

Herbivory and foraging mode in lizards

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Introduction

Active foraging and sit-and-wait predation are often considered as two very disparate foraging strategies (Huey and Pianka, 1981). As implied by the name, active foragers actively search for food and, in the process, will cover large distances. Typical sit-and-wait predators on the other hand will wait motionless for prey to pass by, at which they will dart with a sudden burst of movement. These animals are often cryptically colored and do not move around for prolonged periods of time (see Table 7.1). Herbivores, however, need to forage actively for food, but have radiated extensively within a group of lizards seemingly predisposed to a sit-and-wait strategy.

Differences in foraging mode in lizards seem to be roughly associated with a deep split within the lizard phylogeny: the transition from “fleshy-tongued” Iguania to the “scaly-tongued” Scleroglossa. It has been suggested that this split is tightly associated with evolution of the use of the tongue for chemoreceptive purposes either at the level of the scleroglossans (Schwenk, 1993, 2000; Cooper, 1994) or independently in each of the scleroglossan radiations (Reilly and McBrayer, this volume, Chapter 10). The development of a tongue that allowed animals to detect and assess sedentary prey is thought to have allowed lizards to search extensive areas for prey that would otherwise remain undetected. As a consequence, active foragers tend to consume unpredictably distributed and clumped prey (e.g. termites). Sit-and-wait predators, on the other hand, tend to eat more active and larger prey (Pough *et al.*, 2001). Despite the general consensus that most iguanians are indeed sit-and-wait foragers, Perry (1999) totally rejected the notion that Iguania and Autarchoglossa are dichotomous in foraging mode, and did not detect bimodality between or within either clade.

Surprisingly, herbivores, which are active foragers by definition (waiting motionless for plants to pass by is an unviable evolutionary strategy), are

Table 7.1 *Ecological and morphological characteristics of sit-and-wait predators, active foragers, and herbivores*

Predictions for herbivores clearly have a number of characteristics in common with both sit-and-wait and active foraging lizards. Whereas behaviorally and ecologically herbivores are more like active foragers, morphologically herbivores are expected to be more similar to sit-and-wait predators.

	Sit-and-wait predators	Active foragers	Herbivores
<i>Ecology and behavior</i>			
Prey type	mobile, large, selective, occasional	small, sedentary, clumped, opportunistic, often	sedentary, selective, seasonal
Prey mass/day	low	high	high
Energy requirement	low	high	low
Tongue flicking	no	yes	yes
Escape	camouflage, burst speed	endurance, speed	size/aggression
Home range	small	large	intermediate
<i>Performance</i>			
Endurance	low	high	high
Sprint speed	high	low	low
Bite force	high	low	high
<i>Morphology</i>			
Body size	medium to large	small to medium	large
Body shape	stocky	narrow, elongated	stocky, large body volume
Head shape	large, broad	elongate, narrow	large, broad, short
Tooth structure	robust	narrow, elongate, curved	broad, cusped, resistant to wear
Tongue structure	fleshy	narrow, bifurcated	fleshy, bifurcated
Gut structure	plastic, rapidly upregulated, long	continuous function, short	continuous function, long, partitioned colon

Table modified after Huey and Pianka (1981); Pough *et al.* (2001).

predominantly found among the Iguania. Indeed, roughly 60% of all lizards considered herbivores *sensu stricto* (*s.s.*) are iguanians (Pough, 1973; King, 1996; Pough *et al.*, 2001). This creates an interesting paradox: the radiation within a, by definition, actively foraging niche (herbivory) by members of the clade that seems most constrained to sit-and-wait foraging. However, in a recent paper, Cooper and Vitt (2002) suggested that in contrast to herbivory *s.s.* the number of

origins of omnivory (i.e. partial consumption of plant matter) might in fact be more common among scleroglossans and associated with their ability to assess potential food items by using chemoreception. In this chapter I examine in more detail which characters are traditionally considered to be associated with the two foraging strategies, and compare them with the traits typically associated with a herbivorous life-style. Characters analyzed were chosen because clear predictions could be made regarding their polarity for either foraging mode or dietary groups. I chose to analyze ecological, performance and morphological traits to evaluate the differences between dietary groups and foraging mode on all different levels. Through my examination of characters associated with foraging mode and/or dietary groups, I try to evaluate why so many herbivores *s.s.* have arisen within the Iguania and whether, and how, herbivores transcend the evolutionary impasse of both sides of the foraging paradigm.

Methods

Terminology

In this chapter I use the term omnivore as an indicator of any lizard incorporating plant matter into its diet on a regular basis. I use the term herbivore *s.s.* for those lizards eating only, or predominantly (e.g. over 80% of the diet) plant matter. The term herbivore *s.l.* (*sensu lato*) will be used to define any lizard including plant matter into its diet (i.e. omnivores + herbivores *s.s.*)

Bite forces and head shape Bite force and head shape data were collected for a wide range of lizards including representatives from most major radiations (Table 7.2, Fig. 7.1). Most animals were measured in the field and released at the exact site of capture immediately after the experiments. Data for *Varanus exanthematicus* and *Uromastix acanthinurus* were obtained for captive animals housed at the Antwerp Zoo. Data for *Xenosaurus grandis* were taken from Herrel *et al.* (2001a).

Bite forces were measured by using a Kistler piezo-electric force transducer with portable amplifier as described in Herrel *et al.*, 1999a, 2001a,c. Head dimensions were determined immediately after the bite force trials by using a pair of digital Mitutoyo calipers. Head length was determined from the back of the parietal bone to the tip of the premaxilla; head width was measured at the widest point of the head, just posterior to the orbits, and includes the potential bulging of jaw muscles; head height was measured at highest part of the head, at the level of the frontoparietal suture, and includes the height of the lower jaw and associated muscles; lower jaw length was determined from the back of the retro-articular process to the tip of the lower jaw.

Table 7.2 Head shape, bite forces, and ecology in lizards

Data are means (in millimetres, with the exception of bite force, which is expressed in newtons) from adult male individuals. Classification of species into dietary and foraging categories is based on literature data. The number in parentheses after a species name indicates the sample size.

Species	SVL	Head length	Head width	Head height	Bite force (N)	Diet	Foraging mode
<i>Dipsosaurus dorsalis</i> (10)	125.74 ± 5.7	22.38 ± 0.6	19.15 ± 1.31	14.17 ± 0.87	18.99 ± 2.21	herbivore	active forager
<i>Callisaurus draconoides</i> (12)	83.04 ± 8.18	15.66 ± 0.93	12.59 ± 0.84	8.80 ± 0.48	4.79 ± 1.46	insectivore	sit-and-wait
<i>Sceloporus undulatus</i> (16)	59.64 ± 4.35	12.80 ± 1.11	10.70 ± 1.01	7.17 ± 0.73	3.57 ± 2.54	insectivore	sit-and-wait
<i>Pogona vitticeps</i> (8)	217.76 ± 28.75	38.1 ± 3.00	48.37 ± 6.27	29.06 ± 3.71	112.39 ± 18.32	omnivore	sit-and-wait
<i>Plecoedema stellio</i> (4)	95.79 ± 7.28	23.64 ± 0.79	23.42 ± 0.84	12.93 ± 0.75	22.23 ± 5.01	insectivore	sit-and-wait
<i>Uromastix acanthinurus</i> (4)	159.46 ± 26.11	31.79 ± 4.91	32.69 ± 4.58	18.81 ± 2.56	68.39 ± 23.74	herbivore	active forager
<i>Cordylus mossambicus</i> (5)	109.03 ± 3.17	30.29 ± 0.56	24.93 ± 0.34	13.92 ± 0.45	19.31 ± 0.88	insectivore	sit-and-wait
<i>Eulamprus heatwolei</i> (3)	109.17 ± 10.70	21.37 ± 0.43	13.70 ± 0.83	11.24 ± 0.23	16.66 ± 1.70	insectivore	active forager
<i>Corucia zebrata</i> (2)	275.00 ± 7.07	50.60 ± 4.53	48.88 ± 2.37	36.03 ± 3.01	206.85 ± 69.15	herbivore	active forager
<i>Tiliqua rugosa</i> (13)	282.44 ± 17.07	45.90 ± 3.08	51.64 ± 3.80	33.21 ± 2.54	161.64 ± 30.11	omnivore	active forager
<i>Gallotia galloti</i> (15)	112.03 ± 10.24	30.22 ± 3.19	19.90 ± 2.14	16.31 ± 2.70	107.63 ± 32.24	herbivore	active forager
<i>Psammmodromus algirus</i> (9)	74.84 ± 3.33	18.34 ± 0.78	11.61 ± 0.72	8.77 ± 0.54	11.52 ± 1.65	insectivore	active forager
<i>Podarcis lilfordi</i> (8)	62.08 ± 2.57	16.44 ± 1.34	9.63 ± 0.84	7.71 ± 0.83	10.71 ± 0.81	omnivore	active forager
<i>Cnemidophorus tigris</i> (5)	77.26 ± 9.89	18.97 ± 2.07	10.28 ± 1.75	8.87 ± 1.15	6.69 ± 4.38	insectivore	active forager
<i>Xenosaurus grandis</i> (9)	110.81 ± 7.97	26.55 ± 2.58	21.73 ± 1.80	13.20 ± 0.64	19.91 ± 5.16	insectivore	sit-and-wait
<i>Varanus exanthematicus</i> (7)	237.90 ± 24.38	48.01 ± 4.65	33.58 ± 3.07	23.99 ± 2.94	86.61 ± 21.00	insectivore	active forager

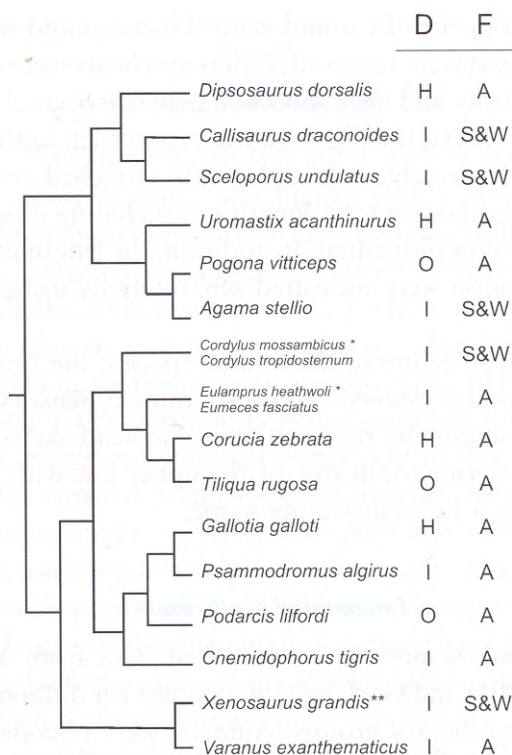


Figure 7.1. Phylogeny depicting the relationships between the species in the analysis. Interfamilial relationships based on Pough *et al.* (2001). Phrynosomatid relationships based on Reeder and Wiens (1996); scincid relationships based on Hutchinson (1980); lacertid relationships based on Arnold (1989). *Xenosaurus grandis* was classified as a sit-and-wait predator based on data in Ballinger *et al.* (1995); *Cordylus tropidosternum* and *C. mossambicus* based on data in Cooper *et al.* (1997). A, active forager; D, dietary classification; F, foraging mode; H, herbivore; I, insectivore; O, omnivore; S&W, sit-and-wait forager. * Species for which only bite force and head shape data could be obtained. For intestinal tract length data the closely related species below was used (see methods). ** Only included in the bite force and head shape data set as no preserved specimens could be obtained for this species or any close relatives.

Intestinal tract and teeth

Preserved adult male individuals of the species included in the bite force and head shape dataset were dissected to extract the digestive tract. As no preserved individuals of the species *Cordylus mossambicus* or *Eulamprus heathwoli* were available, I used two closely related species with similar dietary preferences and foraging mode (*Eumeces fasciatus* and *Cordylus tropidosternum*). First, snout–vent length and head dimensions were determined for each animal.

Animals were then opened by a mid-ventral incision and the entire digestive tract, lungs, and heart were removed. Lungs and heart were carefully removed from the digestive tract and the connective tissue associated with the digestive tract was cut away. Next, the digestive tract from each individual was pinned at its anterior end, straightened, and gently stretched to a fully extended position. The total digestive tract length not including esophagus or rectum was measured for every individual. In addition, the length of the stomach, the intestine and the colon were measured separately by using Mitutoyo digital calipers.

To inspect tooth structure in these same species, the heads were removed from the specimens and cleaned. To do so, muscle, sensory organs and connective tissue were manually removed from the head skeleton. Pictures were taken from the posterior tooth row of the upper jaw with a Nikon Coolpix camera mounted on a Leica dissecting scope.

Locomotor performance

I decided to re-analyze previously published data from Van Damme and Vanhooydonck (2001) and Garland (1999) to test for differences in locomotor performance among dietary groups. Animals were re-coded as being either herbivores *s.l.* or insectivores based on literature data.

Statistical analyses As species are not independent data points, but related through their evolutionary history, I analyzed the data taking into account the phylogenetic relationships between species. I used the same phylogenetic tree as given in Van Damme & Vanhooydonck (2001) and Garland (1999) to analyze the locomotor performance data. To analyze the bite force, head shape, and intestinal tract data, I compiled a tree based on published data (see caption of Figure 7.1 for sources). All data were $\log_{10}$ transformed before analysis, and species means were entered as tip-node values. All analyses were run with the PDAP package (Garland *et al.*, 1999). Branch lengths were set to unity as no data on actual branch lengths could be obtained for all the species in the analysis. I selected Brownian motion as the model of evolutionary change. A thousand simulations were run and analyzed with the PDSIMUL and PDANOVA routines in the PDAP package. F values obtained from the simulation analysis (F_{phy1}) were compared with the F values obtained by doing regular ANCOVAs (F_{95}) in SPSS (v.10). If the F_{95} values were larger than the F_{phy1} values, I considered the results significant. Exact p values were determined by comparing the F_{95} values with the F -table generated by the PDANOVA routine.

Results

Ecology and behavior

Prey type and size (see also Chapter 5)

The original predictions by Huey and Pianka (1981) were that sit-and-wait predators are expected to eat more mobile prey, and that widely foraging lizards should catch more sedentary and unpredictable prey. Additionally, Huey and Pianka (1981) made the argument that active foragers often eat clumped prey such as termites, or large prey such as scorpions (e.g. *Nucras tessellata*). In some cases large prey including small mammals are also captured by actively foraging lizards (i.e. varanids). Later, other authors (see summary table in Pough *et al.* 2001, p. 443) have added an additional component to this scheme that seems contradictory to the original predictions: sit-and-wait predators should also consume, on average, larger prey (see also Andrews, 1979). However, this seems a reasonable assumption as animals that tend to eat infrequently should take the largest possible prey available. This is most exemplary in snakes such as vipers that are extreme sit-and-wait predators and eat large, bulky prey (Cundall and Greene, 2000). Unfortunately, to my knowledge, no quantitative analyses of prey size have been performed to test these hypotheses.

Plants clearly cannot be considered a mobile or active food source. Rather plants are sedentary with a clumped distribution and often of unpredictable availability (e.g. perennial plants or plant parts such as flowers and fruits). These characteristics are generally in accordance with those of food types eaten by active foragers. Yet most plants are large food items that need to be reduced in size before they can be consumed. Although some herbivores will swallow rather big pieces of plants (e.g. *Corucia zebrata*: pers. obs.), most herbivorous lizards effectively crop pieces from plants, thus reducing plant matter to bite-sized pieces (Fig. 7.2). Whereas herbivores typically eat a variety of plants and plant parts (see, for example, Dubuis *et al.*, 1971; Sylber, 1988; Valido & Nogales, 1994), most are selective and select those plants that allow them to obtain a balanced diet (Dearing & Schall, 1992; Rocha, 2000). Omnivores eat plants in variable proportions that may change seasonally, or according to local environmental conditions (Sadek, 1981; Dubas and Bull, 1991; Valido and Nogales, 1994).

Prey detection (see also Chapter 8)

A clear and strong dichotomy has been demonstrated with respect to foraging mode and prey detection capacity in lizards. Whereas active foragers are capable of detecting prey, and even assessing prey quality (i.e. nutrient composition) by using chemical cues, sit-and-wait predators typically are not

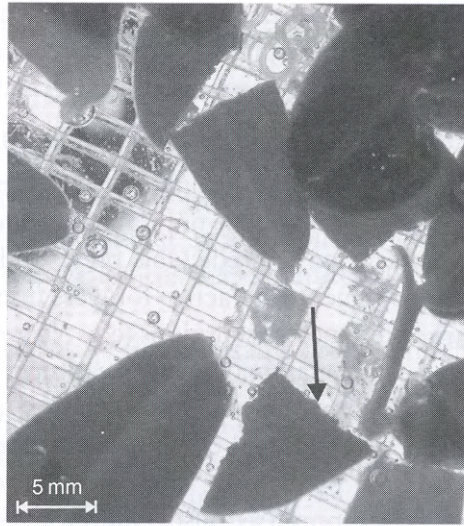


Figure 7.2. Stomach contents of an iguanian herbivore (*D. dorsalis*) obtained after stomach flushing. Note how the leaves are often cut into smaller parts. Note also how the edges of the cut are clean, as if made by a pair of scissors (arrow). Scale bar, 5 mm.

(Cooper, 1994; Cooper *et al.*, 2002). Although there is limited evidence suggesting that some sit-and-wait foragers are capable of recognizing immobile items as potential food by using gustation rather than chemoreception (Herrel *et al.*, 1998b), most sit-and-wait foragers likely rely on visual cues to detect prey (Cooper, 1994; Cooper *et al.*, 2002).

Herbivores, even when belonging to otherwise strictly sit-and-wait foraging clades, are always capable of detecting food items by using chemical cues (Cooper, 1994; Cooper and Vitt, 2002). Because of the tight association between chemosensory prey detection and herbivory, Cooper and Vitt (2002) proposed that the evolution of omnivory would be facilitated in clades of actively foraging lizards. Yet, whereas many actively foraging lizards have made the switch to omnivory (see Cooper and Vitt, 2002), only few have become completely herbivorous (King, 1996).

Energy requirements (see also Chapter 4)

As sit-and-wait predators spend most of their foraging time waiting motionless for prey to pass by, they will obviously be spending less energy than actively foraging lizards (e.g. roughly one third less in lacertid lizards: Huey and Pianka, 1981). Despite their need to forage actively, herbivores are also thought to spend little energy during foraging. The rationale behind this argument is simple: as plants do not escape from a potential forager, the

forager will not need to pursue its food (at high speed) and will thus utilize less energy (Pough, 1973). Body-mass-specific energy requirements are low, herbivores are generally less active and spend considerably less time foraging and thermoregulating (Wilson and Lee, 1974; Gleeson, 1979). Yet, if the cost of transport is similar in herbivores and non-herbivores (which it presumably is; see Gleeson 1979), and if herbivores need to amass more food per unit body mass (as presumably less energy can be extracted per unit mass from plant material; see King, 1996), then the cost of foraging might still be higher for herbivorous lizards. Unfortunately, not enough comparative data on the energetic cost of foraging in lizards are available to test the above mentioned hypothesis.

Home ranges

Despite the results of previous studies (Stamps, 1977, 1983), a recent analysis of home range sizes indicated no differences associated with foraging mode (Perry and Garland, 2002). Rather, home range size seems to scale directly with energetic requirements (Perry and Garland, 2002). Not unexpectedly, home range size did differ significantly between herbivores, omnivores, and carnivores, with omnivores having the smallest, herbivores somewhat bigger, and carnivores having the largest home range sizes.

Performance

Locomotion (see Chapters 2 and 3)

Although it is generally assumed that representatives of the two foraging modes differ in sprint speed and endurance capacity (with active foragers having lower speeds but greater stamina; see Garland, 1994; Miles *et al.*, this volume Chapter 2), this has rarely been tested. However, a recent comparative analysis of sprint speed data by Van Damme and Vanhooydonck (2001) was unable to show differences in sprint speed between active foragers and sit-and-wait predators. Endurance capacity, on the other hand, was shown to be significantly related to quantitative measures of lizard movement patterns under field conditions (Garland, 1999). Consequently, actively foraging lizards are expected to have greater endurance than typical sit-and-wait predators.

To my knowledge, no study has explicitly investigated whether differences in locomotor performance exist between herbivores *s.l.* and non-herbivores. Thus, I decided to re-analyze previously published data from Van Damme and Vanhooydonck (2001) and Garland (1999) to test for differences in locomotor performance. The results from these analyses indicate that there are

significant differences in sprint speed (phylogenetic ANCOVA: $F_{1,97} = 2.57$; $p = 0.5$) or endurance capacity (phylogenetic ANCOVA: $F_{1,22} = 0.02$; $p = 0.96$) when comparing herbivores *s.l.* with other lizards. Although herbivores have to forage actively, they do not show greater endurance capacity than non-herbivores. Moreover, herbivores also show no reduced sprint performance capacity despite the fact that they do not need to pursue prey at high speed. This is all the more surprising given that herbivores are also thought to rely predominantly on their larger size and aggression (for example, *Uromastix* lizards will readily use their spiny tails when confronted with predators) as anti-predator strategies (see Table 7.1).

Bite forces (see also Chapter 9)

Although no explicit predictions exist for differences in bite forces among representatives of the two foraging modes, bite forces can be expected to be higher in sit-and-wait foragers. Not only would high bite forces allow these animals to crush and kill the relatively large prey they feed on (Pough *et al.*, 2001); in addition, high bite forces would ensure that a broad spectrum of potential prey with varying exoskeleton thickness can be handled efficiently. Indeed, high bite forces allow for a faster processing of hard-shelled prey, thus considerably reducing handling time and saving energy (Pough *et al.*, 1997; Verwaijen *et al.*, 2002). However, an analysis of bite forces among a range of lizard taxa (see Figs. 7.1, 7.3; Tables 7.2, 7.3) indicates that sit-and-wait predators do not bite harder than closely related active foragers (irrespective of dietary preference). This result holds when taking into account the evolutionary relationships among species. Thus, it appears that, at least for the species included in the present analysis, sit-and-wait predators do not bite harder than active foragers.

As most plant parts are typically tough and fibrous (with the exception of fruits, buds and young shoots), herbivores are expected to have high bite forces. This would allow them to efficiently crop smaller, bite-size pieces from larger plants (Herrel *et al.*, 1998a). The ingestion of small pieces of plant matter is considered important as this allows for a more efficient digestion (Bjorndal *et al.*, 1990; Bjorndal & Bolten, 1992). A comparison of *in vivo* bite forces among the lizard species in our analysis (Fig. 7.3, Table 7.2) indicates that lizards including plant matter into their diet (herbivores *s.l.*) do indeed bite harder than insectivores (Table 7.3). Even when taking into account the evolutionary relationships among species, herbivores *s.l.* still bite significantly harder than insectivores (Fig. 7.3, Table 7.3). However, no differences could be demonstrated between herbivorous *s.s.* and omnivorous lizards (see Table 7.2), indicating that the increase in bite force is likely associated with the initial transition from insectivory to omnivory.

Table 7.3 Results of phylogenetic analyses of covariance testing for differences in head shape and bite force

Variable	F_{phyl}	F_{95}	p_{95}	p_{phyl}
<i>Test for differences between active and sit-and-wait foragers</i>				
Head length	6.44	0.02	0.90	0.95
Head width	6.27	11.16	0.005	0.009
Head height	6.07	0.72	0.41	0.53
Bite force	6.80	1.14	0.30	0.43
SVL ^a	7.73	0.84	0.38	0.59
<i>Test for differences between herbivores s.l. and other lizards</i>				
Head length	3.86	0.09	0.77	0.75
Head width	3.45	0.13	0.73	0.70
Head height	3.65	3.85	0.07	0.045
Bite force	3.75	5.39	0.04	0.023
SVL ^a	3.67	4.00	0.07	0.041

^aTests for differences in snout-vent length (SVL) are phylogenetic analyses of variance. All other tests are phylogenetic analyses of covariance with SVL as covariate.

Feeding behavior (see also Chapters 9 and 10)

In a recent paper, McBrayer and Reilly (2002) demonstrated that prey processing behavior differs significantly between iguanian and autarchoglossan lizards. Moreover, they showed how certain aspects of prey handling appear to covary with foraging mode in lizards (see Chapter 10). Whereas active foragers use more puncture crushing, sit-and-wait predators used fewer processing cycles on average. Given that sit-and-wait foragers are expected to eat large prey this is rather surprising, especially as bite forces do not differ between members of both foraging modes (see above). Prey capture in sit-and-wait predators also defies the prediction that these animals will eat larger prey on average. Given that adhesive forces are proportional to the contact area between tongue and prey, jaw capture would be expected for animals eating large prey. This is indeed counterintuitive, as most iguanians use their tongue to capture prey. Even more remarkable is the fact that the only scleroglossan known to use their tongues during prey capture have secondarily evolved a sit-and-wait foraging strategy (e.g. *Zonosaurus laticaudatus*: Urbani and Bels 1995; *Gerrhosaurus major*: McBrayer and Reilly, 2002; *Eumeces schneideri*: McBrayer and Reilly, 2002; Chapter 10).

As mentioned earlier, herbivores need to reduce plant matter to optimize digestive efficiency. Interestingly, the one herbivore s.s. (*Ctenosaura*

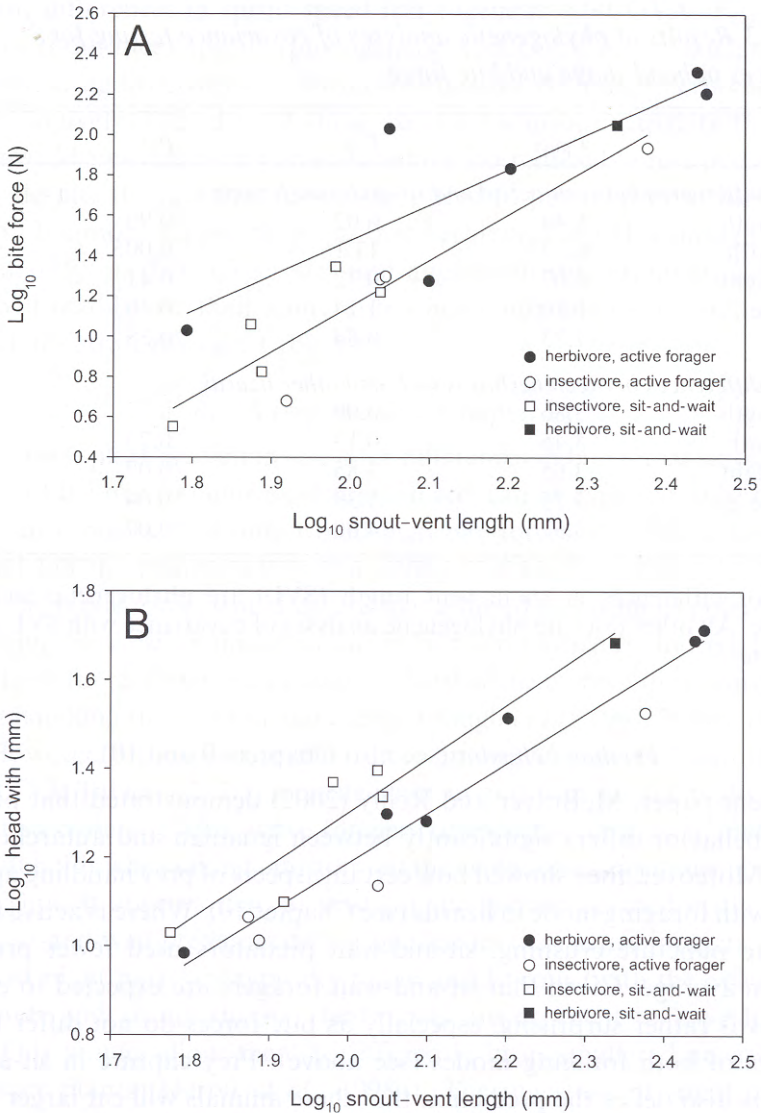


Figure 7.3. Differences in bite force and head shape. (A) Note how herbivores (filled symbols) bite significantly harder than non-herbivores (open symbols) for a given body size. However, no differences are apparent among sit-and-wait predators (squares) or active foragers (circles). (B) Sit-and-wait predators have significantly wider heads than active foragers for a given snout-vent length. No differences in head width are present among dietary categories. Symbols as in (A).

quinquecarinata) included in the dataset by McBrayer and Reilly (2002) uses the most puncture crushing of all iguanids studied. Personal observations of feeding behavior in other herbivores such as *Uromastix acanthinurus* and *Corucia zebrata* indicate that these, too, chew plant matter extensively before

swallowing. Although it has been previously suggested that cranial kinesis would be beneficial for herbivorous lizards (see, for example, King, 1996), data based on cineradiographic recordings of animals during feeding do not support this (Throckmorton, 1976; Herrel *et al.*, 1998a). Given that omnivores eat a wide variety of prey differing in size and other physical attributes (e.g. hardness), I expect extensive modulation capacity. Moreover, well-developed feedback pathways are also likely to be important for omnivorous lizards (Herrel *et al.*, 2001b). The evolution towards 'true' herbivory, on the other hand, might be associated with the loss of functional versatility and flexibility of the feeding system (i.e. a lack of modulatory capacity when confronted with different prey types; see Ralston and Wainwright, 1997) as indicated by data for *Uromastix acanthinurus* (Herrel and De Vree, 2000; pers. obs.). However, it should be noted that this is definitely not the case for all herbivores: *Corucia zebrata* shows no decrease in its modulatory capacity associated with its herbivorous diet (Herrel *et al.*, 1999b).

Morphology

Body size and shape (see also Chapter 2)

Sit-and wait predators are expected to be rather stocky when compared with active predators, as they move less and rely mostly on crypsis as an antipredatory strategy (Huey and Pianka, 1981; Vitt and Congdon, 1978). Additionally, large body and stomach volume is presumably beneficial when eating occasional large prey. Active foragers, on the other hand, are expected to have slimmer and more streamlined bodies. As these animals move about a lot and need to be agile while searching for food in a variety of microhabitats, a lower body mass and smaller overall body size are likely to be beneficial. An analysis of snout-vent length (SVL) data (see Tables 7.3 and 7.5) indicates no systematic differences in body size between active foragers and sit-and-wait predators. However, rather than snout-vent length *per se*, body width and relative body mass (relative to SVL) would be expected to differ between foraging modes.

A classic paper by Pough (1973) predicts that larger-bodied lizards should be herbivorous as they are presumably unable to meet their (absolutely higher) caloric demands based on a diet of insects alone. Herbivory is thus considered a necessary byproduct of large body size in the absence of distinct morphological, physiological, or ecological specializations (Pough, 1973). On the other hand, larger body size presumably also facilitates herbivory, as a large body allows for a large gastrointestinal volume. This is probably important, as herbivores often consume large amounts of plant matter of potentially low nutritional quality in one sitting. For the species included in our analysis

(Table 7.2), differences in snout–vent length between herbivores and insectivores are non-significant. However, when taking into account the evolutionary relationships among species, herbivores *s.l.* are indeed significantly larger than insectivores (Table 7.3). This implies that the evolution towards an omnivorous or herbivorous diet in lizards has occurred in tandem with an increase in body size. Although it should be noted that the list of species included in this analysis is by no means exhaustive, these results confirm earlier observations by Van Damme (1999) for lacertid lizards.

Head size and shape (see also Chapter 9)

One of the interesting predictions of the paradigm is that representatives of the two foraging modes will differ in head shape. As sit-and-wait predators are thought to eat large prey, the prediction is that they should have wide mouths, large gapes, and wide passages to the esophagus, and thus essentially be big-headed. Active foragers, on the other hand, are expected to have rather slender, light, and elongate heads to allow them to move about for prolonged periods of time. An analysis of the external head shape data in Table 7.2 indicates that sit-and-wait predators and active foragers do indeed have differently shaped heads (MANCOVA with SVL as covariate, Wilk's $\lambda = 0.251$; $F_{4,10} = 7.468$; $p = 0.005$). As indicated by subsequent univariate *F*-tests, this difference is mainly due to differences in relative head width (Fig. 7.3, Table 7.3). When taking into account the evolutionary relationships among the different species in the analysis, differences in relative head width are still highly significant (Table 7.3).

Lizards that include plant matter in their diet can also be expected to have differently shaped heads, given that they tend to bite harder than insectivorous lizards (see above) and that head shape has been shown to be correlated with bite force in lizards (Herrel *et al.*, 1999b, 2001a, c). An analysis of the dataset in Table 7.2 indicates that differences in head shape do indeed exist (MANCOVA with SVL as covariate, Wilk's $\lambda = 0.374$; $F_{4,10} = 4.18$; $p = 0.03$) between herbivores and other lizards. Subsequent univariate *F*-tests show that this difference is largely due to differences in head height, with herbivores having taller heads than insectivores (Table 7.3). Phylogenetic analysis indicates that the evolution of herbivory is indeed associated with an evolutionary increase in head height independent of the group to which lizards belong (Table 7.3).

Tooth shape

Although no clear predictions exist with respect to tooth structure, one might expect sit-and-wait predators to have more robust teeth that would allow them to crush large or thick-shelled prey. Active foragers, on the other hand, are

expected to be more agile and would be expected to have light skulls with slender, pointed teeth for puncturing smaller prey. However, even a cursory overview of literature data indicates that this dichotomous view is overly simplistic. Rather, more specific functional adaptations of dentition to diet are observed, irrespective of foraging mode. For example, whereas ant specialistists have numerous, short, peg-like teeth (Hotton, 1955; Montanucci, 1989), durophagous specialists typically have blunt, rounded teeth (Dalrymple, 1979; Rieppel, 1979; Rieppel and Labhardt, 1979).

The plant matter that creates most problems for herbivorous animals consists of leaves, stems and grasses, as these are composed of both tough and fibrous materials (Lucas and Luke, 1984). Tough materials need a lot of mechanical work before fracture occurs as they are generally ductile and resist crack propagation. Similarly, fibrous materials are notch-insensitive (Jeronimidis, 1991) and cracks are readily absorbed at the matrix-fiber interface (Sibbing, 1991). To fracture such materials, tooth penetration is essential. To increase local stresses, a set of carefully aligned opposing blades that pass close to each other (shearing) is presumably optimal (Lucas, 1979, 1982; Lucas and Luke, 1984; Sibbing, 1991). The teeth of herbivorous and even omnivorous lizards examined here (Fig. 7.4) have some of the above characteristics in common: they are mediolaterally flattened, generally robust, and appear blade-like (see also Hotton, 1955; Montanucci, 1968). However, in contrast to data gathered by Hotton (1955) and Montanucci (1968), non-iguaniid herbivores do not always show increased degree of cuspatation of the teeth (Fig. 7.4). Acrodont herbivores differ from this general pattern: species like *Uromastix* have highly specialized but less mediolaterally flattened teeth. Still, the tooth structure as observed in *Uromastix* is highly suited for cropping and cutting up plant matter (Cooper and Poole, 1973; Robinson, 1979; Throckmorton, 1979). Although not related to either group of foraging strategies, the acrodont tooth type appears mammalian-like in some aspects (Cooper *et al.*, 1970) and seems generally predisposed for herbivory owing to its flattened and robust nature. Interestingly, natural history observations indicate that several agamid lizards, although considered typical insectivores, will include plant matter in their diets in times of food scarcity (Greer, 1988; Disi *et al.*, 2001; Spawls *et al.*, 2002) suggesting that the tooth structure observed in acrodonts might indeed facilitate the switch to omnivory.

Digestive tract length and morphology

I was unable to find clear predictions as to what degree differences in digestive tract length and morphology should be expected between actively foraging lizards and sit-and-wait predators. However, if sit-and-wait predators do indeed

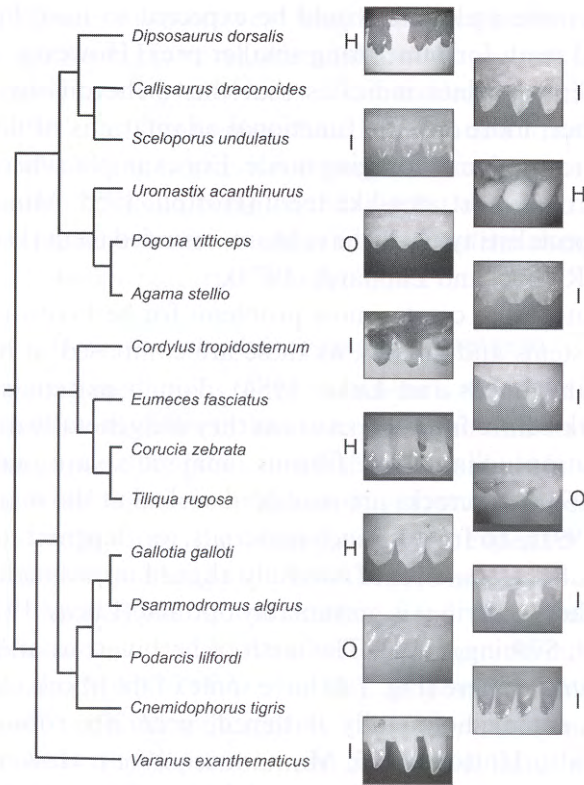


Figure 7.4. Phylogeny depicting the relationships between the species in the analysis. Photographs to the right of the phylogeny show a lateral view of the posterior teeth of the upper jaw for each species (not to scale). Note that herbivores have generally flattened and blade-like teeth. However, only the inguanid herbivore *Dipsosaurus dorsalis* has well-developed excentric cusps on its teeth.

consume larger prey on average, one could predict that these animals would have larger stomachs to allow the digestion of large prey. Additionally, as sit-and wait predators are expected to eat infrequently, the physiologically active tissues should be up- and down-regulated depending on the presence of food (Piersma and Lindstrom, 1997). Many snakes use this strategy; some, such as pythons, are able to increase the size of the active tissues of the small intestine to up to three times the fasting level (Starck and Beese, 2001). However, an analysis of differences in total digestive tract length as well as the length of specific compartments within the digestive tract did not indicate any differences between the active foragers and sit-and-wait predators included in our dataset (phylogenetic ANCOVA, all $p > 0.05$; Table 7.4). This is not completely unexpected, as one might expect differences to be situated in the volume rather than the length of these elements. It would be interesting to test for differences in volume by

Table 7.4 *Intestinal tract and snout–vent length in representative lizard species*

Data represent means (in millimetres) from adult male individuals. Classification of species into dietary and foraging categories is based on literature data. Total intestinal tract length does not include the esophagus or the rectum as these parts could not always be removed intact in all specimens. The number in parentheses after a species name indicates the sample size.

Species	SVL	Stomach	Intestine	Colon	Total length	Diet	Foraging mode
<i>Dipsosaurus dorsalis</i> (1)	110.25	23.15	105.08	19.18	147.41	herbivore	active forager
<i>Callisaurus draconoides</i> (3)	81.59 ± 7.55	27.98 ± 4.36	65.65 ± 10.52	9.98 ± 1.33	103.60 ± 14.86	insectivore	sit-and-wait
<i>Sceloporus undulatus</i> (3)	61.08 ± 3.59	18.89 ± 2.44	45.23 ± 3.50	10.14 ± 3.76	74.26 ± 5.41	insectivore	sit-and-wait
<i>Pogona vitticeps</i> (1)	173.06	49.14	163.36	39.73	252.23	omnivore	sit-and-wait
<i>Plecoedema stellio</i> (2)	104.15 ± 0.05	37.46 ± 0.45	98.28 ± 22.02	21.34 ± 3.27	157.08 ± 18.30	insectivore	sit-and-wait
<i>Uromastix acanthinurus</i> (3)	171.81 ± 4.11	61.74 ± 5.27	126.64 ± 12.96	50.66 ± 2.93	239.04 ± 18.90	herbivore	active forager
<i>Cordylus tropidosternon</i> (2)	87.50 ± 0.60	26.58 ± 1.35	45.52 ± 7.8	15.35 ± 2.89	87.44 ± 9.34	insectivore	sit-and-wait
<i>Eumeces fasciatus</i> (3)	71.35 ± 1.06	26.96 ± 0.78	42.62 ± 5.20	12.63 ± 0.63	82.21 ± 5.41	insectivore	active forager
<i>Corucia zebrata</i> (2)	240.00 ± 0.50	73.41 ± 1.69	164.72 ± 14.72	72.50 ± 3.08	310.62 ± 16.11	herbivore	active forager
<i>Tiliqua rugosa</i> (2)	244.00 ± 29.70	72.66 ± 12.54	214.76 ± 4.99	56.32 ± 2.58	343.73 ± 4.98	omnivore	active forager
<i>Gallotia galloti</i> (4)	116.88 ± 6.79	33.64 ± 2.35	103.03 ± 19.84	28.25 ± 3.37	164.92 ± 17.81	herbivore	active forager
<i>Psammotromus algeris</i> (4)	68.77 ± 3.17	20.53 ± 5.00	40.91 ± 11.64	13.65 ± 4.28	75.09 ± 18.78	insectivore	active forager
<i>Podarcis lilfordi</i> (3)	71.01 ± 6.29	24.36 ± 4.57	73.35 ± 14.21	21.61 ± 4.01	119.32 ± 22.30	omnivore	active forager
<i>Cnemidophorus tigris</i> (3)	83.98 ± 8.48	30.62 ± 8.12	75.73 ± 16.62	16.72 ± 3.03	123.07 ± 25.84	insectivore	active forager
<i>Varanus exanthematicus</i> (2)	261.36 ± 21.79	65.82 ± 1.30	257.04 ± 10.88	57.06 ± 8.42	379.91 ± 20.61	insectivore	active forager

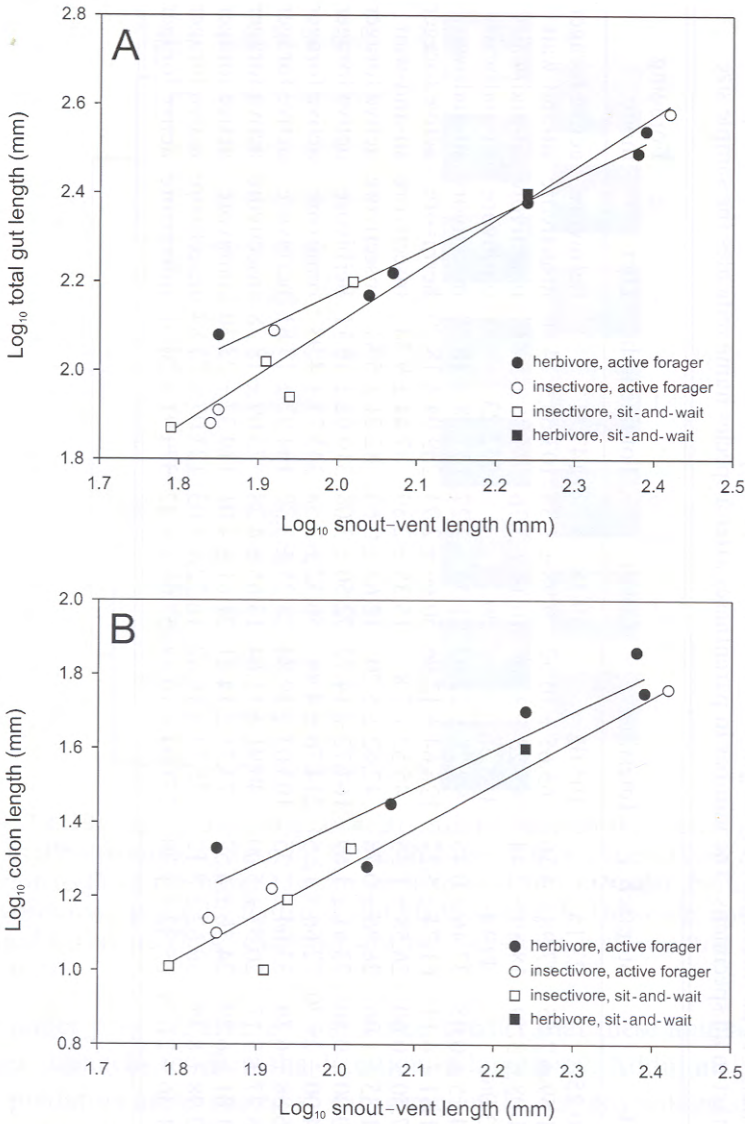


Figure 7.5. Differences in intestinal tract length. Despite the absence of differences in total intestinal tract length (A), herbivores do have longer colons for a given body length (B). In addition, the colon in herbivores has often been modified into a regular cecum with cecal ridges or valves that help slow down the passage of food.

using silicone casts of fresh specimens. Additionally, differences in digestive physiology between active and sit-and-wait foragers are likely to prove an interesting avenue for further research.

As vertebrates rely heavily on commensal microorganisms to digest the cellulose in the cell walls of plants, having a large digestive tract that can be

Table 7.5 Results of phylogenetic analyses of covariance testing for differences in intestinal tract length

Variable	F_{phyl}	F_{95}	P_{95}	P_{ph}
<i>Test for differences between active and sit-and-wait foragers</i>				
stomach	3.35	0.32	0.58	0.5
intestine	3.44	0.92	0.36	0.2
colon	3.59	5.42	0.04	0.0
total length	3.43	1.78	0.21	0.1
SVL ^a	3.00	4.29	0.059	0.0
<i>Test for differences between herbivores s.l. and other lizards</i>				
stomach	8.08	0.01	0.92	0.9
intestine	7.29	0.02	0.90	0.9
colon	7.36	3.31	0.10	0.1
total length	7.72	0.30	0.60	0.7
SVL ^a	7.47	0.10	0.34	0.5

^aTests for differences in snout–vent length (SVL) are phylogenetic analyses of covariance. All other tests are phylogenetic analyses of covariance with SVL as covariate. Differences in esophageal and rectal length were not tested as it was impossible to take out the entire intestinal tract intact in all specimens. Total length was measured from the beginning of the stomach to the end of the colon.

partly modified as a fermenting chamber is expected for any herbivore. Indeed in many herbivorous *s.s.* lizards part of the colon has been modified into a well-developed cecum, often with cecal valves that help slow down the passage of food (Iverson, 1980, 1982). In addition, an increase in the surface area of the digestive tract to allow for maximal resorption of nutrients is probably important. In some herbivorous mammals that feed on bulky, low caloric foods, this is achieved by a dramatic increase in the length of the intestine (up to ten times longer) (see Liem *et al.*, 2001). Data for herbivorous whiptail lizards (*Cnemidophorus murinus*) and lacertid lizards suggest that an increase in intestinal tract length may also be an important evolutionary strategy in omnivorous lizards (Dearing, 1993; A. Herrel *et al.*, unpublished data). An analysis for the species included in Table 7.4 indicates that although no differences in total intestinal tract length exist (phylogenetic ANCOVA, $p = 0.15$, see Fig. 7.5 and Table 7.5), herbivores *s.l.* do differ from other lizards in having a well-developed and significantly longer colon (phylogenetic ANCOVA, $p = 0.026$, see Fig. 7.5 and Table 7.5). This suggests that, rather than a general increase in intestinal tract length, the length of specific physiologically important components may increase as a response to a herbivorous diet. Potentially changes in overall intestinal tract length may only be important when constraints on cecal mass and dimensions are present, as may be the case in

actively moving lizards such as whiptails. All 'true' herbivores examined in the present paper, including the lacertid lizard *Gallotia galloti*, showed well-developed ceca with ridges or valves that probably function to slow down the passage of food. In addition, the omnivorous lacertid lizard *Podarcis lilfordi* as well as the omnivorous scincid *Tiliqua rugosa* showed distinct modifications of the colon, including cecal ridges that presumably also function to slow down the passage of food. The modifications in gut structure in herbivorous lizards probably play an important role in assuring that their digestive efficiency is comparable to that of insectivores (Throckmorton, 1973; Nagy, 1977; Johnson and Lillywhite, 1979).

Tongue structure (see also Chapters 8 and 10)

Among lizards using their tongue to capture and/or transport prey, sit-and-wait foragers would probably benefit from having big tongues, given that the adhesive force exerted by the tongue upon the prey is proportional to the surface area of the tongue itself. In addition, we would expect the tongues of sit-and-wait predators to have large numbers of well-developed papillae to ensure maximal adhesion (i.e. maximize the potential for interlocking). However, this prediction relies strongly on the fact that sit-and-wait foragers are expected to eat large prey. For very large prey, tongue transport is no longer a functional strategy, owing to the disproportionate increase of prey mass to surface area. Active foragers, on the other hand, are likely to benefit from having a long, bifurcated tongue that can be used for chemoreceptive purposes. Actively foraging scleroglossans often also have scaly tongues, which might be better for transport of chemicals to the sublingual plicae and ultimately the vomeronasal organ. As active foragers eat light, small prey they do not need large, fleshy, papillose tongues for transport. In varanid lizards (*Varanus*) and some tegus (*Tupinambis*) that eat very large prey, inertial rather than lingual transport is used (Gans, 1969; Elias *et al.*, 2000; Schwenk, 2000).

Herbivores presumably do not need a large and fleshy tongue as they tend to eat rather light food items. In addition, as the tongue is used for chemoreceptive purposes, one would expect herbivores to have longer and more deeply bifurcated tongues. However, as in most lizards, the tongue is still of prime importance in transporting the food to the esophagus. As iguanians rely strongly on gustation to assess prey chemicals, herbivores are also expected to have a larger number of taste buds on the tongue and associated tissues. As herbivorous iguanians also use vomerolfactive cues (Cooper and Alberts, 1991; Cooper, Chapter 8), one would also expect a more strongly developed vomeronasal organ. It is noteworthy to mention that, at least in one iguanian herbivore for which data on tongue structure are available, the papillae on the

tongue were strongly reduced and resembled the more scaly tongue structure of scleroglossan lizards (see Fig. 3 in Herrel *et al.*, 1998b). Omnivores would, contrast to herbivores, be expected to have rather big and fleshy tongues to pick up and/or transport a wide range of vegetable and animal food items.

Discussion

How similar are herbivores to sit-and-wait predators and active foragers? Although herbivores are, by definition, active foragers, the data presented here indicate that they are unique and highly specialized, possessing an array of both sit-and-wait and active foraging traits. Although herbivores need to forage actively to find their food, the food itself must be reduced extensively before being swallowed. The clumped and often unpredictable nature of certain plant foods is, however, reminiscent of foods eaten by active foragers. One aspect of foraging where herbivores have clearly adopted a typical active forager trait is prey detection. All herbivores tested to date, whether nested within sit-and-wait clades or not, use prey chemical cues to identify and assess food items. Owing to the sessile nature of their food, herbivores have relatively low energy requirements despite their active mode of foraging (see above). As a result of their relatively low energy requirements, herbivores also have home ranges that are smaller than those of insectivores (Perry and Garland, 2002).

The analysis of locomotor performance data indicates that herbivores are again different from active foragers in that they do not have an increased endurance capacity. Although herbivores need to forage actively, they presumably cover smaller distances (smaller home ranges) and do not need to sustain fairly high locomotor speeds, as the food does not move. Herbivores differ from both active foragers and sit-and-wait predators in having large bite forces. This seems to be a trait essential for the evolution of a herbivorous lifestyle in lizards. The feeding behavior, on the other hand, is more similar to that of an active forager, with an emphasis on prolonged chewing. Obviously, this is important as prolonged chewing increases the amount of plant cell wall directly broken (which frees the content to be digested), and increases the surface area of the plant food for digestion by commensal organisms.

Morphologically, herbivores are a mixed bag, with some traits more like those of sit-and-wait predators, but also with a whole suite of derived and highly specialized characteristics. Although herbivores have the wide, stocky body and head in common with sit-and-wait predators, they have uniquely thin heads and specialized, mediolaterally flattened and blade-like teeth. The digestive tract is also uniquely specialized in herbivores, with an elongated colon that is often modified into a regular cecum inclusive of cecal ridges.

and valves. The tongue of herbivores is often broad and fleshy, which may aid in the transport of plant matter, but presumably possesses a specialized epithelium and more taste buds than is typical for sit-and-wait predators. Unfortunately, quantitative data on tongue structure are largely lacking, thereby making tests for differences in tongue structure impossible.

One of the major issues related to the foraging paradigm is the seemingly rigid association of morphological and ecological traits with foraging mode. Because foraging mode is tightly associated with phylogeny (with iguanians being mostly sit-and-wait predators and scleroglossans being mostly active foragers) it is hard to test whether the invariance of character states associated with foraging mode is due to phylogenetic inertia or the result of true adaptive evolution. However, herbivores may offer some unique insights as they have arisen independently in both Iguania and Scleroglossa and appear to possess a number of very specific adaptations, unrelated to foraging mode as well as characters that are probably associated specifically with foraging mode. The results presented here clearly indicate that most of the characters typically tightly associated with foraging mode do change when evolving a herbivorous lifestyle (morphology, locomotor performance, energy requirements, etc.). In addition, some of the characters typically associated with a certain foraging mode show reversals in herbivores. For example, iguanian herbivores that arose within a sit-and-wait clade all evolved the use of chemosensory prey detection typically associated with an actively foraging lifestyle. Scleroglossan herbivores, on the other hand, evolve large stocky bodies and big heads typically associated with iguanian sit-and-wait foragers. Clearly, many of these traits are not constrained by phylogeny, suggesting that the ecological and morphological character suite associated with foraging mode is a true adaptive phenomenon.

Given that many of the traits associated with herbivory are uniquely derived, independent of the ancestral condition, the question of why there are so many 'true' herbivores among the Iguania becomes even more pertinent. What are the differences between omnivores and 'true' herbivores as judged from the previous overview? Apparently, very few if any quantitative differences can be discerned in traits examined here for omnivores and true herbivores. The one character uniquely associated with true herbivores seems to be the high degree of specialization of the colon with very prominent ridges or valves. Yet this trait too seems unconstrained by phylogeny, as at least two scleroglossan herbivores *s.s.* possess this derived morphology (*Corucia zebrata* and *Gallotia galloti*). Could it be that, rather than being a real phenomenon, the apparent lack of scleroglossan herbivores *s.s.* is due to our limited knowledge of herbivory among scleroglossans? An overview of literature data

indicates that data for iguanian herbivores are indeed much more common than for scleroglossans. Yet most of the new herbivores that are being 'discovered' are small scleroglossans, suggesting that our current understanding might indeed be taxonomically biased.

Conclusions

What can we conclude regarding foraging strategy and herbivory in lizards? Is there really a paradox? Where do herbivores fit in? How do they support or challenge to support the supposed dichotomy between active foragers and sit-and-wait predators? Although the data presented here raise as many questions as can be answered, one thing the analyses clearly show is that there is no evidence of lizards being constrained or predisposed with respect to dietary mode because of their ancestry. For iguanians, sit-and-wait predators readily evolve the ability of chemosensory cues to recognize and judge the quality of plant matter, and on the scleroglossan side active foragers grow bigger and develop broader and higher heads. Regardless of foraging mode, the change to a herbivorous diet is universally associated with the evolution of flat blade-like teeth, high bite forces, larger body size, and a longer colon. As most of these traits are already observed in omnivorous lizards, this suggests that it is the transition to an omnivorous diet that may be the crucial step in the evolution of herbivory. It may then be surprising that, even though independent origins of omnivory are likely to be more common among scleroglossans (Cooper and Vitt, 2001), most herbivores *s.s.* are Iguania. If the crucial transitions indeed take place going from an insectivorous to an omnivorous diet, why are there not many scleroglossan herbivores *s.s.*? The current knowledge of the distribution of herbivory within lizards and of the associated ecological and morphological traits is unfortunately insufficient to answer this question.

Unresolved questions, future directions

The often heard, but often justified, cry for more quantitative data is applicable here too. Clearly, more data are needed on all aspects of herbivory, especially in scleroglossan lizards. Cordylid (e.g. *Angolosaurus skoogi*), anguillid (which species if any might be herbivores?) and xantusiid (e.g. *Xantusia riversiana*) herbivores are largely unstudied, but could provide significant insights into the evolution of herbivory within scleroglossan taxa. More quantitative data on foraging behavior (i.e. quantifying movement during foraging) and associated morphological traits would be equally beneficial to our understanding of the co-variation and co-evolution of dietary specialization and foraging.

mode in lizards. Wider sampling of herbivorous and non-herbivorous taxa is thus essential to allow a quantitative test for associations between foraging mode and herbivory (see Cooper and Vitt, 2002). In addition, I think it would be most important to identify current, and ongoing, transitions from insectivory to omnivory, and from omnivory to herbivory. Clearly, we also need to document the ecological, behavioral and functional changes that accompany these transitions. Lizards showing large amounts of population-level variation in the degree of herbivory (e.g. lacertid lizards of the genus *Gallotia*) would be especially suited for these types of analyses and might offer truly exciting windows into adaptive evolution in action.

Acknowledgements

I thank Jay Meyers for sharing unpublished data. Bieke Vanhooydonck, Raoul Van Damme, and Jay Meyers are gratefully acknowledged for stimulating discussions on aspects of this work. I also thank the Antwerp Zoo for allowing me to use the animals in their care. A. H. is a postdoctoral fellow of the Fund for Scientific Research, Flanders, Belgium (FWO-VI).

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