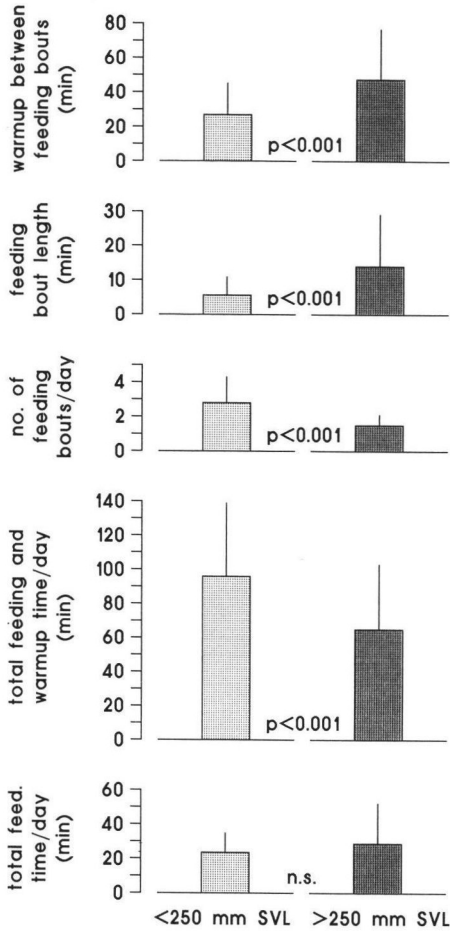


Fig. 1. Comparison between the foraging behavior of small (SVL < 250 mm) and large (SVL > 250 mm) marine iguanas (means \pm 95% confidence interval; between columns, significances of differences between the data for small and large animals based on Mann-Whitney U-tests). Small marine iguanas warm up for shorter periods between feeding bouts (top panel), have shorter feeding bouts (second panel), but make more feeding bouts per day (third panel), and their foraging activity (total feeding and warm-up time) extends over a longer period of time per day than that of larger animals (fourth panel). As a result, small and large animals reach similar total feeding time per day (sum of all individual feeding bout lengths) (lowest panel).

0.48). They were $13 \pm 7\%$ stationary, $27 \pm 5\%$ running, and $60 \pm 3\%$ feeding.

Small animals preferred to forage in the warmer upper IT where they went foraging every day (days between foraging 1.07 ± 0.1 ; $N = 187$), except on days with extremely high wave activity (score 4). Large animals foraged every second day only (1.8 ± 0.24 days between foraging; $N = 32$), mostly in the lower IT. Small animals started feeding before the large ones entered the IT foraging area and left the feeding area later (Fig. 1, fourth panel). Most animals made more than one, and hatchlings up to 8 feeding bouts per day during low tide. Large animals rested longer to warm up between foraging bouts (Fig. 1, upper panel). Small animals had shorter feeding bouts (Fig. 1, second panel), shuttled faster between IT areas and basking places, and, therefore, made more foraging bouts per day (during the low tide period) than large animals (2.8 vs 1.2) (Fig. 1, third panel). First and last bouts were shorter than the bouts around lowest low tide (lowest low tide equals time zero, bout length for absolute time from lowest low tide: $r_s = 0.35$, $N = 827$, $p < 0.001$). For the total feeding time (exclusive of warm-up), there was no significant difference between the two groups, although larger animals showed a tendency to forage slightly longer than small ones (Fig. 1, lowest panel).

Environmental influences.

Apart from the hour of low tide (TRILLMICH & TRILLMICH, 1986), tide level and wave activity strongly influenced foraging time. High low-tide levels coincided with shorter feeding bouts (Kruskal-Wallis, $H = 2.78$, $p < 0.01$, $df = 3$, $N = 1304$ feeding bouts on 37 days of 219 animals). Feeding bouts of hatchlings declined from a median of 9 min at 0 m low tide level to 3 min at 0.6 m, and total feeding time from 29 min to 9 min (Kruskal-Wallis, $H = 2.3$, $df = 3$, $p < 0.05$, $N = 812$ feeding bouts on 37 days of 71 animals).

In a simultaneous multiple regression analysis of length of feeding bouts of marine iguanas of all sizes, the variables 'wave activity', 'time of low tide' and 'body mass' of the animal explained most of the variance. Other variables (cloud cover, water temperature, warm-up time before the feeding bout, height of low tide, and rock temperature) had no significant (all $p > 0.05$) effect on the fit of the model as a whole ($F = 76$, df

= 1305, $p < 0.01$, $r = 0.5$). Low tide height and wave activity in the IT zone are independent effects that can act in concert or opposing each other and thus both were entered.

The number of feeding bouts per day showed no correlation with wave activity in large animals, but small animals made significantly more feeding bouts at medium wave activity (score 2: 4.6 ± 1.1 bouts/day) than at both low (score 1: 3.8 ± 0.9 bouts/day) and high (score 3: 3.5 ± 1.0 bouts/day) wave activity (Kruskal-Wallis test, $H = 14.2$, $p < 0.001$, $N = 197$ foraging days of 78 individuals). Total feeding time per day showed no dependence on wave activity in large animals, but varied significantly with wave activity in small animals (ANOVA, $F = 7.2$, $df = 3$, $p < 0.001$; wave activity 0 = 23 ± 4 min, 1 = 26 ± 6 min, 2 = 21 ± 4 min, 3 = 13 ± 8 min). Warm-up times of individuals were shorter on sunny days (27 ± 20.7 min, cloud cover 0-4) than on cloudy days (33.2 ± 20.3 min, cloud cover 5-8)(Mann-Whitney U-test, $Z = 2.32$, $N_1 = 235$, $N_2 = 178$, $p < 0.05$). Obviously, small animals showed most changes in foraging behavior under adverse environmental conditions.

Subtidal foraging.

In Santa Fé, only 5% of 800 marked animals foraged in the ST (population composition of marked animals: 436 males from 125 to 412 mm SVL, 364 females from 123 to 321 mm SVL). No female was found diving on Santa Fé. All 40 subtidally foraging males were large enough to become territorial (median mass of subtidal feeders: 2790 g, $N = 40$), but only 60% were territorial. Male marine iguanas dived in areas with big boulders in 3-5 m depth. 98% of ST feeding activity occurred between 10:30 and 15:00 hours. ST feeding hardly ever occurred around low tide, because even big males were more likely to forage in the IT area at low tide. When low tide occurred in the early morning hours, these males foraged less in the IT (correlation with hour of low tide: $r_s = 0.56$, $N = 484$, $p < 0.001$) and more in the ST (for low tides between 06:00 and 09:00 hours, 72 ± 31 foraging trips in the ST/day, 19 ± 18 foraging trips in the IT).

The higher the water temperature, the more marine iguanas went foraging in the ST ($r_s = 0.47$, $N = 18$ days, $p < 0.05$). On days of strong wave action, fewer ST feeders were observed (Kruskal-Wallis H-test, $H =$

10.5, $df = 3$, $p < 0.05$). Neither cloud cover nor rock temperature significantly influenced the proportion of animals that fed subtidally each day.

Before foraging, marine iguanas had T_b 's of $36.7 \pm 0.9^\circ\text{C}$ (mean \pm SD, $N = 11$). ST feeders waited near the cliff for a big wave to carry them out to sea. Then, they slowly swam 30 m offshore, where they submerged with a strong tail undulation. Animals stayed in the water for 13.7 min (median) and returned to shore with an average T_b of $23.8 \pm 0.9^\circ\text{C}$ ($N = 14$), which was only slightly higher than sea surface temperature ($21.7 \pm 0.5^\circ\text{C}$). The median number of diving bouts per day was 2 (range 1-10). When rock temperature was higher, duration of diving bouts was longer ($r_s = 0.37$, $N = 35$ animals, $p < 0.05$). At a rock temperature of 29°C dive bouts lasted on average 5 min, and 7.5 min at 42°C rock temperature. More diving bouts were performed when rocks were warmer ($r_s = 0.66$, $N = 40$ animals, $p < 0.001$). At 29°C the mean was 1.5 bouts per day, at 42°C 2.3 bouts/day. Single dives lasted from 57 sec to 732 sec with a median of 230 sec ($N = 116$). Lengths of dives were not correlated to individual properties of animals (SVL, weight, tail length, condition), nor to wave action or water temperature. Dive duration declined as more dives were performed per foraging bout (Kruskal-Wallis H-test, $H = 15.6$, $N = 41$, $p < 0.001$).

The total duration of all observed diving bouts, per animal and day of foraging, averaged 465 sec (± 240 s, $N = 41$) with a minimum of 117 sec and a maximum of 1920 sec (32 min). Total diving time per animal and day increased with time in the water (regression, see Fig. 2; $r = 0.68$, $p < 0.001$, $N = 39$). This is not self-evident because some iguanas need much longer than others to leave the water or to swim to their ST foraging sites. According to the best fitting function (see legend Fig. 2) doubling time in the water only resulted in prolonging the total diving time by a factor 1.75.

Comparison of subtidal and intertidal feeding.

All subtidally foraging males, except the largest one, foraged in both the ST and the IT area. The larger and heavier an animal, the more it foraged in the ST (body mass: $r_s = 0.41$, $p < 0.01$, $N = 40$; SVL: $r_s = 0.51$, $p < 0.001$, $N = 40$). The slope of the regression of percent ST foraging

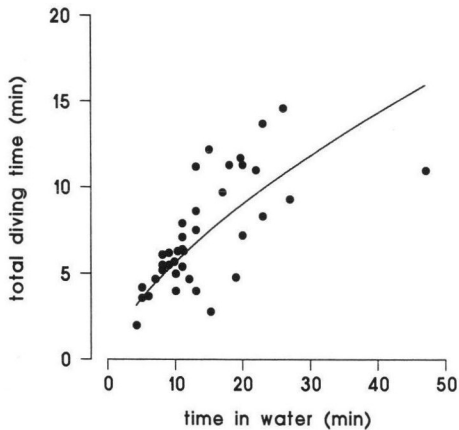


Fig. 2. The longer male marine iguanas stayed in the water, the lower the proportion of time spent diving. A non-linear model fitted significantly better than a linear regression (equation: diving time (min) = $1.1969 \times \text{time in water}^{0.673}$; $r = 0.75$, $N = 39$, $p < 0.001$).

against body mass was 0.29 ($r^2 = 0.3$, $df = 38$, $p < 0.001$). There was no significant difference in body condition between mainly subtidally and mainly intertidally feeding animals. Every foraging day, individuals spent more time foraging in the IT (median = 30.4 min) than in the ST (median = 13.7 min) (Wilcoxon test, $Z = 2.83$, $N = 28$, $p < 0.001$).

Influence of territoriality on foraging.

Morphologically, territorial and non-territorial subtidally foraging males were not different (Mann-Whitney U-tests, all $p > 0.05$ for SVL, tail length, weight, condition). Foraging modes differed during and after the reproductive season (Table 1) with less ST feeding in the latter by both territorial and non-territorial males (Table 1; $\chi^2 = 6.158$, $df = 1$, $p < 0.05$).

During the reproductive season, territorial males were slightly more likely to adopt the ST feeding strategy (76.6%) than non-territorials (66.6%), (Mann-Whitney U-test, $Z = 1.91$, $N_1 = 13$, $N_2 = 23$, $p = 0.056$). Territorial males left the resting sites significantly later for foraging in the IT than non-territorial males with a mean time lag of 42 min (Mann-Whitney U-test, $Z = 2.87$, $N_1 = 69$, $N_2 = 65$, $p < 0.001$), and a mean time

TABLE 1. Total foraging times of marine iguana males in minutes (mean \pm SD (N))

Males	Season		Non-reproductive				
	Reproductive						
non-territorial	ST	a)	10.6 \pm 1.8	(35)	b)	15.0 \pm 3.5	(59)
	IT	c)	43.0 \pm 12.6	(32)	d)	37.0 \pm 13.2	(14)
territorial	ST	e)	14.1 \pm 1.6	(24)	f)	17.0 \pm 2.7	(109)
	IT	g)	10.0 \pm 3.5	(42)	h)	46.0 \pm 14.1	(20)

Significant differences by Mann-Whitney U-Test exist between c) and g) ($p < 0.05$), a) and e) ($p < 0.05$), and g) and h) ($p < 0.001$).

lag of 17 min when they left their territory to forage subtidally (Mann-Whitney U-test, $Z = 2.39$, $N_1 = 146$, $N_2 = 183$, $p = 0.01$). Territorial males fed less time than non-territorials in the IT, but longer in the ST (Table 1). After a foraging bout, territorial males immediately went back to their territories, whereas non-territorial males stayed basking on the first warm rocks they found ashore.

After the reproductive season, formerly territorial males fed in the ST area more often than formerly non-territorial males ($\chi^2 = 5.58$, $df = 1$, $p < 0.05$, $N = 193$). All males had longer feeding times per day than during the reproductive season (Table 1), and previously territorial males left not significantly later or earlier than former non-territorial males to the IT and ST.

Physiological parameters influencing foraging.

Besides thermal influences and reproduction, wave action influenced foraging decisions most. We therefore tried to elucidate how wave forces act as a size-related constraint on foraging.

Grip strength.

Gripping strength strongly influenced an iguana's ability to resist wave currents in the IT. Grip strength was expected to increase with animal size and decrease with T_b . As expected, gripping strength increased linearly with increasing body size ($r = 0.98$, $N = 43$, $p < 0.001$; Fig. 3a), but it did not change with T_b (Wilcoxon test, $Z = 0.79$, $p = 0.42$). At low wave activity, waves exerted a force of 1.4 N on the wooden hatchling model, 2.6 N on the juvenile model and 5.0 N on the adult model. At high

wave activity the forces were 2.8 N for the hatchling model and 4.1 N for the juvenile model and only estimated for the adult model (Fig. 3a). The maximum gripping strength of the animals usually exceeded the force exerted on the wooden models by waves. Wave drag equalled or even exceeded gripping force only for hatchlings during high wave activity. The gripping strength of adults was always higher than wave drag (Fig. 3a).

Speed.

Running speed decreased with T_b (Wilcoxon test, $Z = 4.8$, $N = 25$, $p < 0.001$) (Fig. 3b). Mean sprint speed at high T_b was 1.4 m/sec (SD ± 0.64),

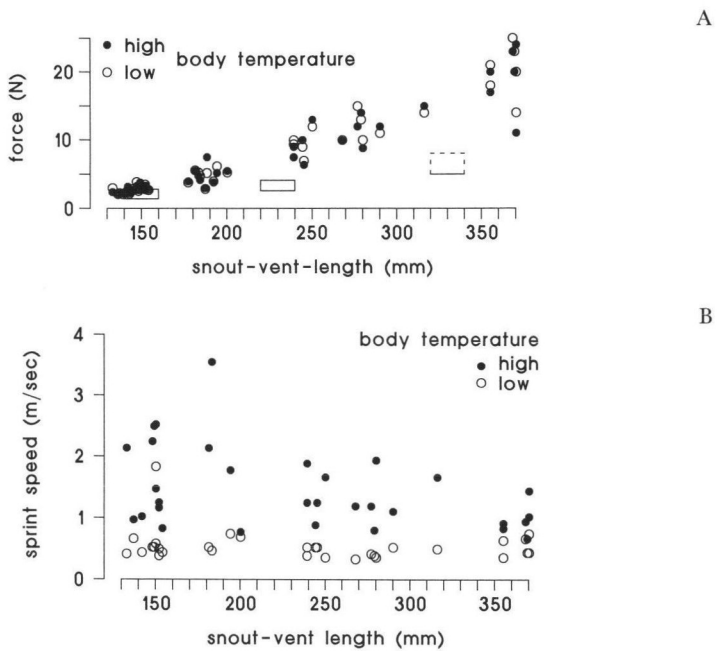


Fig. 3. a) Large marine iguanas keep a stronger grip on wire mesh than small ones. The strength of each individual was tested twice, at high (approx. 35°C) and low (approx. 25°C) T_b . No difference in strength was found between high (closed circles) and low (open circles) T_b . The open boxes represent the range of drag force of waves upon wooden iguana models. The hatched bar represents a lower estimate only, because at greater wave strength the researcher was swept away. b) Marine iguanas run faster at high (approx. 35°C) than at low T_b (approx. 25°C, open circles). Sprint speed of each individual was tested once at high and once at low T_b . At low T_b , all individuals ran at similar maximum speed.

at low T_b 0.53 m/sec (SD \pm 0.25) (*cf.* VAN BERKUM *et al.*, 1989; HUEY *et al.*, 1990). When animals foraged in the lower IT they were not able to run to a safe place, because high waves came at irregular intervals and reached them within approximately 2 sec, too short a time to allow them to leave the foraging area (a distance of at least 4 m). Animals foraging in the lower IT had to grip the rocks and hide behind a barnacle or in a crevice to resist the strength of the waves.

Natural cooling.

As found earlier (TRILLMICH & TRILLMICH, 1986), the smaller an animal, the higher was its T_b when it returned from foraging (Fig. 4 top). Large

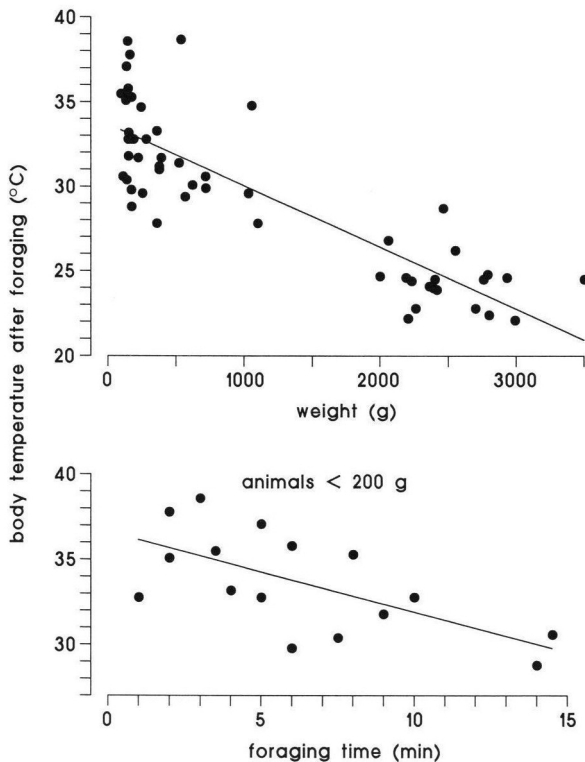


Fig. 4. Small marine iguanas return from foraging with much higher T_b than large animals (top). In the largest marine iguanas, T_b sometimes fell almost to water temperature (22° vs 21°C, respectively). High variance occurs because data from all environmental conditions and foraging bout lengths were pooled. In small marine iguanas (T_b after foraging decreased with foraging bout length (bottom).

males above 350 mm SVL cooled down to T_b 's nearly equal to water temperature, whereas hatchlings sometimes returned from foraging with T_b above 37°C. However, beyond this well established fact, the high variance within the group of animals below 200 g was explained by the length of individual feeding bouts (Fig. 4 bottom). The longer a hatchling foraged in the IT area, the lower its T_b when it returned from foraging. The data did not allow to test this for animals above 120 mm SVL.

Bite rate.

Frequency of bites (per 30 sec) declined linearly with the time the animals were feeding (Fig. 5; $r = -0.44$, $N = 43$, $p < 0.01$). Bite frequency in the first half of each feeding bout was higher (median 24/30 sec) than in the second half (median 19/30 sec) (Wilcoxon test, $Z = 3.04$, $N = 27$, $p < 0.001$). Differences in bite frequencies were found between age classes. Hatchlings and juveniles had median rates of 23 bites and adults 16 bites per 30 sec (Mann-Whitney U-test, $Z = 2.46$, $N_1 = 130$, $N_2 = 76$, $p < 0.05$).

The influence of rate of heat exchange on foraging decisions.

Thermal constraints, related to body mass, obviously influenced foraging decisions. We therefore altered the radiative heat gain of 2 small and 2 large marine iguanas by painting them white. Painted animals showed

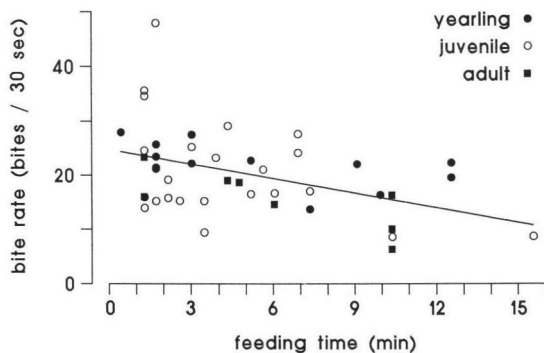


Fig. 5. Marine iguanas feed with high bite rates when entering the foraging area. The longer animals stay in the IT, the lower the bite rate (bite rate = $24.7 - 0.01 \times$ time in IT (min); $F_{1,42} = 10.1$, $r^2 = 19.4$). High variance results from pooling data from marine iguanas of all sizes and from all environmental conditions.

normal behavior in terms of daily feeding activity, site fidelity, and interactions with conspecifics. They lost the white color after 15-20 days.

White-painted marine iguanas warmed up slower than equally-sized unpainted iguanas (Fig. 6). The warm-up curves of white-painted animals were similar to those of animals larger than the experimentals.

Painted animals did not change warm-up time between feeding bouts (Fig. 7, top) (Wilcoxon test, NS), however, length of feeding bouts declined in all four animals (Fig. 7, second panel) (Wilcoxon test, $T = 5$, $N = 15$, $p < 0.01$ for the small and $T = 15$, $N = 13$, $p < 0.05$ for the large animals). The median number of feeding bouts per day increased after painting (small iguanas: 4.5 to 7, large iguanas 2.5 to 4; Fig. 7, third panel). The painted small iguanas only increased total feeding and warm-up time on 2 days with low wave activity; on days with high wave activity, total feeding and warm-up time was similar before and after painting. The large iguanas increased their total feeding and warm-up time from 94 min before to 143 min after painting (Fig. 7, fourth panel). Total feeding time per day of the small iguanas decreased after painting (from 26 min to 15 min), but did not change for the large iguanas (25 min vs 24.5 min) (Fig. 7, lowest panel).

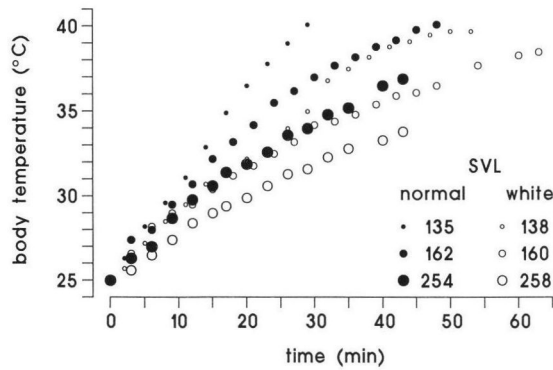


Fig. 6. The heating curve of marine iguanas of different sizes and colors: marine iguanas with normal (brownish-black = 'natural') coloration are compared to animals painted white. At similar sizes, the white colored marine iguanas warm-up slower than black control animals. The heating curves of white painted animals resemble those of larger normal animals (160 mm SVL white is similar to 254 mm SVL normal) or those during cold or cloudy weather (not shown). Two further animals (SVL 203 and 207 mm) were also measured, but are not shown here for graphical clarity.

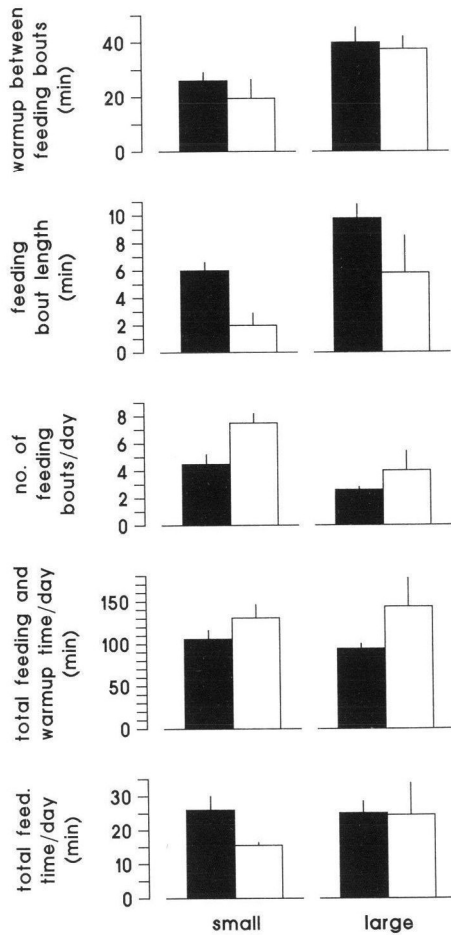


Fig. 7. Comparison of the foraging behavior of one small and one large marine iguana (mean \pm 95% confidence interval) before (black bar) and after (white bar) painting them white. The other two animals showed similar behavior and were omitted for graphical clarity. See text.

Discussion

Even though they live under tropical sun, marine iguanas have to forage in a cool (14-23°C) intertidal or marine environment. Within the foraging areas of marine iguanas (upper and lower IT, ST) there is a gradient of decreasing ambient temperature but increasing availability of food; algal digestibility is similar across the entire gradient (WIKELSKI *et al.*, 1993).

Small marine iguanas stayed in the upper IT where they made short but frequent feeding excursions. Medium sized animals foraged exclusively in the IT and made most use of the lower parts of it and only a few large males additionally exploited the ST algal fields by diving. On other islands, where marine iguanas become larger, more of them turn to a pure ST foraging strategy (*e.g.* on Fernandina; TRILLMICH & TRILLMICH, 1986). Thus, changes in body size during ontogeny result in different foraging behavior. The differences in foraging behavior of small and large marine iguanas can be explained by mass-related changes in cooling and heating rates combined with an ontogenetic shift in upper and lower threshold temperature for, respectively, initiating and ending foraging. Despite the apparent differences in foraging behavior, marine iguanas may follow the same decision rules during foraging over their entire lifetime.

The 'sawtooth-model' of foraging decisions.

These results can be summarized in a somewhat idealized way by the 'sawtooth' model (Fig. 8). With this model we attempt to make the effect of size on foraging behavior understandable as a consequence of changing patterns of thermoregulatory shuttling. It also serves to point out where further more detailed information on thermoregulation is needed. Animals of all sizes enter the foraging area with high T_b . They appear to heat up as much as possible before entering the cool foraging areas. We measured a T_b of 43°C in one hatchling, well above the 39.5°C maximum value of body temperature recorded by WHITE (1973). While foraging in the IT, animals cool down and eventually return to basking places to warm up again. This cycle is repeated until either the stomach is filled or wave action increases to a point (with the incoming tide) where further foraging becomes ineffective.

Two factors seem responsible for the interruption of foraging and the move from the IT to basking places when body temperature has fallen. Firstly, small animals which have relatively low gripping strength (Fig. 3a) cannot escape fast enough from approaching waves when cool because their running speed decreases with T_b (Fig. 3b) thus they may get swept away. This leads to a twofold cost: (i) loss of time (swimming back to land and rewarming), and (ii) at least for small animals, a serious risk of

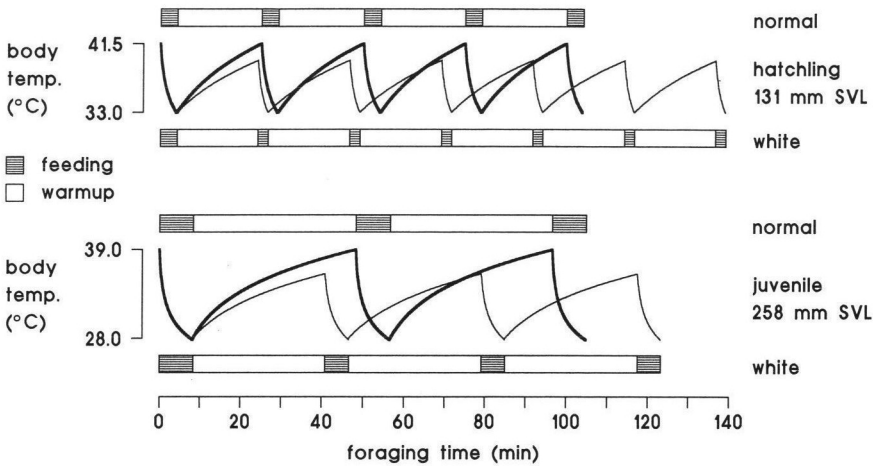


Fig. 8. The 'Sawtooth-Model' of marine iguana foraging behavior. During the daily foraging period, marine iguanas alternate between feeding and warm-up. The body temperature decreases and increases as shown (in an idealized way). Hatchlings and juveniles may have different upper and lower mean threshold temperatures. Thick line shows idealized foraging behavior before (top bar, foraging bout hatched), thin line after painting the animals white (lower bar) (see text and Figs. 4 and 7).

predation by large predatory fish (COOPER & LAURIE, 1987; own obs.). To avoid these costs, animals must return to dry land to increase body temperature once they reach a lower, size-dependent threshold of body temperature before they can continue to forage. Secondly, the decrease in bite rate over the period of a feeding bout (Fig. 5) diminishes foraging efficiency. This is another reason to terminate a foraging bout in order to warm up on land, and then return to forage at higher efficiency. The change in bite rate with decreasing T_b is essential to explain the shuttling of larger animals between the IT and basking sites. Otherwise they should forage without interruption as long as the tide level permits, as they do under conditions of warmer water temperature on other islands (unpubl. data) or when the sea is extremely calm and consequently the intertidal unusually warm.

Foraging marine iguanas provide an ideal example of thermoregulatory shuttling in ectotherms and conform to the model postulated by DREISIG (1984, 1985). They are constrained in their foraging time by the duration of low tide and the low temperature in the IT. Within these

constraints, they forage when warm and cease foraging when cold (dual set point model; COWLES & BOGERT, 1944; HEATH, 1965, 1970; BARBER & CRAWFORD, 1977). This thermoregulatory behavior leads to the behavior pattern described by the time budget model (shuttle between warm and cold areas to maximize foraging time; DREISIG, 1984, 1985). The two models describe two aspects of foraging behavior, its regulatory mechanism and the behavioral results of that regulation, which are schematically summarized for the case of marine iguanas in Fig. 8. Differences in details of foraging behavior patterns among individuals are related to body size and the correlated upper and lower threshold body temperatures as also suggested by DREISIG (1985), and to heating and cooling rates of animals of differing size. Because of the resulting shape of the T_b curve we call our schematic representation the 'sawtooth-model'.

The experiment in which heating rates were changed by painting animals white showed the strong influence of thermal factors on foraging behavior. Animals cycled faster between foraging and basking since foraging bouts were shorter. The animals apparently lower the upper threshold of T_b . An animal of 170 mm SVL lowered its T_b before foraging from $40.4 \pm 1.8^\circ\text{C}$ ($N = 14$) to $37.9 \pm 1.9^\circ\text{C}$ ($N = 12$) after it had been painted white, whereas the T_b at the end of a foraging bout remained unchanged ($33.1 \pm 2.4^\circ\text{C}$; $N = 15$ before *versus* $32.8 \pm 2.7^\circ\text{C}$; $N = 13$ after painting)(unpubl. telemetry data of M.W. from 1993). Larger animals tend to return at lower T_b from foraging than small ones (Fig. 4; TRILLMICH & TRILLMICH, 1986), and also do not heat to the same upper T_b as smaller animals before foraging (unpubl. data of M.W. from 1993: regression of T_b at the start of a feeding bout as a function of body mass is: $T_b = -0.002 \times \text{mass (g)} + 40.2$; $N = 9$; $r = 0.47$, $p < 0.05$). The idea of a threshold temperature does not imply rigidly fixed switch point temperatures since upper and lower temperatures during foraging are expected to vary (1) depending upon environmental constraints (*e.g.* insolation, time of day, wave action) as well as (2) the internal state of an animal (*i.e.* its motivation, status, and level of body reserves).

Physiological parameters directly influencing foraging behavior.

According to our measurements of sprint speed and gripping force a change in threshold temperatures with body size is adaptive (*cf.* KAUFMANN & BENNETT, 1989). Smaller animals live in a relatively more

hostile environment (*cf.* ZIMMERMANN & TRACY, 1989). Relative to wave forces on a small body, young animals have a smaller safety margin when caught by a wave during foraging (Fig. 3). The shift in threshold temperature thus correlates with relative safety conferred by size: the bigger an animal the lower it allows its T_b to drop (Fig. 4) (BARTHOLOMEW, 1982; TRILLMICH & TRILLMICH, 1986). In addition, our strength measurements are probably overestimates of actually achieved holding ability, because when given the choice, marine iguanas in the IT preferred to grip onto a wire mesh rather than onto the lava substrate when washed over by waves.

The thermal sensitivity of sprint speed and the insensitivity of gripping strength suggests that only the speed of the muscular response was affected by T_b , not the maximum force developed (*cf.* HUEY, 1982; GLEESON & HARRISON, 1988). Alternatively, two types of muscle fiber may be responsible for the different abilities or the iguanas may lock their toe nails in gripping position with only a minor need for muscular force, an alternative explanation suggested on theoretical grounds by VAN MARKEN LICHTENBELT (*pers. comm.*).

Black coloration is of obvious advantage when fast warm-up is required during foraging interruptions (BARTHOLOMEW, 1982). Similar adaptations are also found in other ectotherms (HUEY & KINGSOLVER, 1989). Alternatively, black coloration may be interpreted as camouflage in a lava environment (*cf.* ENDLER, 1978). But land predation is negligible around the foraging areas. At the post-hatching stage of the life cycle when predation on marine iguanas is highest, black coloration even prevents camouflage because most sandy nesting areas are lighter in color than the surrounding lava fields. Therefore, the black color of marine iguanas is best interpreted as a thermoregulatory adaptation.

Foraging on steeply inclined rocks or on cliff faces enables small marine iguanas to maintain high T_b 's and bite rates for a longer time than in flat parts of the IT zone since in the former habitat it is easier to avoid waves (*cf.* WALDSCHMIDT & TRACY, 1983). They can thus feed approximately as long as older animals using the same decision rules as these.

Changes in foraging strategy.

Cold seawater prevents small animals from foraging subtidally (via increased risk at low T_b). Subtidally foraging animals on Santa Fé had

higher food intake rates than intertidally foraging ones (WIKELSKI *et al.*, 1993). But due to shorter foraging time, pure ST feeding led to lower daily food intake. Exactly at which body size ST foraging becomes the better option will therefore depend on food availability in the ST *vs* IT, and on water temperature. To achieve maximal energy intake, large marine iguanas on Santa Fé fed in both areas, thus maximizing intake per day by using all available foraging time. For very large animals (3-6 kg) in a more productive environment, *e.g.* on Fernandina, a pure ST feeding strategy has been documented (TRILLMICH & TRILLMICH, 1986).

Not only thermal problems constrain foraging. There also exist motivational influences. During the reproductive season, males are less likely to go foraging (TRILLMICH, 1983) because they almost continually attend their territories, presumably in order not to lose matings (Table 1; TRILLMICH, 1983; Dellinger, 1991). Given this time constraint on foraging, they try to maximize intake *rate* rather than net intake, *i.e.* they behave as time minimizers (SCHOENER, 1971, but see also PYKE *et al.*, 1977) by drastically shortening IT foraging time but maintaining ST foraging duration (Table 1). Moreover, territorial males departed to the foraging ground later than non-territorial males. Immediately after foraging, non-territorial males cannot sneak copulations while territorials are away foraging because the former's T_b has dropped to approximately 3 °C above water temperature during foraging (about 25 °C; BARTHOLOMEW, 1966). They first have to warm up (*cf.* WHITE, 1973; MAGNUSON *et al.*, 1979), because low T_b prevents marine iguanas from mating (DELLINGER, 1991, pers. obs.). In contrast, the T_b of territorial males can decrease only slightly during their short foraging bouts in the IT and thus almost continuous mating competence is ensured.

The change in foraging behavior of reproductive males can be understood as an increase of the lower threshold temperature (Fig. 8) caused by aggressive and/or sexual motivation. Longer foraging of territorials after the reproductive season also demonstrates that foraging decisions are strongly influenced by internal state, in this case the low level of body reserves resulting from prolonged partial fasting during the reproductive season (TRILLMICH, 1983; DELLINGER, 1991).

The painting experiments further showed that foraging decisions are flexibly adjusted to heating and cooling rates and that changes in foraging behavior with size are not caused by fixed size- or age-related changes in

decision mechanisms. Animals changed their behavior following the artificial change in heating rate (Fig. 6, 7) and made more, but shorter feeding bouts in response to our manipulation.

The observed age-related changes in foraging behavior can therefore be explained by postulating a rule of the form 'forage while warm and warm up when getting inefficient at biting and running'. The fact that occasionally animals stop feeding before the end of low tide when sea conditions are particularly calm force one trivial addition to the above rule namely, 'stop feeding when your stomach is full or when there is no food left'. Internal motivational state, and changes in heating and cooling with increasing size during ontogeny are the two factors influencing the decision at which T_b to switch from foraging to warming-up and back. The changes in switch point described in this paper allow the animals to respond adaptively to changing costs and benefits of foraging in a cool environment.

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