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Frugivory in polychrotid lizards: effects of body size

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Abstract As more data have become available on lizard diets in the past few decades, researchers have stressed the importance of lizards as pollinators and seed dispersers. Whereas large body size has been traditionally put forward as a major biological factor “allowing” herbivory and frugivory in lizards, a recent review of frugivory and seed dispersal by lizards showed that frugivory might be considered to be a typical island phenomenon, independent of body size. Here we show that frugivory is correlated with lizard body size among a group of syntopic *Anolis* species in Jamaica, with larger species eating more fruit. Additionally, the size of the fruits consumed is significantly related to lizard body size. Multiple regression analyses show that this is largely a pure body size effect as head shape or residual bite force are uncorrelated to overall fruit size. Moreover, we demonstrate that among polychrotid (*Anolis*-like) lizards in general, those that consume fruit are on average larger than those that do not. Lizards from the mainland were not significantly different in body size from island species. We thus suggest that fruit consumption in polychrotid lizards is mediated by large body size whether living on islands or not.

Keywords Diet · Evolution · Ecomorphology ·
Herbivory · *Anolis*

Introduction

Previous authors have asserted that lizards are (with some exceptions) generalised insectivores (e.g., Greene 1982; Schwenk 2000). However, this assumption is increasingly being challenged as more dietary data become available. The accumulation of evidence that many lizard species include vegetative plant parts, flowers, fruits, and even nectar in their diet has led to the realization that lizards may engage in important mutualistic interactions with plants (e.g., Iverson 1985; Traveset 1990; Valido and Nogales 1994; Nogales et al. 1998; Castilla 1999, 2000; Shanahan et al. 2001; Benitez-Malvido et al. 2003). Whereas enlarged body size has been traditionally put forward as a major biological factor facilitating herbivory and frugivory in lizards (see Schoener et al. 1982; Van Damme 1999; Cooper and Vitt 2002), a recent review of frugivory and seed dispersal by lizards suggested that frugivory should be considered an island phenomenon, independent of the effects of body size (Olesen and Valido 2003).

Several lines of evidence suggest that increased size should indeed correlate with frugivory or herbivory. First, as large lizards may be less adept at catching small insects, and as they have greater absolute energetic requirements, the switch from mobile to stationary food items (e.g., plants) may be associated with substantial energetic benefits (e.g., see Pough 1973; Van Damme 1999). Second, in absolute terms, the head of a larger lizard is bigger and is thus likely better at processing and swallowing large food items, such as fruits. For example, the higher bite forces of larger lizards (Herrel et al. 1999, 2001a, b) may allow them to consume relatively large and hard fruits (e.g., most figs are harder than most other fruits; see Dumont 1999; Aguirre et al. 2003). However, variation in head shape or relative bite force may also mediate the consumption of large or hard food items irrespective of an animal's absolute size (Herrel et al. 2002).

However, other ecological factors may also play a key role in determining whether lizards become frugivores. For

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example, lizards on islands may be more likely to consume plant matter (including fruit and nectar) as island lizard densities are often high, and interspecific competition is often lower than on the mainland (see Case et al. 1979; Olesen and Valido 2003). This may allow lizards to expand their diets to include novel food items such as fruit. Alternatively high lizard densities (strong intraspecific competition) may also force certain individuals to include alternative food items in their diet (i.e., density compensation; see MacArthur et al. 1972; Case 1975; Case et al. 1979). Additionally, as the number and diversity of lizard predators is often much lower on islands compared to mainland areas, this may allow animals to forage for longer periods of time, and to spend more time digesting plant matter (Szarski 1962).

However, few studies have systematically addressed how body size and the degree of frugivory are related either among or within lizard species. Here we test whether frugivory is associated with body size both within and among species by examining dietary patterns in polychrotid lizards. Polychrotid lizards are typically small, diurnal lizards that occur throughout the neotropics (Zug et al. 2001). Although generally considered insectivores, many species include fruit in their diet (Schwartz and Henderson 1991). Moreover, *Anolis* lizards have radiated extensively on a large number of Caribbean and Pacific islands as well as on the mainland of Central and South America, thus making them an ideal group with which to investigate whether frugivory is associated with the island conditions that are expected to lead to frugivory (i.e., fewer predators and interspecific competitors but generally large densities). In the present study, we quantitatively examine the prevalence of fruit consumption among different age/sex classes within and among four syntopic species of Jamaican *Anolis* lizards. Because these different groups (adult males, adult females, and juveniles) differ dramatically in size, we can test how size affects patterns of frugivory, both within each species, and among the four species. We also investigate whether variation in head shape and relative bite force (independent of variation in body size) can explain why particular species or age/sex classes consume fruit. Additionally, we test whether larger individuals eat fruits as this may in turn help explain why larger species eat more fruit. Finally, we gathered previously published data from the literature to examine whether frugivorous polychrotid lizards are generally larger than insectivorous ones, both among island and mainland anoles.

Materials and methods

Study animals

Individuals of four species of *Anolis* lizards were caught by noose or by hand at the Discovery Bay Marine Laboratory, Discovery Bay, Jamaica between 21 January 2002 and 2 February 2002. In total, we captured 45 *Anolis grahami*, 123 *A. lineatopus*, 48 *A. valencienni* and 13 *A. garmani*. Snout-vent length of all individuals was measured from the tip of the snout to the posterior edge of the anal

scale; head length was measured from the back of the parietal bone to the tip of the upper jaw; head width was measured at the widest part of the head (at the level of the jugal bones) and head height was measured just posterior to the orbits. All measurements were taken using digital callipers (Mitutoyo CD-15DC; precision 0.01 mm).

Measurement of bite capacity

We measured *in vivo* bite forces for all individuals using an isometric Kistler force transducer (type 9203) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5995; see Herrel et al. 1999 for a detailed description of the set-up). Where needed, we induced the lizards to bite the force transducer by tapping them gently on the side of the mouth. The tapping readily resulted in a characteristic threat response where the jaws are opened maximally. The free ends of the holder (the bite plates) were then placed in between the jaws, which immediately resulted in fierce and prolonged biting. As body temperature is known to affect performance capacity in lizards, we placed the lizards outside in the shade in individual bags at least half an hour prior to experimentation and in between trials. In doing so, the lizards attained body temperatures equal or close to the environmental temperature ($29 \pm 2^\circ\text{C}$). At least five "good" bites were obtained for each lizard. As an estimate of maximal bite capacity, we used the highest bite force out of the five bites for each individual.

Stomach content analysis

Lizards were stomach flushed directly after capture using a syringe with a ball-tipped steel needle attached. The size of the syringe and needle was adjusted to the size of the animal. Lizards were tapped gently on the sides of the jaw, which resulted in a threat response where the jaws are opened widely. A small plastic ring was inserted in between the jaws to allow unhindered flow of the water and food out of the digestive tract. The needle was gently inserted into the pharynx and pushed further down the digestive tract until the end of the stomach. Next, water was gently squeezed out of the syringe while massaging the stomach of the lizard. Water was added until the food was regurgitated or pushed out with the water. Stomach contents were placed in individual vials with 70% ethanol and labeled. Animals were marked with a non-toxic marker and allowed to recover from stomach flushing for at least 12 h before being returned to their exact site of capture.

Stomach contents were analysed down to the lowest possible taxonomical order (invertebrates), and were measured. Length and width of all intact food items were determined using digital callipers (Mitutoyo CD-15DC; precision 0.01 mm). The mass of each intact food item was determined using a Denver Instruments electronic balance (precision 0.01 mg). For seeds and intact fruits, we determined the two greatest linear dimensions and mass using digital callipers and an electronic balance as mentioned above. While stomach flushing lizards in the field, we noticed that two fruit types were disproportionately common in the stomachs of the species examined. Of these fruits, fresh samples of fruits and leaves were taken back to the laboratory at Tulane University and were identified by Anne S. Bradburn, Curator of the Tulane University Herbarium, as *Canella winterana* and *Ficus cotenifolia*. Where appropriate, fruits or seeds in the stomachs were classified as *Canella* or *Ficus*.

Statistical analyses

To test whether body size was a good predictor of frugivory in the Jamaican anoles, we regressed the log₁₀-transformed body size against the arcsin-transformed proportion of animals with fruit in their stomach for each species. We also regressed the log₁₀-transformed head dimensions and bite forces against the arcsin-

	male	female	fruit	island/mainland
<i>Polychrus marmoratus</i> ^{1,4}	126	144	Y	M
<i>Polychrus acutirostris</i> ²⁹	124	146	Y	M
<i>Anolis smallwoodi</i> ²⁴	190	165	Y	I
<i>Anolis equestris</i> ^{3,6,10,22,12}	188	170	Y	I
<i>Anolis richardi</i> ²³	140	77	Y	I
<i>Anolis griseus</i> ²³	136	86	Y	I
<i>Anolis aeneus</i> ²³	77	55	Y	I
<i>Anolis roquet</i> ²³	86	66	N	I
<i>Anolis vermiculatus</i> ²³	123	83	Y	I
<i>Anolis bahorucoensis</i> ²⁴	51	44	N	I
<i>Anolis coelestinus</i> ²⁴	84	60	Y	I
<i>Anolis olssoni</i> ²⁶	50	44	N	I
<i>Chamelinorops barbouri</i> ¹⁶	44	55	N	I
<i>Anolis strahmi</i> ²³	79	64	N	I
<i>Anolis armouri</i> ¹⁹	67	56	N	I
<i>Anolis whitemani</i> ^{7,8}	67	54	N	I
<i>Anolis cybotes</i> ^{14,24}	77	66	Y	I
<i>Chameleolis barbatus</i> ²³	170	157	N	I
<i>Chameleolis porcus</i> ²³	162	171	N	I
<i>Anolis cuvieri</i> ^{20,21}	122	87	Y	I
<i>Anolis barahonae</i> ⁵	160	148	Y	I
<i>Anolis bimaculatus</i> ¹⁷	123	70	Y	I
<i>Anolis ferreus</i> ²³	119	65	N	I
<i>Anolis gingivus</i> ²³	72	53	N	I
<i>Anolis lividus</i> ²³	70	52	N	I
<i>Anolis oculatus</i> ²	96	64	N	I
<i>Anolis distichus</i> ^{7,24,9,11}	58	48	Y	I
<i>Anolis cristatellus</i> ^{23,18}	75	76	N	I
<i>Anolis monensis</i> ²³	57	57	Y	I
<i>Anolis gundlachi</i> ²³	68	45	N	I
<i>Anolis pulchellus</i> ²³	47	36	N	I
<i>Anolis krugi</i> ²³	45	36	N	I
<i>Anolis evermani</i> ²³	70	45	N	I
<i>Anolis stratulus</i> ²³	44	46	N	I
<i>Anolis scriptus</i> ²³	76	64	N	I
<i>Anolis alutaceus</i> ²³	37	37	N	I
<i>Anolis angusticeps</i> ²³	53	47	N	I
<i>Anolis allisoni</i> ¹⁸	82.5	65.5	N	M
<i>Anolis smaragdinus</i> ²³	64	51	N	I
<i>Anolis porcatus</i> ²³	73	51	N	I
<i>Anolis sagrei</i> ^{18,23}	70	46	N	I
<i>Anolis ophiolepis</i> ²³	35	30	N	I
<i>Anolis humilis</i> ^{2,27,30}	37	40	N	M
<i>Anolis nitens</i> ^{29,32}	72	74	N	M
<i>Anolis biporcatus</i> ^{18,30}	105	105	N	M
<i>Anolis pentaprion</i> ¹⁸	65	50	N	M
<i>Anolis capito</i> ^{18,30}	91	95	N	M
<i>Anolis oxylophus</i> ³⁰	72	72	N	M
<i>Anolis limifrons</i> ^{2,27,30}	39	41	N	M
<i>Anolis ortonii</i> ^{1,13}	57	52	N	M
<i>Anolis fuscoauratus</i> ^{1,13}	49	50.5	N	M
<i>Anolis carpenteri</i> ³⁰	41	41	N	M
<i>Anolis lemuringus</i> ^{18,30}	67	69.5	N	M
<i>Anolis trachyderma</i> ^{1,13,32}	49.1	55	N	M
<i>Anolis lineatopus</i> ^{this study}	70	47	Y	I
<i>Anolis reconditus</i> ¹⁵	100	84	N	I
<i>Anolis valencienni</i> ^{this study}	80	65	Y	I
<i>Anolis grahmi</i> ^{this study}	75	64	Y	I
<i>Anolis garmani</i> ^{25,this study}	131	80	Y	I
<i>Anolis opalinus</i> ²³	53	44	N	I
<i>Anolis auratus</i> ¹	50	37	M	I

◀ **Fig. 1** Composite phylogeny representing the relationships between the species included in the comparative analysis (see Materials and methods). Also indicated are the maximal male and female body size (mm), whether species consume fruit (*Y*) or do not consume fruit (*N*), and whether species live on islands (*I*) or on the mainland (*M*). 1Avila-Pires (1995), 2Andrews (1979), 3Barbour and Ramsden (1919), 4Beebee (1944), 5Bowersox et al. (1994), 6Brach (1976), 7Burns et al. (1992), 8Carr et al. (1989), 9Cast et al. (2000), 10Colette (1961), 11Cullen and Powell (1994), 12Dalrymple (1980), 13Duellman (1978), 14Fobes et al. (1992), 15Hicks (1973), 16Howard et al. (1999), 17Lazell (1972), 18Lee (1996), 19Lenart et al. (1994), 20Perez-Rivera (1985), 21Rivero (1978), 22Ruibal (1964), 23Schwarz and Henderson (1991), 24Sifers et al. (2001), 25Simmonds (1958), 26Smith et al. (1994), 27Talbot (1979), 28Vitt and Lacher (1981), 29Vitt and Zani (1998a), 30Vitt and Zani (1998b), 31Vitt et al. (2001), 32Vitt et al. (2002)

transformed proportion of animals with fruit in their stomachs to test whether head dimensions and bite force were associated with fruit consumption. Next, we calculated head shape variables and residual bite forces by extracting the residuals of the regression of the log₁₀-transformed head dimensions and bite force against log₁₀-transformed snout-vent length for each sex separately. To test whether head shape and residual bite force were good predictors of frugivory, we regressed these variables against the arcsin-transformed proportion of animals with fruit in their stomach. Additionally, we ran a stepwise multiple regression analysis with snout-vent length, the head shape variables and residual bite force as independent variables and the arcsin-transformed proportion of individuals with fruit in their stomachs as the dependent variable. All data were analyzed for males and females separately. Although the data points in our regression analysis are not entirely independent (belonging to closely related species), our sample size does not allow regressions on species means using independent contrasts.

To test whether larger individuals consumed larger fruits, we regressed the average log₁₀-transformed size (length, width and mass) of the fruits consumed by each individual lizard against log₁₀-transformed body size across all individuals of the four species for each sex separately. Next we calculated head shape variables and residual bite force for each sex as above and regressed both those and the raw log₁₀-transformed head size and bite force data against the average log₁₀-transformed fruit size per individual. Additionally we ran a stepwise multiple regression with snout-vent length, the residual head dimensions and residual bite force against the respective fruit dimensions (mass, length and width).

Comparative analysis

To test whether the trends observed for the Jamaican *Anolis* species could be extrapolated to Polychrotid lizards in general, we gathered diet and body size data from literature from both island and

mainland species and tested whether frugivores (i.e., all species that were reported to include fruit in their diet and for which body size data were available) were larger than non-frugivores (species for which dietary and body size data were available, but that were not reported to eat fruit). Additionally we tested whether lizards living on islands were larger than their mainland congeners using the same data set. It should be noted, however, that the results of this last analysis should be interpreted with caution due to the unequal sample size (45 insular vs. 16 mainland species). We only included species for which we could find data on diet, adult male and female body size and for which the phylogenetic relationships were known. This resulted in a total of 61 species that were included in the comparative analysis (Fig. 1).

As species are related through their evolutionary history, we conducted these analyses in a phylogenetic framework (Felsenstein 1985, 1988; Harvey and Pagel 1991). To do so, we constructed a composite phylogeny of the 61 species based on molecular phylogenies reported in Jackman et al. (1999, 2002), Glor et al. (2001) and Nicholson (2002). The tree we use should be considered only as an estimate of the relationships among these species. As we were unable to find divergence times for all species in the analysis, all branch lengths were set to unity (Martins and Garland 1991; Diaz-Uriarte and Garland 1998). We used the PDAP package (Garland et al. 1999) for our analysis.

We inspected the diagnostic graphs and statistics in the PDTREE program to verify that our constant branch lengths were adequate for all traits (see Garland et al. 1999). Maximal body sizes log₁₀-transformed for males and females separately were used as our variables of interest. To test whether frugivores differed from non-frugivores, and island from mainland species in maximal body size, simulation analyses were performed using the PDSIMUL and PDANOVA programs (Garland et al. 1993). In the PDSIMUL program, we used Brownian motion as our model for evolutionary change and ran 1,000 unbounded simulations to create an empirical null-distribution against which the *F*-value from the original data could be compared. In the PDANOVA program, diet (frugivore vs. non-frugivore) or insularity (island vs. mainland) was entered as a factor, and maximal male and female body size were used as independent variables. We considered differences among categories significant if the original *F*-value was higher than the *F*₉₅-value derived from the empirical distribution.

Results

Stomach content analysis of Jamaican *Anolis* lizards

Fruits were a common food item in the stomachs of *Anolis* lizards from Discovery Bay, Jamaica. In some species (*A. garmani*, *A. valencienni*), a third or more of the

Table 1 Occurrence of fruit in the stomach of Jamaican *Anolis* lizards. Table entries are numbers of lizards with fruits in their stomachs (*Fruit*) vs. total number of lizards examined (*Total*).

Species	Total no. of individuals		Males		Females		Juveniles		Total no. of fruits	Fruits/individual
	Fruit	Total	Fruit	Total	Fruit	Total	Fruit	Total		
<i>A. lineatopus</i>	5 4.27%	117	3 5.36%	56	2 4.76%	42	0 0%	19	6	1.2
<i>A. garmani</i>	5 38.46%	13	2 40%	5	3 37.5%	8	–	–	5	1.0
<i>A. grahami</i>	8 19.05%	42	6 25.03%	24	2 13.33%	15	0 0%	3	10	1.25
<i>A. valencienni</i>	14 29.17%	48	7 28.00%	25	7 33.33%	21	0 0%	2	22	1.57

Percentages indicate relative abundance of fruit in the stomach of each species, sex and age class. Also shown are the total number of fruits and the mean number of fruits per individual

individuals had fruits in their stomachs (Table 1). Two fruits (*C. winterana* and *F. cotenifolia*) were disproportionately common in the diet and together comprised up to 50% of the total number of fruits in the diet of the four species combined. Whereas all four species ate *Canella*, only the larger three ate *Ficus*. Most lizards had only a single fruit in their stomach, with the exception of *A. valencienni* where individuals had two items on average in their stomach. Whereas *A. garmani* (fruit mass, 0.11 ± 0.04 g; length, 13.01 ± 4.85 mm; width, 5.96 ± 1.91 mm; means ± SD) and *A. valencienni* (fruit mass, 0.11 ± 0.13 g; length, 8.21 ± 3.61 mm; width, 4.96 ± 1.89 mm) ate relatively large fruits, the other two species typically ate smaller fruits (*A. lineatopus*, fruit mass, 0.02 ± 0.02 g; length, 6.12 ± 4.25 mm; width, 2.11 ± 1.26 mm; *A. grahami*, fruit mass, 0.04 ± 0.04 g; length, 7.30 ± 1.29 mm; width, 3.23 ± 1.19 mm).

When examining the relationships between lizard body size (see Table 2) and the proportion of animals with fruit in their stomach, a significant correlation was found for females ($r^2=0.90$, $P=0.049$) despite the low sample size (i.e., four data points). Regressions for males showed a

strong trend but were not significant ($r=0.87$, $P=0.068$; see Fig. 2).

Only regressions of snout-vent length against the proportion of individuals with fruit in their stomachs showed significant positive relationships in females, with regressions for head length ($r^2=0.82$, $P=0.092$) and bite force ($r^2=0.81$, $P=0.098$) approaching significance. For males, regressions against head length ($r^2=0.87$, $P=0.07$), head height ($r^2=0.86$, $P=0.071$) and bite force ($r^2=0.88$, $P=0.063$) approached significance. A multiple regression analysis with snout-vent length and the residual head dimensions and residual bite force was highly significant model with snout-vent length, residual head height and residual head width ($r^2=1$; $P<0.001$) for females. For males, however, no model was significant and thus retained.

An analysis of the size of the fruits eaten showed that among males, larger individuals ate significantly wider fruits (Table 3). Among females, larger individuals ate both wider, longer and heavier fruits (Table 3). A multiple regression analysis with snout-vent length and residual head dimensions and residual bite force as independent variables, and the respective fruit dimensions as dependent variables, was a significant model with snout-vent length as the only predictor for males (fruit width, $r^2=0.40$, $P=0.012$). Also for females, models were retained with snout-vent length only (fruit mass, $r^2=0.62$, $P=0.001$; fruit length, $r^2=0.48$, $P=0.006$; fruit width: $r^2=0.35$, $P=0.026$). Regressions of residual head dimensions and residual bite force against fruit dimensions were not significant, indicating that the relationship between head dimensions and fruit size is purely a consequence of body size in these lizards (all $P>0.05$).

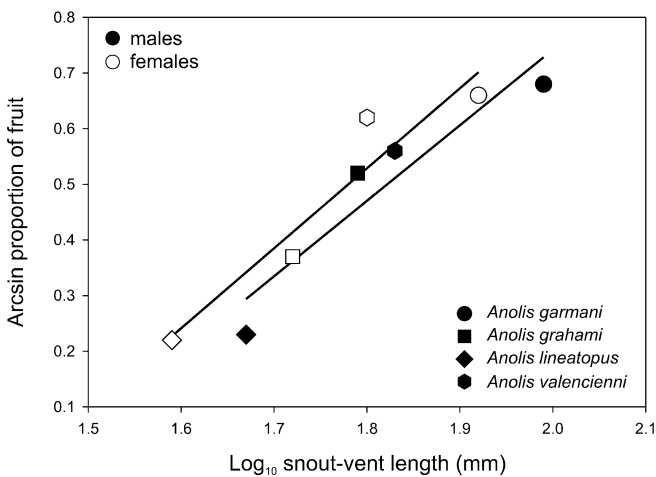


Fig. 2 Graphs representing the relationship between lizard size (snout-vent length) and the occurrence of fruit in the diet for males and females of the four species of Jamaican *Anolis* lizards. Note how females tend to eat more fruit for a given snout-vent length than males (not significant)

Comparative analysis

We obtained diet data from the literature for 61 species of polychrotid lizards (Fig. 1). The majority of the species were island species (45 species=70%). Whereas only two of the mainland species consumed fruit (10% of the species), fruit consumption was relatively common for island species (30% of the species are known to consume fruit).

Table 2 Morphometric characterisation of the species examined in this study. Table entries are averages ± SDs. Numbers in parentheses indicate the sample size for each sex and age class. BF Bite force, F female, HH head height, HL head length, HW head width, J juvenile, M male, SVL snout-vent length

Species	Sex	SVL (mm)	Mass (g)	HL (mm)	HW (mm)	HH (mm)
<i>A. lineatopus</i>	M (58)	51.6±5.9	3.1±1.2	15.9±2.1	8.4±1.1	6.3±0.8
	F (45)	44.0±2.2	1.9±0.5	13.0±0.6	6.8±0.3	5.1±0.3
	J (20)	31.3±5.0	0.7±0.3	10.1±1.1	5.4±0.5	4.2±0.4
<i>A. garmani</i>	M (6)	102.9±12.1	27.2±10.8	29.2±3.6	16.2±2.3	12.9±1.8
	F (7)	81.7±3.5	13.0±2.0	22.2±0.8	12.3±0.6	9.5±0.5
<i>A. grahami</i>	M (23)	59.6±4.4	5.5±1.5	17.8±1.3	10.2±1.0	7.3±0.8
	F (17)	45.2±3.3	2.4±0.7	13.5±1.0	7.3±0.6	5.3±0.5
	J (5)	29.8±6.1	0.4±0.1	9.8±1.7	5.3±0.6	4.0±0.5
<i>A. valencienni</i>	M (25)	65.5±8.3	5.1±1.9	19.3±2.7	9.3±1.3	7.7±1.3
	F (21)	60.1±5.7	4.0±1.0	16.8±1.3	8.0±0.7	6.4±0.5
	J (2)	35.2±6.8	0.9±0.9	10.4±1.8	5.4±0.7	4.7±0.1

Table 3 Regressions of log10-transformed SVL, parameters of head size and BF against the log10-transformed fruit size across all individuals with fruit in their stomach. For abbreviations, see Table 2

	Fruit mass		Fruit length		Fruit width	
	<i>r</i> ²	<i>P</i>	<i>r</i> ²	<i>P</i>	<i>r</i> ²	<i>P</i>
Males (<i>n</i>=18)						
SVL (mm)	0.19	0.11	0.11	0.23	0.40	0.012
HL (mm)	0.16	0.13	0.12	0.21	0.42	0.009
HW (mm)	0.10	0.26	0.10	0.25	0.28	0.041
HH (mm)	0.22	0.08	0.16	0.15	0.44	0.007
BF (N)	0.08	0.30	0.07	0.33	0.31	0.030
Females (<i>n</i>=14)						
SVL (mm)	0.62	0.001	0.48	0.006	0.35	0.026
HL (mm)	0.60	0.001	0.47	0.007	0.35	0.027
HW (mm)	0.43	0.011	0.39	0.018	0.25	0.072
HH (mm)	0.46	0.008	0.34	0.030	0.25	0.072
BF (N)	0.62	0.001	0.53	0.003	0.38	0.018

Our analysis shows that polychrotid frugivores are significantly larger than non-frugivores (males, 118 ± 39.64 mm vs. 71.53 ± 28.58 mm, $F_{1,59}=22.76$, $P<0.001$; females, 94.35 ± 42.00 mm vs. 63.08 ± 27.65 mm, $F_{1,59}=12.93$, $P=0.001$). For both male and female lizards the difference remains significant when taking into account the evolutionary relationships (phylogenetic; phyl) between species (males, $F_{\text{phyl}}=12.08$, $P=0.005$; females, $F_{\text{phyl}}=12.57$, $P=0.048$).

An analysis of body size indicates that species living on islands are not significantly larger than their mainland congeners (males, 87.42 ± 40.97 mm vs. 70.41 ± 28.58 mm, $F_{1,59}=2.38$, $P=0.13$; females, 69.07 ± 36.19 mm vs. 74.61 ± 35.17 mm, $F_{1,59}=0.54$, $P=0.50$). This result remains when the relationships between the species are taken into account (males, $F_{\text{phyl}}=28.44$, $P=0.60$; females, $F_{\text{phyl}}=31.09$, $P=0.81$).

Discussion

Frugivory in Jamaican *Anolis*

An unexpected finding from our data was that frugivory was relatively common among Jamaican *Anolis* lizards. All four species investigated consumed some fruit, with larger species consuming more fruit than smaller ones (see Fig. 2). No juveniles of any of the four species of Jamaican anoles examined, consumed fruit. Additionally, our data show that among Jamaican *Anolis* lizards, larger lizards generally eat larger fruits (see Table 3). Additionally, our comparative data confirmed the results of the within-island analysis, and show that frugivores are on average, larger than non-frugivores.

Two fruits (*C. winterana* and *F. cotenifolia*) were disproportionately common in the diet of the Jamaican anoles examined. Whereas all Jamaican species consumed *Canella*, three of the four species also consumed *Ficus*.

That three of the four Jamaican *Anolis* species consumed figs is unexpected, as there are only a few documented cases of lizards eating figs (see Whiting and Greef 1997; Shanahan et al. 2001). Whether this relatively common fig-eating is related to the specific habitat sampled, the time of year, or other extrinsic factors cannot be determined at this point. A more extensive sampling of the diets of Caribbean *Anolis* lizards on different islands and at different time periods is currently being undertaken and will allow us to test the generality of these observations.

Why larger lizards in general eat fruit remains unclear at this point. However, as larger lizards have larger gapes and bite disproportionately harder than small lizards, this might enable them to chew or bite off pieces from large fruits more effectively, or to swallow small fruits whole (which was observed regularly in the Jamaican *Anolis*). This hypothesis was supported by the fact that larger lizards also eat larger fruits. Additionally, our data also indicate that larger lizards eat relatively more figs (relative to other fruits eaten), again suggesting that absolute bite force, or maximal mouth opening capacity might be important. Figs are known to be relatively hard fruits (Dumont 1999; Aguirre et al. 2003), and previous analyses have demonstrated that, at least in bats, fig-eating species show distinct behavioural modifications that enhance bite force generation, thus allowing them to consume these relatively hard fruits (Dumont 1999). Among the lizards examined in this study, *A. grahami* consumed a disproportionate amount of figs (50% of the fruits found in its stomach), but is a fairly small species (see Table 2). If bite force is important in facilitating the consumption of hard fruit, than we would expect this species to have relatively high bite forces. However, *A. grahami* does not bite disproportionately hard for its body size when compared with the other small species in our analysis, *A. lineatopus* [analysis of covariance (ANCOVA), $F_{1,163}=6.28$, $P<0.05$, with *A. lineatopus* biting harder than *A. grahami*]. However, *A. grahami* does have relatively longer jaws (ANCOVA, $F_{1,163}=4.04$, $P<0.05$), suggesting that *A. grahami* can open its jaws further than *A. lineatopus*. This indicates that rather than bite force, gape distance or mouth opening capacity might be the important performance variable that allows smaller lizards to consume relatively large fruits.

Whereas no distinct changes in head shape or bite force were observed that were correlated with the prevalence of fruit in the diet in males, in females residual head height and residual head width were also retained in a multiple regression model with the proportion of fruit as dependent variable. This suggests that female lizards with relatively wider and higher heads eat more fruit, confirming the importance of large gape (animals with higher and wider heads will have a wider passage for fruits to be transported into the pharynx). Variation in fruit size, however, was not correlated with specific head shape variables or residual bite force. This suggests that, in general, any advantages conferred by larger heads, and larger bite forces, are a consequence of body size. *Anolis* lizards thus seem to be

opportunistic frugivores with larger animals eating more fruit because they are capable of doing so. However, gape distance and bite force are not the only attributes that covary with body size. For instance, larger lizards are typically subjected to lower predation pressures, thus allowing them to spend considerable amounts of time searching for and processing fruits (Szarski 1962). Larger lizards also have a larger absolute intestinal tract volume and surface area, thus facilitating the resorption of nutrients from food (King 1996). Moreover, large lizards might consume fruit disproportionately more than smaller lizards due to their larger absolute energetic demands (Pough 1973).

Effects of insularity on frugivory?

Our comparative data for polychrotid lizards suggest that within this group frugivores are more common on islands (30% of the species on islands vs. 10% on the mainland). However, island species in our data set are generally not bigger than mainland species (but see Schoener 1967, 1968; Schoener and Gorman 1968), suggesting that island phenomena such as density compensation or temporal fluctuations in prey abundance may force larger lizards to include fruits in their diet (see Olesen and Valido 2003). It should be noted, however, that the observed difference in number of frugivorous species on islands compared to the mainland, might potentially be a consequence of differences in sampling effort. Indeed, many more studies have focussed on insular *Anolis* lizards, especially Caribbean forms (almost 75% of data comes from studies on Caribbean *Anolis*).

If frugivory is brought about by processes such as density compensation, then it would be expected to be most common on small islands where interspecific competition is low (e.g., see Olesen and Valido 2003). Yet, Jamaica is a large island ($\pm 11,000$ km²), harbouring a complex anole fauna, and most of the traditionally recognised ecomorphs are present (with the exception of the grass-bush anole; Losos 1990). Additionally, previous analyses have shown that interspecific competition has been a key factor in the evolution of Jamaican anoles (Losos 1994; Roughgarden 1995) thus making it unlikely that reduced interspecific competition has led to the occurrence of frugivory on this island. Moreover, as literature data indicate (see Fig. 1), larger Caribbean islands with complex faunas often contain large numbers of frugivorous species (Fig. 1). Preliminary data of *Anolis* diets from very small Bahamian islands, often containing only one or two species of *Anolis* lizards, indicate very small amounts of fruit consumed, despite the availability of fruit to lizards. Another prediction inherent to density compensation is that high lizard densities (strong intraspecific competition) should force individuals towards frugivory. However, on many Caribbean islands, the *Anolis* species occurring in the highest densities are usually small (i.e., grass-bush anoles) and typically do not consume fruit (Fig. 1). Also, among the Jamaican *Anolis*

the most abundant species (*A. lineatopus*) consumes the least fruit of all four species examined.

These two lines of evidence suggest that density compensation (i.e., the presence of high lizard densities and reduced interspecific competition on small islands) may not explain the occurrence of frugivory in *Anolis* lizards. Moreover the observed *within*-island trend between body size and frugivory is also not consistent with hypotheses proposed by Olesen and Valido (2003), suggesting that at least in Caribbean *Anolis* lizards and potentially in polychrotid lizards in general, frugivory is not the result of island phenomena such as density compensation.

However, other ecological phenomena associated with insularity may have played an important role in creating the observed bias towards frugivory on islands. Temporal food scarcity, for example, is likely more common on islands (especially on small ones; see Van Damme 1999; Cooper and Vitt 2002 and references therein) and might force insular lizards towards frugivory or herbivory in general. The observation that larger islands most often harbour frugivores does not support this suggestion as fluctuations of food availability are likely buffered on these large tropical islands. Low predation pressures are often associated with insular habitats and may also promote frugivory by allowing lizards to forage for longer periods of time, and spend more time digesting food. Whereas data on predation pressures in insular vs. mainland habitats are scarce, it is unlikely that large islands with complex faunas (which often contain the largest numbers of frugivores) would show strongly decreased predation pressures. Thus, although it seems that frugivory in polychrotid lizards is more common on islands, none of the “traditional” explanations seem to hold. Clearly, further quantitative data on diets of polychrotid lizards will be needed before this paradox can be resolved.

In summary, our data show that: (1) within a single island radiation of *Anolis* lizards, strong correlations exist between body size and the prevalence of fruit in the diet. Moreover, our data also indicate that larger lizards tend to eat larger fruits: (2) polychrotid frugivores are, on average, larger than non-frugivores and (3) polychrotids living on islands are, on average, not larger than those on the mainland. Thus, while our data are consistent with previous studies that show that frugivores are more common on islands, we also contend that body size is a key factor in determining whether species are frugivorous.

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References

- Aguirre LF, Herrel A, Van Damme R, Matthyssen E (2003) The implications of food hardness for diet in bats. *Funct Ecol* 17:201–212
- Andrews RM (1979) Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. *Breviora Mus Comp Zool* 454:1–51
- Avila-Pires TCS (1995) Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zool Verh Rijksmus Nat Hist Leiden* 299:1–706
- Barbour T, Ramsden CT (1919) The herpetology of Cuba. *Mem Mus Comp Zool* 47(2):71–213
- Beebe W (1944) Field notes on the lizards of Kartabo, British Guiana and Caripito, Venezuela. Part 2. Iguanidae. *Zoologica* 29(14):195–216
- Benitez-Malvido J, Tapia E, Suazo I, Villasenor E, Alvarado J (2003) Germination and seed damage in tropical forest plants ingested by iguanas. *J Herpetol* 37:301–308
- Bowersox SR, Calderon S, Powell R, Parmelee JS Jr, Smith DD, Lathrop A (1994) Nahrung eines Riesenanolis, *Anolis barahonae*, von Hispaniola, mit einer Zusammenfassung des Nahrungsspektrums westindischer Riesenanolis-Arten. *Salamandra* 30:155–160
- Brach V (1976) Habits and food of *Anolis equestris* in Florida. *Copeia* 1976:187–189
- Burns JK, Cunningham CA, Dupuis RA, Trask MN, Tulloch JS, Powell R, Parmelee JS Jr, Kopecky KL, Jolley ML (1992) Lizards of the Cayos Siete Hermanos, Dominican Republic, Hispaniola. *Bull Chicago Herpetol Soc* 27:225–232
- Carr DK, Powell R, Parmelee JS Jr, Smith DD (1989) *Anolis whitemani whitemani*, food habits. *Herpetol Rev* 20:53
- Case TJ (1975) Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology* 65:3–18
- Case TJ, Gilpin ME, Diamond JM (1979) Overexploitation, interference competition and excess density compensation in insular faunas. *Am Nat* 113:843–854
- Cast EE, Gifford ME, Schneider KR, Hardwick AJ, Parmelee JS Jr, Powell R (2000) Natural history of an anoline lizard community in the Sierra de Baoruco, Dominican Republic. *Caribb J Sci* 36:258–266
- Castilla AM (1999) *Podarcis lilfordi* from the Balearic islands as a potential disperser of the rare Mediterranean plant *Whitania frutescens*. *Acta Oecol* 20:103–107
- Castilla AM (2000) Does passage time through the lizard *Podarcis lilfordi*'s guts affect germination performance in the plant *Whitania frutescens*? *Acta Oecol* 21:119–124
- Colette BB (1961) Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bull Mus Comp Zool* 125(5):137–162
- Cooper WE, Vitt LJ (2002) Distribution, extent, and evolution of plant consumption by lizards. *J Zool* 257:487–517
- Cullen DJ, Powell R (1994) A comparison of food habits of a montane and a lowland population of *Anolis distichus* (Lacertilia: Polychrotidae) from the Dominican Republic. *Bull Md Herpetol Soc* 30:62–66
- Dalrymple GH (1980) Comments on the density and diet of a giant anole *Anolis equestris*. *J Herpetol* 14:412–415
- Diaz-Uriarte R, Garland T Jr (1998) Effects of branch length errors on the performance of phylogenetically independent contrasts. *Syst Biol* 47:654–672
- Duellman WE (1978) The biology of an equatorial herpetofauna in Amazonian Ecuador. *Univ Kansas Mus Nat Hist Misc Publ* 65:1–352
- Dumont ER (1999) The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): an experimental study. *J Zool* 248:219–229
- Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1–15
- Felsenstein J (1988) Phylogenies and quantitative characters. *Annu Rev Ecol Syst* 19:445–472
- Fobes TM, Powell R, Parmelee JS Jr, Lathrop A, Smith DD (1992) Natural history of *Anolis cybotes* (Sauria: Polychrotidae) from an altered habitat in Barahona, Dominican Republic. *Caribb J Sci* 28:200–207
- Garland T Jr, Dickerman AW, Janis CM, Jones JA (1993) Phylogenetic analysis of covariance by computer simulation. *Syst Biol* 42:265–292
- Garland T Jr, Midford PE, Ives AR (1999) An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral states. *Am Zool* 39:374–388
- Glor RE, Vitt LJ, Larson A (2001) A molecular phylogenetic analysis of diversification in Amazonian *Anolis* lizards. *Mol Ecol* 10:2661–2668
- Greene HW (1982) Dietary and phenotypic diversity in lizards: why are some organisms specialized? In: Mossakowski D, Roth G (eds) *Environmental adaptation and evolution*. Fischer, Stuttgart, pp 107–128
- Harvey PH, Pagel MD (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford
- Herrel A, Spithoven L, Van Damme R, De Vree F (1999) Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Funct Ecol* 13:289–297
- Herrel A, De Grauw E, Lemos-Espinal JA (2001a) Head shape and bite performance in Xenosaurid lizards. *J Exp Zool* 290:101–107
- Herrel A, Van Damme R, Vanhooydonck B, De Vree F (2001b) The implications of bite performance for diet in two species of lacertid lizards. *Can J Zool* 79:662–670
- Herrel A, O'Reilly JC, Richmond AM (2002) Evolution of bite performance in turtles. *J Evol Biol* 15:1083–1094
- Hicks RA (1973) New studies on a montane lizard of Jamaica, *Anolis reconditus*. *Breviora Mus Comp Zool* 404:1–23
- Howard AK, Forester JD, Ruder JM, Parmelee JS Jr, Powell R (1999) Natural history of a terrestrial Hispaniolan anole: *Anolis barbouri*. *J Herpetol* 33:702–706
- Iverson JB (1985) Lizards as seed dispersers? *J Herpetol* 19:292–293
- Jackman TR, Larson A, De Queiroz K, Losos JB (1999) Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. *Syst Biol* 48:254–285
- Jackman TR, Irschick DJ, De Queiroz K, Losos JB, Larson A (2002) Molecular phylogenetic perspective on evolution of lizards of the *Anolis grahami* series. *J Exp Zool* 294:1–16
- King G (1996) *Reptiles and herbivory*. Chapman & Hall, London
- Lazell JD (1972) The anoles (Sauria, Iguanidae) of the lesser Antilles. *Bull Mus Comp Zool* 143:1–115
- Lee JC (1996) *The amphibians and reptiles of the Yucatan peninsula*. Comstock, Ithaca, N.Y.
- Lenart LA, Powell R, Parmelee JS Jr, Smith DD, Lathrop A (1994) The diet and a gastric parasite of *Anolis armouri*, a cybotoid anole from montane pine forests in southern Hispaniola. *Herpetol Nat Hist* 2:97–100
- Losos JB (1990) Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol Monogr* 60:369–388
- Losos JB (1994) Historical contingency and lizard community ecology. In: Vitt LJ, Pianka ER (eds) *Lizard ecology*, 2nd edn. Princeton University Press, Princeton, N.J., pp 319–334
- MacArthur RH, Diamond JM, Karr JR (1972) Density compensation in island faunas. *Ecology* 53:330–343
- Martins EP, Garland T Jr (1991) Phylogenetic analyses of correlated evolution of continuous characters: a simulation study. *Evolution* 45:534–557
- Nicholson KE (2002) Phylogenetic analysis and a test of the current infrageneric classification of *Norops* (Beta *Anolis*). *Herpetol Monogr* 16:93–120
- Nogales M, Delgado JD, Medina FM (1998) Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Aleganza, Canary Islands). *J Ecol* 86:866–871

- Olesen JM, Valido A (2003) Lizards as pollinators and seed dispersers: an island phenomenon. *Trends Rev Ecol Evol* 18 (4):177–181
- Perez-Rivera R (1985) Notas sobre el habitat, los habitos alimentarios y los depredadores de los lagartos *Anolis cuvieri* (Lacertilia: Iguanidae) de Puerto Rico. *Caribb J Sci* 85 (21):101–103
- Pough FH (1973) Lizard energetics and diet. *Ecology* 54:837–844
- Rivero JA (1978) Los anfibios y reptiles de Puerto Rico. Universidad de Puerto Rico, San Juan
- Roughgarden J (1995) *Anolis* lizards of the Caribbean: ecology, evolution and plate tectonics. Oxford University Press, Oxford
- Ruibal R (1964) An annotated checklist and key to the anoline lizards of Cuba. *Bull Mus Comp Zool* 130(8):475–520
- Schoener TW (1967) The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155:474–477
- Schoener TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49(4):704–726.
- Schoener TW, Gorman GC (1968) Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. *Ecology* 49 (5):819–830
- Schoener TW, Slade JB, Stinson CH (1982) Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus* of the Bahamas. *Oecologia* 53:160–169
- Schwartz A, Henderson RW (1991) *Amphibians and Reptiles of the West Indies*. University of Florida Press, Gainesville, Fla.
- Schwenk K (2000) Feeding in lepidosaurs. In: Schwenk K (ed) *Feeding: form, function and evolution in tetrapod vertebrates*. Academic, San Diego, Calif., pp 175–292
- Shanahan M, So S, Compton SG, Corlett R (2001) Fig-eating by vertebrate frugivores: a global review. *Biol Rev* 76:529–572
- Sifers SM, Yeska ML, Ramos YM, Powell R, Parmelee JS Jr (2001) *Anolis* lizards restricted to altered edge habitats in a Hispaniolan cloud forest. *Caribb J Sci* 37:55–62
- Simmonds FJ (1958) The effect of lizards on biological control of scale insects in Bermuda. *Bull Entomol Res* 49:601–612
- Smith JW, Powell R, Parmelee JS Jr, Smith DD, Lathrop A (1994) Natural history notes on a population of grass anoles, *Anolis olssoni* (Sauria: Polychrotidae), from the Dominican Republic. *Bull Md Herpetol Soc* 30:67–75
- Szarski H (1962) Some remarks on herbivorous lizards. *Evolution* 16:529
- Talbot JJ (1979) Time budget, niche overlap, inter- and intraspecific aggression in *Anolis humilis* and *A. limifrons*. *Copeia* 1979:472–481
- Traveset A (1990) *Ctenosaura similis* Gray (Iguanidae) as a seed disperser in a Central American deciduous forest. *Am Midl Nat* 123:402–404
- Valido A, Nogales M (1994) Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70:403–411
- Van Damme R (1999) Evolution of herbivory in lacertid lizards: effects of insularity and body size. *J Herpetol* 33:663–674
- Vitt LJ, Lacher TE (1981) Behavior, diet, and reproduction of the iguanid lizard *Polychrus acutirostris* in the caatinga of northeastern Brazil. *Herpetologica* 37(1):53–63
- Vitt LJ, Zani PA (1998a) Prey use among sympatric lizard species in lowland rain forest of Nicaragua. *J Trop Ecol* 14:537–559
- Vitt LJ, Zani PA (1998b) Ecological relationships among sympatric lizards in a transitional forest in the northern Amazon of Brazil. *J Trop Ecol* 14:63–86
- Vitt LJ, Sartorius SS, Avila-Pires TC, Esposito MC (2001) Life on the leaf litter: the ecology of *Anolis nitens tandai* in the Brazilian Amazon. *Copeia* 2001:401–412
- Vitt LJ, Avila-Pires TC, Zani PA, Esposito MC (2002) Life in the shade: the ecology of *Anolis trachyderma* (Squamata: Polychrotidae) in Amazonian Ecuador and Brazil, with comparisons to ecologically similar anoles. *Copeia* 2002:275–286
- Whiting MJ, Greef JM (1997) Facultative frugivory in the cape flat lizard *Platysaurus capensis* (Sauria: Cordylidae). *Copeia* 1997:811–818
- Zug GR, Vitt LJ, Caldwell JP (2001) *Herpetology: an introductory biology of amphibians and reptiles*. Academic, San Diego, Calif.