The evolution of foraging behavior in the Galápagos marine iguana: natural and sexual selection on body size drives ecological, morphological, and behavioral specialization

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Introduction

Each year thousands of tourists visit the Galápagos Islands and become intrigued by the unique habits of the world's only sea-going lizard, the Galápagos marine iguana (*Amblyrhynchus cristatus*), as it swims offshore and dives under the waves to feed. One of the islands' first visitors, Charles Darwin, reported fascination with watching these creatures forage, and he

opened the stomach of several, and in each case found it largely distended with minced sea-weed . . . [that] grows at the bottom of the sea, at some little distance from the coast. (Darwin, 1839)

We now know that the Galápagos marine iguana is the only terrestrial vertebrate that forages almost exclusively on macrophytic marine algae. Although marine iguanas are active foragers, their short, intense bouts of foraging activity more closely resemble the activity pattern of sit-and-wait foragers. To understand why these endemic lizards have adapted such a unique foraging strategy and how it differs from the general pattern of foraging in lizards, we must examine the social and environmental selective pressures that are unique to this species and its environment.

The Galápagos marine iguana is a model system to understand how natural and sexual selection drive morphological and behavioral adaptations. In this chapter we will show how the unique foraging strategy of the marine iguana is an adaptation resulting from the forces of both sexual selection, acting through their unique social system, and natural selection by a harsh and variable environment. We will explore a variety of environmental and physiological constraints (e.g. tidal cycle, the rapid loss of body heat during foraging, variation in body size) that act as overriding selective forces, and are not as salient to their terrestrial counterparts. Finally, we will examine how these constraints have resulted in the adaptation of a variety of unusual morphological characteristics that enable efficient foraging. Thus, we hope to demonstrate how contrasting social and environmental selective pressures on body size have shaped this unique foraging strategy and have resulted in the unusual morphological and behavioral characteristics that first caught Darwin's eye.

Natural and sexual selection

Marine iguanas are highly sexually dimorphic: adult males weigh approximately 70% more than adult females (Laurie and Brown, 1990a). This size dimorphism is driven primarily by sexual selection: females display a strong preference for mating with bigger males in this lekking, or arena-mating, species (Trillmich, 1983; Wikelski et al., 1996, 2001, 2005; Partecke et al., 2002). Male mating success is highly skewed (Mackenzie et al., 1995); and a single male may be responsible for 35% of the copulations on a lek (Wikelski et al., 1996, 2001). Despite sexual selection for large size, body size varies substantially between islands: maximum adult male body mass ranges from 1 kg on the island of Genovesa to 12 kg on southern Isabela Island (Laurie, 1983, 1989; Wikelski et al., 1997). These differences in maximum body size are due to variability in algal productivity and sea surface temperature between islands (Wikelski and Trillmich, 1997; Wikelski and Romero, 2003; Wikelski, 2005). Large body size, however, comes at a high cost: members of the biggest size classes experience greatly increased mortality risks during periods of food shortage (Laurie and Brown, 1990b; Wikelski and Trillmich, 1997; Wikelski, 2005) owing to their higher total caloric requirement (Wikelski et al., 1997). El Niño events, which result in a sharp decline in food availability, occur frequently in the Galápagos Islands, averaging once every 3.8 years (Quinn et al., 1987; Laurie, 1989). Moreover, during these periods of food shortage reproductive failure may be complete (Wikelski and Trillmich, 1997). Thus, marine iguanas are subject to competing pressures of natural and sexual selection that determine optimal (and maximal) body size, which in turn shapes their unique foraging behavior.

Foraging behavior

Diet choice and foraging strategies

Although the seas around the Galápagos Islands are among the most productive in the world, marine iguanas are constrained in their foraging abilities by the cold and rough surface waters, as well as the restricted types of macrophytic marine algae upon which they can feed. Together, these constraints necessitate active foraging during a greatly restricted period that is ultimately regulated by the tidal cycle. Marine iguanas have evolved highly unique and efficient foraging strategies to overcome the temporal and spatial constraints associated with foraging on marine algae, allowing them to maximize energy intake and ultimately body size.

The preferred diet of marine iguanas consists primarily of two species of red alga (*Centroceras* sp. and *Gelidium* sp.) and one species of green alga (*Ulva sp.*), although at least ten genera of alga are consumed regularly across the archipelago (Carpenter, 1966). The preferred algal species varies among islands (Wikelski *et al.*, 1993; Wikelski and Wrege, 2000; Rubenstein and Wikelski, 2003), although the preferred types appear to be those with the highest nutritional quality of the species present; on Santa Fe this is *Gelidium*, which has both the highest carbon and nitrogen content and C:N ratio (Rubenstein and Wikelski, 2003). Choice tests conducted on Santa Cruz Island confirmed the iguanas' preference for red algae over green algae, such as *Gelidium pusillum* var. *pacificum* and *Hypnea spinella* over *Ulva lobata* (Shepherd and Hawkes, 2005). As in their terrestrial relatives (Troyer, 1982), digestion of plants (i.e. algae) is achieved by specialized hindgut endosymbionts, shown to be capable of hydrolyzing and fermenting plant polymers that are indigestible to the host (Mackie *et al.*, 2004).

Given the strong selection for large body size and the constraints caused by variable food availability (Rubenstein and Wikelski, 2003) and environmental conditions, marine iguanas have evolved highly efficient methods of foraging to maximize energy intake. The total daily active period for marine iguanas lasts between one third and one half of the duration of their closest relative, Conolophus pallidus (Christian and Tracy, 1985; Wikelski and Trillmich, 1994; Drent et al., 1999). Marine iguanas forage actively by grazing on intertidal and/or subtidal algae (Hobson, 1965; Carpenter, 1966; Trillmich, 1979; Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994). Although marine iguanas are famed for their unique diving habits, the majority of animals forage intertidally, grazing at low tide on exposed algae. Only about 5% of each population forages subtidally by diving beneath the sea surface to feed on offshore algal beds (Wikelski and Trillmich, 1994). Body condition (body mass (g) $\times 10^6$ / SVL³) (Laurie, 1989) does not differ between marine iguanas utilizing these two modes of obtaining energy (Wikelski and Trillmich, 1994). Subtidal and intertidal foragers may differ in the proportion of various algal species contained in the diet, but the quality of these diets is not significantly different (Wikelski et al., 1993). Individuals are highly consistent in the foraging strategy used, and the choice of this strategy is dependent upon body size (Trillmich and Trillmich, 1986): most females and smaller males forage intertidally, whereas larger animals typically forage subtidally. A small group of intermediate-sized iguanas may exploit both strategies (Trillmich and Trillmich, 1986). The minimum size of diving iguanas varies widely between islands and may depend on population density, algal abundance, and the size and topography of the site (Trillmich and Trillmich, 1986; Wikelski and Trillmich, 1994). Minimum body size of subtidal foragers ranges over a fivefold difference, from 600 g on Genovesa to 3000 g on Fernandina.

Temporal and spatial constraints on foraging

Given the similar diet quality and relative energetic benefits of foraging intertidally vs. subtidally, why are there size-associated differences in foraging strategy? The shift from intertidal to subtidal foraging appears to be due to the higher total caloric requirement of large animals (despite a reduced relative energetic requirement) (Wikelski and Trillmich, 1997; Wikelski et al., 1997). Intertidal foragers are both temporally and spatially constrained, whereas subtidal foragers experience reduced temporal constraints and can predominantly avoid spatial constraints. Intertidal foraging is limited to the period of low tide, when algal beds are accessible (Hobson, 1965; Trillmich and Trillmich, 1986; Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994; Rubenstein and Wikelski, 2003). Environmental effects significantly impact the duration of intertidal foraging: rough seas and high low-tide levels decrease the total time devoted to foraging (Trillmich and Trillmich, 1986; Wikelski and Trillmich, 1994). The pattern of foraging is also dependent upon environmental conditions on land: on sunny days marine iguanas are able to increase body temperature more quickly following foraging, and thus shorten re-warming duration between successive bouts (Buttemer and Dawson, 1993; Wikelski and Trillmich, 1994). Foraging efficiency is constrained by body temperature: marine iguanas prefer to maintain a body temperature between 35 and 39 °C (White, 1973; Bartholomew et al., 1976; Wikelski and Trillmich, 1994), much warmer than the usually cool (11-23 °C) Galápagos sea surface temperature. Voluntary body temperatures of up to 43 °C have been observed in hatchling marine iguanas before foraging. Body temperature declines linearly throughout a foraging bout, resulting in a decreasing bite rate and reduced energy intake (Fig. 16.1) (Wikelski and Trillmich, 1994). The speed of digestion also decreases at lower temperatures: gut passage time in marine iguanas has a Q_{10} of approximately 2.5 (Wikelski *et al.*, 1993).

Because of these temperature constraints, intertidally foraging marine iguanas prefer to graze during morning or midday low tides, because these



Figure 16.1. Maximum bite rate of intertidally foraging marine iguanas increases linearly with body temperature, as measured by implanted radiotelemetry tags on Santa Fe (redrawn from Wikelski and Trillmich, 1994).

periods offer both the lowest tide levels and the fastest re-warming after foraging. If low tides occur during early morning, marine iguanas are less able to achieve the warm body temperatures necessary for a successful foraging bout; if they occur in the late afternoon, animals have a difficult time re-warming sufficiently after returning from the water. When the low tide occurs after 1600 h, animals switch from foraging during the early afternoon to the subsequent morning low tide. This shift takes place approximately every 14 days (Trillmich and Trillmich, 1986; Wikelski and Hau, 1995; Rubenstein and Wikelski, 2003). Marine iguanas foraging intertidally in cold waters further maximize their body temperature by foraging slightly after low tide in the morning, and ahead of low tide in the afternoon (Trillmich and Trillmich, 1986).

The timing of intertidal foraging is also affected by algal spatial constraints. Algal blade length is greater at increased intertidal depths (Rubenstein and Wikelski, 2003). Algae grow quickly when submerged during high tide, but are rapidly grazed down by foraging iguanas. This competition causes marine iguanas on some islands to anticipate the tides, arriving at the foraging grounds prior to the time of low tide and thereby gaining a competitive advantage (Wikelski and Hau, 1995). Anticipation is greatest on islands with lower food supplies, and during the periods of poor foraging conditions associated with El Niño events. During a long-term El Niño on the island of Genovesa (which has relatively poor food availability even during 'good' years), marine iguanas that arrived at the foraging grounds earlier had higher survival rates (Wikelski and Hau, 1995). Anticipation is reduced when low tide occurs earlier in the day, and increases during afternoon low tides. Early foraging may not be efficient near the beginning of the day, when iguanas have had insufficient time to achieve warmer body temperatures. The increased anticipation exhibited during low tides occurring later in the day may result from the need for sufficient re-warming subsequent to foraging and prior to the drop in ambient temperature associated with the onset of darkness.

Ontogenetic and sexually dimorphic patterns of foraging

Subtidal foragers are not subject to the same temporal or spatial constraints as intertidal foragers. Dives are not timed to coincide with low tide (Hobson, 1965; Buttemer and Dawson, 1993), although some populations of subtidal foragers display a preference for foraging during high tides (Rubenstein and Wikelski, 2003). In general, however, the suitable foraging window is not as restrictive as it is in intertidal foraging. Subtidal foraging occurs between late morning and early afternoon (Trillmich and Trillmich, 1986); this allows re-emergence at the hottest period of the day to maximize re-warming rate (Buttemer and Dawson, 1993). Subtidally foraging animals are also able to feed during a much greater range of weather conditions. Moreover, foraging duration is more plastic in subtidal than in intertidal foraging bouts. The duration of foraging dives averages approximately three minutes, although individuals may remain voluntarily submerged for over 45 min (Hobson, 1969; Trillmich and Trillmich, 1994; M. Wikelski, personal observation). Dive duration is inversely related to algal productivity (Fig. 16.2), whereas the duration



Sea surface temperature (°C)

Figure 16.2. Subtidally foraging iguanas show increased dive durations during periods of high sea surface temperature and low algal productivity, and decreased dive length when sea surface temperature is low, indicating high productivity of preferred algal species (from Wikelski and Trillmich, 1994).



Figure 16.3. The duration of intertidal foraging bouts within a site remains constant with changing algal biomass, except below a threshold level of $5 \text{ g}/100 \text{ cm}^2$, when intertidal foraging duration increases.

of intertidal foraging bouts within a site remains constant, except at very low algal biomass (Fig. 16.3).

The total time devoted to foraging varies between populations: on some islands subtidal foragers spend significantly more time feeding, whereas on others intertidal foragers devote more time to obtaining energy (Trillmich and Trillmich, 1986; Wikelski and Trillmich, 1994; Drent *et al.*, 1999). The total time spent foraging in the intertidal zone varies. Intertidal foragers show much greater variance in the duration of foraging bouts than subtidal foragers, and more frequently fast for up to several days between foraging bouts (Trillmich and Trillmich, 1986).

Despite the reduced temporal and spatial constraints associated with subtidal foraging, it is not an effective or efficient method of foraging for smaller marine iguanas; the energetic costs appear to outweigh the benefits. Larger animals are much more efficient swimmers, as both swimming speed and power generated per body undulation are directly related to body size (Bartholomew *et al.*, 1976; Vleck *et al.*, 1981). Smaller iguanas may not be able to generate enough power to overcome the buoyancy that results from diving with inflated lungs (Bartholomew *et al.*, 1976). Smaller animals also lose heat more rapidly than larger individuals (Bartholomew and Lasiewski, 1965). Because of the difference in heat loss, smaller iguanas would be forced to return to land to warm up more frequently than larger animals, or face inefficient foraging due to the temperature-associated decrease in bite rate. An increased locomotory shuttling between cold water and warm land would greatly increase the cost of subtidal foraging (Trillmich and Trillmich, 1986). Intertidal foragers, in particular small or young iguanas, remain above the water the majority of the time, and are never far from rocks on which they can warm themselves; thus, this foraging strategy is much less expensive for smaller individuals. In fact, the smallest iguanas foraging intertidally on Santa Fc island attain body temperatures of up to 43 °C before foraging, and remain in the intertidal area for only a few minutes, departing with body temperatures of 37 °C, having never been washed over by a wave.

Hatchlings and juveniles display ontogenetic differences in foraging strategy. For the first several months after hatching, iguanas predominantly forage on the feces of conspecifics (Boersma, 1983) that enable them to obtain the endosymbiotic bacteria necessary for successful digestion of algae (Troyer, 1982; Mackie *et al.*, 2004). Although older hatchlings and juveniles forage intertidally, they are restricted to foraging in the upper intertidal region. Smaller individuals are subject to the competing demands of a higher relative energetic requirement, coupled with a decreased ability to retain heat when exposed to cold sea water (Wikelski *et al.*, 1993). Running speed decreases with body temperature, and this limits the ability of smaller iguanas to elude large waves. Gripping strength, an important indicator of the ability of marine iguanas to maintain their position on rocks in the intertidal zone when buffeted by high surf, is also positively correlated with body size (Wikelski and Trillmich, 1994).

Small individuals are restricted to foraging in the upper intertidal zone where they have a reduced chance of encountering large waves that would cool them more quickly and might sweep them off of rocks. A juvenile swept into the ocean would face a much higher relative energetic cost of swimming back to shore than a large individual, and might face the additional danger of being consumed or injured by large predatory fish and marine invertebrates (Wikelski and Trillmich, 1994; M. Wikelski, personal observation; H. Snell, personal observation). Although foraging in the upper intertidal zone provides many advantages to small marine iguanas, the shorter algal blade lengths and higher density of foraging animals result in increased competition for scant resources.

Surviving times of crisis

Although large animals are generally able to obtain sufficient energy by foraging subtidally, they suffer much higher mortality during conditions of low food availability (Laurie and Brown, 1990a). Marine iguanas experience frequent but unpredictable declines in food availability during El Niño events, in which warming sea-surface temperatures (up to 32 °C) and a failure of the upwelling of cold, nutrient-rich water induces massive dieback of the preferred

algal species (*Gelidium* spp., *Centroceras* spp., *Ulva* spp. and *Spermothamnium* spp.) (Laurie, 1987, 1989; Rubenstein and Wikelski, 2003). Subsequently, intertidal zones are colonized and grown over by a species of brown alga, *Giffordia mitchelliae*. Marine iguanas face difficulties digesting these brown algae, possibly because iguanas lack the hindgut endosymbionts to digest *G. mitchelliae* (Laurie, 1989; Cooper and Laurie, 1987). As a consequence, iguanas experience greatly increased mortality rates during El Niño events, due to starvation. The 1982–3 El Niño resulted in 60% mortality across the archipelago (Laurie, 1990). Mortality rates of up to 90% have been recorded on individual islands (Seymour Norte in 1997–8 and Genovesa in 1991–4) (Wikelski and Wrege, 2000; Romero and Wikelski, 2001).

During El Niños there is differential mortality among size classes, with the highest mortality rates found in the largest animals, owing to higher absolute caloric requirements (Laurie and Brown, 1990b; Wikelski and Trillmich, 1997; Wikelski *et al.*, 1997), and in the smallest size classes, which are restricted to foraging in the upper intertidal zone and thus may be subject to the strongest resource competition (Laurie and Brown, 1990a,b). The foraging efficiency of marine iguanas, measured as intake/bite (mg g^{-0.8}), declines with increasing size (Fig. 16.4), which may further contribute to the high mortality rates observed. An additional factor constraining small animals during El Niños may be the rising sea-surface level in the Galápagos, which can climb more than 30 cm above normal, causing the total submergence of the preferred algal species typically located in the intertidal region.

Uniquely among lizards, marine iguanas may have evolved the ability to reduce their body length during periods of food shortage to improve their



Figure 16.4. Foraging efficiency of intertidally foraging marine iguanas differs between islands (different symbols) and is negatively related to body size (redrawn from Wikelski and Romero, 2003).

survival probability. During El Niño events, marine iguanas appear to be able to decrease body length by as much as 20% (6.8 cm) within two years. Reduction of this magnitude cannot be accounted for solely by reducing cartilage and connective tissue, which together account for only c. 10% of body length, and suggests that these animals are resorbing bone mass (Wikelski and Thom, 2000). The amount of shrinkage is significantly associated with survival, owing to both increased foraging efficiency and decreased energy expenditure of smaller individuals. The magnitude of decrease in body length is greatest among the largest size classes, which are typically those that suffer the highest mortality during El Niño events (Wikelski and Thom, 2000).

A unique instance of dietary niche expansion

A subpopulation of marine iguanas on Seymour Norte Island found a unique way to increase maximum body size through dietary niche expansion, thereby gaining an advantage in sexual selection (Wikelski and Wrege, 2000). These iguanas exhibited the distinctive foraging behavior of supplementing their algal diet with the beach plant Batis maritima both before and after foraging intertidally. Although the nutrient value of *Batis* is lower than that of marine algae, and assimilation efficiency is likely to be much lower, Batis foraging is not subject to the same time constraints (tidal cycle and decreasing body temperature) as intertidal foraging. Through expanding dietary niche breadth Batis foragers were able to increase maximum body size by nearly 100% when compared with non-Batis eaters. The decreased dependence on algal abundance appears to have increased survival of the Seymour Norte Batis foragers during historic El Niño events: despite the near-total mortality of individuals in the largest size classes on many islands during El Niños, many large Batis-foraging males, some in excess of 2 kg, survived. During the 1997-8 El Niño, however, high sea-surface levels flooded and killed the entire population of Batis plants on which the Seymour Norte subpopulation fed. Without supplementation from Batis, the unusually large individuals were unable to survive the period of food deprivation, and the entire subpopulation of Batis foragers perished (Wikelski and Wrege, 2000). Some juveniles from this subpopulation that did not feed on Batis in 1997 were permanently marked, and in 2003 were observed ingesting a variety of land plants (Galápagos Naturalists Guides, personal communication). It will be interesting to follow their ontogeny to determine whether this subpopulation's tradition of terrestrial foraging will be successfully passed down to this generation, and whether it will enable the development of larger body size.

Morphology, behavior, and physiology Endogenous rhythms and foraging patterns

The precise timing of foraging during the tidal cycle is vitally important to intertidally foraging marine iguanas, and may be regulated by an endogenous rhythm (Wikelski and Hau, 1995). Iguanas that have been resting out of view of the ocean for several days will arrive at the foraging grounds not at the previous time of foraging, but rather at the predicted time of low tide (or prior to low tide in populations that anticipate tidal changes). Moreover, marine iguanas experimentally housed in darkened enclosures retain foraging activity rhythms with a mean period of 24.5 h, although the period of their apparently free-running endogenous rhythm is sometimes longer or shorter than the tidal cycle. Captive animals will also shift activity levels from the evening to the morning low tide at the appropriate time during the 14-day low tide cycle. Foraging behavior does not appear to be synchronized by social cues, as initially synchronous animals housed together in darkened enclosures may develop asynchronous periodicity (Wikelski and Hau, 1995). Experimentally altering the onset of light in animals enclosed away from the shoreline does not shift their activity rhythm, indicating that foraging activity is not primarily cued by the light-dark cycle. Finally, foraging time is more closely related to the calculated time of low tide than to the actual time at which the intertidal algae beds are exposed. These results suggest that marine iguanas possess either a circatidal (c. 12.4 h) or circalunadian (c. 24.8 h) oscillatory system that enables them to predict the timing of low tide, and thus the most appropriate period for foraging (Wikelski and Hau, 1995).

Algal quality cues reproduction

Food availability also has implications for the timing of reproduction. Marine iguanas breed seasonally only once a year. Males typically establish territories two months prior to the start of reproduction (Trillmich, 1983; Partecke *et al.*, 2002). The reproductive period varies by several months across islands, with the mean copulation date ranging from mid December on Santa Fe and Genovesa to February–March on Española and southern Isabela (Trillmich, 1979; Laurie, 1984). Within each population copulation is relatively synchronous, with all matings on a particular island occurring over a 20–25 d period (Trillmich, 1979; Partecke *et al.*, 2002; Rubenstein and Wikelski, 2003). The timing of synchronized reproduction varies by up to several weeks each year within a population, and coincides with the peak nutritional quality of

the preferred algal species (Rubenstein and Wikelski, 2003). In years when sea-surface temperatures are higher, both the median date of copulation and the peak algal quality occur earlier. This indicates that marine iguanas may use changes in algal quality, associated with seasonal but variable changes in water temperature, as a cue to initiate breeding (Rubenstein and Wikelski, 2003).

Foraging energetics

Marine iguanas have developed a variety of morphological adaptations to maximize foraging efficiency. They possess blunt heads with tricuspid teeth that are flattened laterally, enabling effective grazing on marine algae (Darwin, 1839), as well as long and sharp claws with a powerful ability to grip onto the lava (Carpenter, 1966). Their tails are flattened compared with those of other iguanids, and thereby adapted for efficient swimming (Tracy and Christian, 1985). Black coloration and circulatory heat shunts help to maintain preferred body temperature during foraging bouts in the cold sea water. Marine iguanas also possess highly developed salt glands that allow them to excrete the excess salt ingested while foraging in sea water (Dunson, 1969), and harbor endosymbiotic bacteria that allow efficient digestion of marine macrophytes. Some of these morphological adaptations contribute to a greatly decreased cost of locomotion in water compared with the cost of walking at the same speed: at 1.0 km/h, swimming has been estimated to use only one quarter of the energy expended on terrestrial locomotion (Gleeson, 1979). Marine iguanas do not, however, appear to have adapted physiologically to the low sea-surface temperatures characteristic of their foraging environment by lowering the temperature at which they can be maximally active (Bartholomew, 1966; Dawson et al., 1977; Trillmich and Trillmich, 1986). Foraging behavior is therefore highly constrained by body temperature (Fig. 16.5). Foraging accounts for approximately 8%-10% of average daily energetic expenditure, as determined by both heart rate energetics (M. Vitousek and M. Wikelski, unpublished data) and the doubly labeled water method (Gleeson, 1979; Nagy and Shoemaker, 1984; Drent et al., 1999). Energetic expenditure on foraging varies widely, however, ranging from 0 (no foraging) to over 40 kJ/d. Intertidally foraging animals may spend more than 75% of their total daytime expenditure on foraging behaviors (Fig. 16.6) (M. Vitousek, unpublished data).

Unlike many lizards, marine iguanas of different sex and size classes do not differ in diet composition, diet quality, or digestive efficiency (which, at 70%, is higher than that of most herbivorous lizards: Wikelski *et al.*, 1993). Size



Figure 16.5. Schematic variable sawtooth model of foraging behavior of iguanas. Iguana body temperature (curved line) falls from around 40 °C while foraging and rises while basking in a sawtooth manner. Iguanas stop feeding when full or cold, whichever happens first. Curves are steeper in the cool season than in the hot season. When algal biomass is high a single feeding excursion per low tide is sufficient. Letters indicate: a, Academy Bay, Santa Cruz, in the cool season (this study); b, Tortuga Bay, Santa Cruz, in the hot season (this study); b, Tortuga Bay, Santa Cruz, in the hot season (this study) (if algal biomass were low, as is more common in the cool season, the iguana might require two or more feeding excursions); c, Santa Fe in the cool season (Wikelski and Trillmich, 1994; Wikelski *et al.*, 1997); d, Fernandina in the cool season (after Wikelski *et al.*, 1997).

classes also do not differ in time devoted to foraging on a given island (Wikelski and Trillmich, 1994). Larger iguanas have a higher total intake of dry algal mass than small animals; however, the difference between food intake and energetic expenditure is much lower in large animals, indicating that these individuals are barely meeting their energetic requirements whereas small iguanas have an energetic surplus (Wikelski *et al.*, 1997; Drent *et al.*, 1999; Romero and Wikelski, 2003).

The average daily energetic expenditure of intertidal and subtidal foragers does not differ, although on some islands subtidal foragers spend significantly more time foraging than intertidal foragers (Drent *et al.*, 1999). Daily energetic expenditure varies between islands; this difference probably



Figure 16.6. The amount of daily energetic expenditure devoted to foraging is highly variable both between and within individuals. Data show the percent of daytime energetic expenditure devoted to foraging (n = 4 Santa Fe females), as determined through implanted heart rate – body temperature. Symbol types represent individual females; closed symbols are from 1999, open symbols from 2003.

results from differences in resource availability. Both subtidal and intertidal foragers have a higher energetic expenditure on Santa Fe, an island with relatively low sea-surface temperature, rough seas, and high total algal productivity, than on neighboring Genovesa, which is characterized by warmer water, smoother seas, and a lower total algal productivity (Drent *et al.*, 1999).

Conclusion

The combination of unique social and environmental selective pressures faced by the Galápagos marine iguana have resulted in the development of a foraging style that is unique, not only among iguanids, but among all reptiles. In order to meet the energetic demands associated with large (sexually selected) body size, marine iguanas have evolved unique foraging strategies specialized for the consumption of marine macrophytic algae, which is both temporally and spatially constrained. The short, intense, and energetically costly grazing bouts of marine iguanas combine the leisurely grazing of herbivorous lizards with the active-searching foraging style of carnivorous lizards. In addition, they have evolved morphological adaptations, such as blunt heads, black coloration, and salt glands, that help them maximize energy intake during their costly foraging bouts. In summary, the Galápagos marine iguana is a model system to understand how natural and sexual selection drive morphological and behavioral adaptations.

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LIZARD ECOLOGY

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Lizard Ecology

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