Body size, prey size and herbivory in the Galápagos lava lizard, Tropidurus

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Body size and diet were studied in Tropidurus in relation to food supply, to evaluate the hypothesis that body size is adapted to efficient exploitation of available foods. The results suggest that size is adapted to a particular degree of herbivory (i.e. a mixture of plant and animal food) rather than arthropod prey size. Body size and prey size were only weakly associated in T. pacificus, and comparison with other studies suggests this results from a large mean adult body size relative to the most common prey sizes. Balanced-diet effects on prey choice were not detected. The total quantity of animal food in the diet was not related to body size. Tropidurus size on different islands was unrelated to mean prey size available. However, degree of herbivory usually increased with increasing body size in T. pacificus. Mean body size of this population is approximately the size expected for an iguanid exhibiting its degree of herbivory. Tropidurus body size on different Galápagos islands is inversely related to arthropod abundance, and some data suggest that degree of herbivory varies in correspondence. The results support the hypothesis that body size is adapted to food, though the possible importance of other factors needs to be investigated.

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Определяли размеры тела и состав пищи у Tropidurus в зависимости от запаса пищи, для проверки гипотезы о том, что размер тела адаптирован для наиболее эффективного использования доступной пищи. Результаты показали, что размеры адаптированы к степени частичной фитофагии (т.е. смеси растительной и животной пищи), скорее, чем к размеру жертв из числа членистоногих. Размеры тела и размеры жертв лишь слабо связаны у T. pacificus, и сравнение с результатами других исследований позволяет предполагать, что это – следствие крупных средних размеров тела взрослых особей в сравнении с размерами большинства обычных жертв. Влияние сбалансированного рациона на выбор жертв не установлен. Общее количество животной пищи в рационе не связано с размером тела. Размеры Tropidurus на разных островах не связаны с средними размерами доступных жертв. Однако, степень растительноядности обычно возрастает с увеличением размеров тела у T. pacificus. Средние размеры тела у этой популяции примерно соответствуют ожидаемым размерам игуан, с соответствующей степенью фитофагии. Размеры тела Tropidurus на разных Галапагосских островах обычно пропорциональны обилию членистоногих, и некоторые данные показывают, что степень растительноядности варьирует соответственно. Результаты подтверждают гипотезу о соответствии размеров тела составу пищи, хотя возможные значения других факторов нуждаются в дальнейшем изучении.

1. Introduction

Theoretical models of foraging, and their success in laboratory situations, have revived interest in quantitative field studies of diets (e.g., Smith et al. 1978, Doble and Eggers 1978, Craig 1978, Schluter 1981, 1982a, Stamps et al. 1981, Sherry and McDade 1982). This is chiefly because the models hold promise that bewildering variation in diets in nature may be predicted by a small number of factors, particularly the profitability and abundance of foods (e.g., MacArthur and Pianka 1966, Schoener 1971). However, there is a second benefit to be derived from such models: since food profitability is a function of predator size and shape, it may be possible to predict predator morphology from considerations of feeding efficiency and food abundance (Schoener 1969, Belovsky 1978, Case 1979a,b, Schluter and Grant 1984).

I investigated the diet of the lava lizard *Tropidurus pacificus* on Isla Pinta Galápagos, to test the hypothesis that body size is adapted to food. *Tropidurus* was of interest for several reasons. First, the genus is widespread in the Galápagos and has differentiated morphologically among islands (Van Denburgh and Slevin 1913, Carpenter 1970). Hence body size on any particular island (e.g. Pinta) may be an evolutionary response to local food conditions. Second, individual *T. pacificus* feed on a wide variety of food types, especially plant parts and arthropods. Both the size of arthropod prey consumed by lizards, and the degree of herbivory exhibited, are expected to be related to body size (Schoener and Gorman 1968, Schoener 1969, Pough 1973, Case 1979a,b). Finally, there is at most one *Tropidurus* species on any Galápagos island, and it is the only small diurnal terrestrial lizard there. This permits an investigation into causes of *Tropidurus* size uncomplicated by the presence of closely related competitor species.

I begin this paper by describing the diet of adult *T. pacificus* in terms of the types of prey taken, the sizes of arthropods consumed, and the extent of herbivory. I then examine arthropod prey size and degree of herbivory as alternate explanations for body size, through tests of predictions with field data. If body size is adapted to efficient exploitation of arthropod prey sizes, then 1) a correlation is expected between body size and prey size among individual *T. pacificus;* and 2) differences among islands in *Tropidurus* size should be associated with island differences in available prey sizes. Alternatively if body size is adapted to a mixed diet of plant and animal foods, then 1) degree of herbivory among *T. pacificus* individuals should be related to body size; 2) mean body size of *T. pacificus* should be intermediate between strictly carnivorous and strictly herbivorous lizards (Pough 1973); and 3) differences among islands in *Tropidurus* body size should be associated with island differences in the supply of plant and/ or animal foods.

Finally, I discuss other possible explanations for body size in *Tropidurus*.

2. Methods

The Pinta study was conducted in two 1-ha sites on the south slope in 1979. The first site, located in the arid zone (Wiggins and Porter 1971) was relatively sparsely vegetated. *Bursera graveolens, Castela galapageia, Chamaesyce punctulata* and *Rynchosia minima* were the most common plant species. The substrate was largely bare rock, and soil and litter was uncommon and patchy. This contrasts with the second site located in the upper transition zone, a grassland-type habitat just below the humid forest (Wiggins and Porter 1971). Ground cover was dense, dominated by *Paspalum galapageia* and *Rynchosia minima*. Soil litter was abundant, and bare rock virtually absent. Tree cover, chiefly *Zanthoxylum fagara,* was sparse. These two sites are the same as sites 1 and 5 in Schluter (1982b) where they are described in more detail.

Diets were studied in both February and November. The first month corresponded to the early wet season, a season of heavy but infrequent rains, sunny skies, and warm temperatures (Wiggins and Porter 1971, Grant and Boag 1980). In November, the late dry season, temperatures were cooler and skies were generally cloudy until 1–2 PM daily. Arthropod abundance and activity, and flower and fruit production was greatest in the wet season.

Fifteen *T. pacificus* were collected over several days from each site in each month. Collections were made at approximately the same time of day, in mid-afternoon. About half of each sample were males, and half were females. Each lizard was weighed to the nearest 0.1 g with a spring balance, and snout-vent length was measured to 1 mm with a ruler. Measurements are summarized in Tab. 1.

Guts were removed and stored in alcohol. Stomach contents were later identified and measured in the laboratory. Plant and animal portions were separated, dried and weighed. While total lengths of available prey were measured in the field (see later), it was not possible to determine the original length of arthropod prey in the gut. Instead, width of the head capsule was used as a measure of prey size in the diet. The hindgut was also dissected and head widths of all arthropods were measured, excluding ants. Ants were very common in the

Tab. 1. Mean snout-vent length (mm) and body mass (g) for 60 *Tropidurus pacificus* collected. Standard deviations are in parentheses.

Sex	SVL	Mass	N
Male	96.4 (6.1)	24.4 (5.5)	31
Female	80.3 (5.8)	15.1 (3.4)	29

diet, but the vast majority were uniform in size (0.3–0.6 mm head capsule width). Since their abundance tended to overwhelm statistical characteristics of diet, ants are considered separately.

Food supply was assessed in the two Pinta sites in both months. To better estimate food characteristics for the whole island, four other sites were also sampled, in different habitats (Schluter 1982b). Food was also sampled in different years in sites on four additional islands where *Tropidurus* is present (Schluter and Grant 1984): San Salvador (wet season 1978, dry season 1981; 3 sites), Marchena (wet and dry seasons 1979; 2 sites), Fernandina (dry season 1981; 4 sites), and Española (dry season 1981; 3 sites). The sampling procedure followed Abbott et al. (1977), and is described in Schluter (1982b). Briefly, 25 (50 in site 1, November) random 1 m² quadrats were located in each site and month. Percent cover of the vegetation was estimated by eye, and the number of fruits and flowers on the vegetation was counted. All litter and surface soil in two 25 × 25 cm subquadrats was collected in a plastic bag. Within 12 h of collection these samples were carefully inspected for arthropods, using an enamel tray to prevent escape. The length of each arthropod was determined with a ruler. Arthropods were stored in alcohol for later drying and weighing. I did not collect ants, because their numerical abundance and small size made collection impractical. Arthropods less than 2 mm in length were also excluded, because they were more difficult to detect than larger prey.

This sampling procedure provides a reasonable estimate of food supply for *T. pacificus*. Individual lizards take most arthropod prey from the ground, especially in the dry season. However, since some prey (e.g., lepidoptera) are taken also from the vegetation arthropod availability may be underestimated, particularly in the wet season. Silverfish and isopods were common in ground samples but were virtually absent from stomachs; these two arthropod types were therefore excluded from estimates of food supply.

3. Results and discussion

3.1. Feeding description

T. pacificus exploited an unusual diversity of foods and feeding positions (Tab. 2). Ants dominated the animal portion of the diet numerically in all situations, though many other arthropod groups were taken. Plant items were common, particularly flowers, and especially in the wet season (February). Berries were eaten frequently in site 1, where *Lantana peduncularis* is present; the enclosed seeds pass through the gut undigested. Parts of *Opuntia* cactus were exploited in site 1, the frequency of exploitation increasing in the dry season (November). *Opuntia* was absent in site 5. Leaves of

other plants were also taken. Overall, averaging across sites and months, about 63% of the diet by weight was plant material.

The diversity of food items in the diet results from a wide range of foraging positions and methods. Many prey are snatched from the ground when discovered from a stationary position in classic sit-and-wait behavior (Pianka 1966). However the lizards also actively search for prey. Subsurface neuroptera and beetle larvae are often obtained through "digging": the head and forelegs are used to shove aside litter and soil (see also Carpenter 1970). Lizards take *Lantana* flowers and fruits from the tips of slender branches, either by climbing the shrub or by leaping from the ground. Individuals also climb *Opuntia* trees, 5 m or more in height, to exploit its leaves and flowers.

Tab. 2. *Tropidurus* diet summary: The summed total number of items in 15 stomachs per site and month. In the case of *Opuntia* individual items could not usually be enumerated; *nx* refers to the number of lizards with that food type in the stomach.

Food Type	Site 1		Site 5	
	Feb	Nov	Feb	Nov
Arthropods				
Pseudoscorpions	1	1		
Spiders	1	3	14	7
Acarina	2	1	1	5
Isopods			1	1
Orthoptera	1	3	6	3
Termites			1	
Hemiptera		2	10	25
Homoptera	9	2	4	4
Neuroptera	6	1		1
Beetles (ad.)	7	4	12	9
Beetles (larv.)	29	5		
Lepidoptera (ad.)	7	1	9	3
Lepidoptera (larv.)	23	3	31	23
Diptera	1		2	4
Ants	158	263	233	421
Hymenoptera (excl. ants)	7	12		1
Centipedes		2	1	1
Other Animal				
Tropidurus skin		2	2	4
Tropidurus tail			1	
Flowers				
Rynchosia minima	122		130	
Lantana peduncularis	152			
Other	9		1	30
Berries				
Lantana peduncularis	29			
Other	6		2	1
Leaves				
Various	15	2	7	38
Opuntia				
Flower	2x	1x		
Leaf	2x	10x		
Fruit		1x		
Ex.-fl. nectaries	1x	4x		
Seeds without Fruits				
Various	7		3	2

3.2. Prey size hypothesis

3.2.1. Prey size in T. pacificus

Body size in lizards is frequently considered to be an adaptation to the frequency distribution of available prey sizes (Schoener 1969, Case 1979b). The argument assumes that body size strongly determines prey choice. In this section I examine the relationship between body size and prey size in *T. pacificus*. The effect of food abundance on this relationship is also evaluated.

There was no correlation between body size (snout-vent length) and the mean size of arthropod prey in the diet (ants excluded, stomach and hindgut combined) ($r=0.08$, $n=60$, $P>0.05$). Deletion of one conspicuous outlier improves the trend slightly ($r=0.26$, $P=0.05$). This relationship between body size and prey size is shown in male-female comparisons in Fig. 1, summarized in Tab. 3. Mean prey size in females was significantly less than the mean for males in 3 of 4 cases. The differences are small, however, and this is surprising considering the large differences between the sexes in body size (Tab. 1). The maximum observed difference in mean prey size was 0.24 mm, a value smaller than some differences between sites and months for a given sex (Tab. 3).

The relatively weak relationship between body size

and prey size in *T. pacificus* contrasts with the results of some other lizard studies showing a strong positive association between these two variables (Schoener and Gorman 1968, Sexton et al. 1972, Roughgarden 1974, Pianka and Parker 1975, Stamps et al. 1981). However, these other studies all show that the greatest effect of increased body size is to increase the upper limit of prey sizes chosen, while the lower limit increases more slowly; hence variance in prey size also increases with body size. In *T. pacificus* males tended to take fewer small prey than females (Fig. 1), but the maximum prey size in both their diets was essentially identical. Thus females usually consumed slightly smaller prey on average than did males, but variance in prey size may often have been greater in females (Tab. 3).

Observation suggests that both males and females will readily attack and consume prey much larger than any found in their guts (pers. obs., R. Reynolds pers. comm., Stebbins et al. 1967). But large prey were in general eaten only infrequently, and sampling indicates that they were very rare. A large absolute body size relative to the size of the most common prey thus accounts for the weak effect of variation in body size on prey sizes consumed by *T. pacificus*. This contradicts the hypothesis that body size is adapted to available prey sizes.
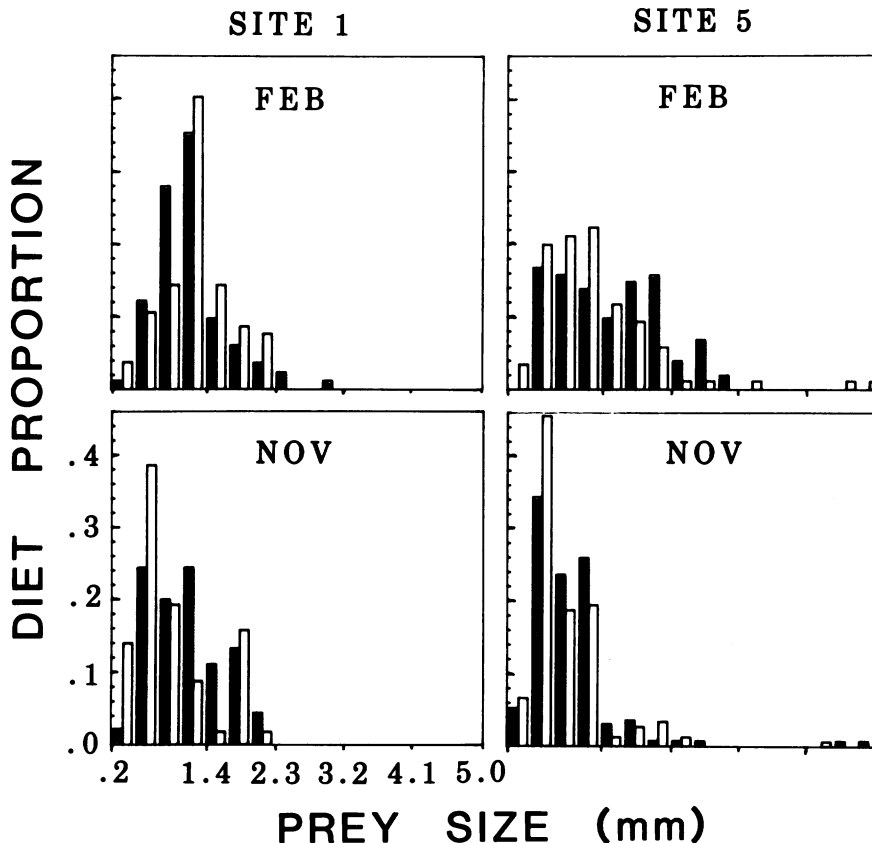

Fig. 1. Frequency distribution of prey sizes in diet of male (shaded) and female *T. pacificus*. Prey size refers to the width of arthropod head capsules in the stomach and hindgut combined. Ants are excluded from this comparison; the majority would be in the first size class (0.3–0.5 mm).

Tab. 3. Sample mean and variance for prey size in the diet (ants excluded). Data are from Fig. 1. P-values are for differences between males and females (t-tests and Levine's tests on log-transformed data); NS refers to P>0.10. Both parameters differ among sites and months when the sexes are pooled (Kruskall-Wallis, P<0.001; Levine's test, P<0.001).

Site	Month	Mean		P	Variance		P
		Males	Females		Males	Females	
1	Feb	1.19	1.22	NS	0.20	0.19	NS
1	Nov	1.12	0.92	<0.01	0.21	0.24	NS
5	Feb	1.51	1.27	<0.01	0.44	0.57	NS
5	Nov	0.99	0.90	<0.01	0.36	0.26	NS

The distribution of prey sizes in lizard guts varied with site and date, possibly indicating an effect of food abundance on prey choice. Tab. 4 documents absolute abundance of ground arthropod prey in each site and month. Abundance was highest in site 5, where it declined in the dry season. Observations on foraging success of birds removing lepidoptera larvae from the vegetation (unpubl. obs.) indicates that the abundance of this food was also lower in the dry season in both sites.

If absolute food availability affects diet, diet diversity will be highest when availability is low (MacArthur and Pianka 1966, Schoener 1971). However, in this study variance in prey size was greatest in site 5 (Tab. 3), where food abundance was highest. When food availability declined in November, variance in prey size also declined in site 5, though it may have increased slightly in site 1. Mean prey size in both sexes also varied erratically with total food abundance (Tabs. 3,4). Thus, variation between sites and months in the mean and variance in prey size might be mainly attributable to variation in relative food availability rather than absolute food availability. In support of this, declines in the mean and variance of prey size in the diet in site 5 between February and November (Tab. 3) are associated with significant declines in the mean and variance of available prey lengths (Wilcoxon and Levine tests, P<0.05). I cannot repeat this test for site 1 since the number of arthropods collected there was too low.

That relative prey abundance may have been more important than absolute prey abundance is not surpris-

ing, since in all sites and months the range of prey sizes chosen was extremely broad (Fig. 1). Most available prey types lay between these limits, and the diet of an opportunistic predator is expected to closely reflect relative prey availability (MacArthur and Pianka 1966).

3.2.2. Prey choice: opportunism or balanced diets?

Stamps et al. (1981) suggested an alternate explanation for why absolute prey abundance may not greatly influence diet: lizards seek a balanced diet in terms of nutrients and hence choose prey somewhat independently of their absolute abundance. Conceivably this effect could also explain the weak relation between body size and prey size in *T. pacificus*. Models predicting body size generally assume that foraging is opportunistic, and that diet, feeding efficiency and food abundance are uncomplicated by major nutrient considerations (e.g., Schoener 1969). The possibility of strong balanced-diet effects on prey choice (and consequently body size) in *T. pacificus* is thus worth considering.

Stamps et al. (1981) concluded that juvenile *Anolis* chose a balanced diet, but the statistical tests they used were inappropriate. If balanced-diet considerations strongly influence prey choice then individuals in any given situation should choose a diet *more similar* to each other than chance alone would dictate. This was tested for *T. pacificus* first by examining the frequency distribution of different prey types in the stomachs of individual lizards using χ^2 contingency tables. In 8 of 8 comparisons (by sex, site and month) the diets of indi-

Tab. 4. Mean quantity of animal and plant food in the diet, and food abundance. Available animal is the biomass of arthropods in ground samples, excluding ants. Available plant is the density of berries and flowers, including only those species found in the diet. All means are significantly different across site-months (Kruskall-Wallis, P<0.001). Percent herbivory is the dry weight proportion of plant food in all stomachs combined.

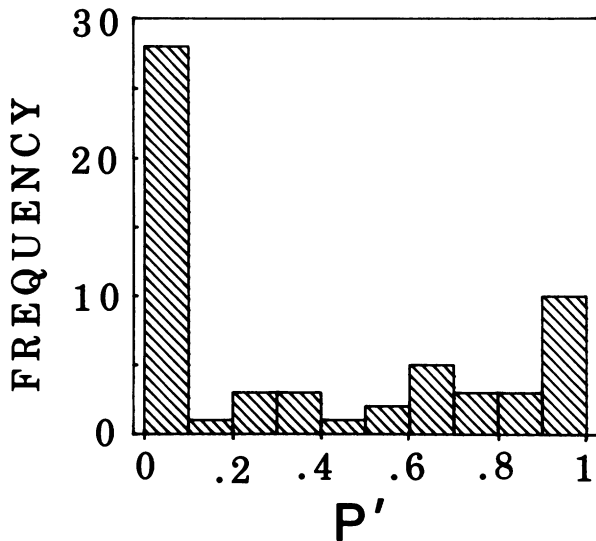| Site	Month	Animal		Plant		Percent Herbivory
		Diet (mg stomach^{-1})	Available (mg m^{-2})	Diet (mg stomach^{-1})	Available (No. m^{-2})	
1	Feb	14.7	1.9	48.9	17.0	77
1	Nov	6.2	2.5	22.4	1.4	78
5	Feb	39.4	53.6	38.6	13.0	49
5	Nov	15.7	21.4	13.3	3.4	46

Fig. 2. Frequency of P' values for 60 lizards. The nonuniform distribution indicates significant dissimilarity among individual lizards in the distribution of prey sizes consumed.

square (N-1) distribution. Under the null hypothesis P' will be uniformly distributed between 0 and 1, but under the balanced diet hypothesis values for P' should cluster about the midpoint, 0.5. Fig. 2 shows that P' is non-uniform, but is usually close to 0 or 1, not 0.5. Individuals thus differ significantly from one another in the distribution of prey sizes chosen, contra the balanced-diet expectation.

Both stomach and hindgut data were used in this analysis, so the differences among individuals are not the short-term consequence of only one or two feeding bouts. Differences are also not due to morphological differences among individuals: within classes, variance and mean in prey size in guts is not correlated with body size (all $P > 0.05$). The number of ants in the stomachs of individuals is also highly heterogeneous with respect to the number of other arthropods ($P < 0.001$). The most likely explanation for nonrandom differences is that individuals encounter different distributions of prey in the habitat, possibly as a consequence of territorial behavior (Werner 1978). This result further implicates variation in relative prey abundance as an important determinant of diet in *T. pacificus*.

In sum, the conclusion that *T. pacificus* is opportunistic in its choice of arthropod prey is supported by additional analysis. Note that this result is consistent with other studies that have shown lizard diets to be not greatly modified when prey abundance varies (Sexton et al. 1972, Stamps et al. 1981), in that in both these other studies absolute prey availability changed, but relative prey availability remained quite constant (e.g., Stamps et al. 1981:1084).

3.2.3. Body size and prey size across islands
If body size in *Tropidurus* is adapted to efficient exploitation of arthropod prey sizes, then body size on different islands should be positively correlated with available arthropod size. This is tested in Tab. 5. Lizard size on five Galápagos islands (data from Carpenter 1970) is not correlated with the mean size of arthropods present ($r = -0.17$, $P > 0.10$); indeed the trend is in the opposite direction to that expected. I repeated this comparison using a weighted mean prey length for islands (Tab. 5),

vidual lizards were actually more different from one another than expected, not more similar as predicted by a balanced-diet hypothesis.

P-values for the above tests were small (seven $P < 0.05$) but unreliable, since the expected number of prey per cell was often very small. A second test was therefore performed. Let VAR be the observed variance in prey size for the combined gut contents of lizards within a given sex-site-month class, and let s^2 be the observed variance for an individual lizard. If the N prey items in that individual's gut constitute a random sample from the pooled variance for its class, then $(N-1)s^2/VAR$ will be approximately chi-square distributed with N-1 df (e.g., Snedecor and Cochran 1967). I computed this ratio for all 60 lizards. Data were first log-transformed, since the test assumes a normal distribution for the pooled prey sizes. P' was then computed for each lizard, which is the probability of a value smaller than the observed $(N-1)s^2/VAR$ under a chi-

Tab. 5. Body size of *Tropidurus* on several Galápagos islands as a function of arthropod abundance. Body size is the modal SVL for males, given in Carpenter (1970: Fig. 1). Mean prey size (SE in parentheses) and arthropod abundance are averages from 2–6 sites sampled in the dry season; differences among means are significant (Kruskall-Wallis, $P < 0.001$). Weighted means are weighted by prey mass, assumed proportional to length^3.

Species	Island	SVL (mm)	mean prey size (mm)	Weighted mean prey size (mm)	arthropod abundance (mg m^{-2})
T. delanonis	Española	125	3.8 (0.88)	8.6	0.9
T. albemarlensis	Fernandina	115	3.5 (0.33)	14.3	3.8
T. habelii	Marchena	105	12.3 (2.40)	21.5	7.7
T. albemarlensis	San Salvador	95	4.3 (0.20)	16.8	26.1
T. pacificus	Pinta	90	5.1 (0.52)	12.3	23.2

where the weighting for an individual arthropod was its dry mass (assumed proportional to length[3]). The result was similar (r = –0.40, P>0.10). Ants were not included in this comparison, but they are present on all islands and their size is small and approximately equal on each; including them would not alter the basic result. These data contradict the prey size hypothesis.

3.3. Herbivory hypothesis

3.3.1. Herbivory in T. pacificus

In addition to prey size, herbivory is a second dietary factor thought to influence body size in lizards (Pough 1973, Case 1979a). The argument assumes that body size strongly determines the relative amounts of plant and animal foods consumed. This section examines the relationship between body size and food quantity in *T. pacificus*.

The number of plant and animal items in stomachs was significantly heterogeneous among individuals in all four site-months (χ^2 contingency tests, P<0.05), but in no situation was the mass of plant material in the gut correlated with the mass of animal material (|r|=0.03–0.21, P>0.10). Partial correlations, holding the effects of body size (SVL) fixed, gave the same result. Lizards thus did not compensate for a lack of one food type by consuming more of the other food, nor did they balance the amounts of these two foods, on a short term basis. For this reason percent herbivory, which is the proportion of the diet comprised of plant food, is analysed by separately considering the absolute quantities of animal and plant food consumed.

The amount of animal food in the diet was uncorrelated with body size in any site or season (Tab. 6). Correspondingly, sexes did not differ significantly or consistently in the mean amount of animal food (t-tests, P>0.10). Trends were similar within the sexes. Tab. 4 also suggests that the mean total amount of animal food in the stomach was related to arthropod availability (see also earlier).

In contrast to animal food, the quantity of plant food in the diet was significantly positively correlated with body size in two situations (Tab. 6). A weak positive trend was present in a third case. Correspondingly, in

February in both sites there were significant differences between the sexes in the amount of plant food in the diet (P<0.05) males had almost twice the amount of females. Within each sex similar trends were detected, although none was significant. These trends may have resulted from limitations to stomach storage capacity. For example in three of the four situations scatter diagrams indicated a consistent upper limit to the amount of plant food in the gut, for a given body size. Additionally, the strength of the correlation between body size and the quantity of plant food in the gut varied in correspondence with the mean total amount of plant food in the stomach (Tabs. 4,6). Tab. 4 indicates that this latter variable was associated with the quantity of plant food available.

In summary, the amount of plant food in the diet was often positively related to body size, while the amount of animal food did not change with size. Degree of herbivory in *T. pacificus* was thus positively related to body size, and this is consistent with the herbivory hypothesis.

3.3.2. Comparison with other lizards

Pough (1973) showed that herbivory is related to body size in many lizard groups, and he argued that this results from the effects of size on the efficiencies of plant and animal food consumption. Thus a simple prediction of the herbivory hypothesis is that *T. pacificus* should be intermediate in size between carnivorous and herbivorous lizards. Fig. 3 estimates the relationship between body size and percent herbivory in the Iguanidae, using data from the literature. The curve shows that small iguanids are largely carnivorous, and large iguanids are largely herbivorous. Body size in *T. pacificus* corresponds to the size expected for a lizard exhibiting its degree of herbivory.

3.3.3. Body size and food supply across islands

A third test of the herbivory hypothesis considers the effects of alternative food supplies on *Tropidurus* body size. Fig. 3 shows that the transition from low to high herbivory occurs within a narrow region of lizard sizes. Since *T. pacificus* occurs within this region, as do other *Tropidurus* populations (Tab. 5), body size in the genus should be particularly responsive to variation in the relative benefits of herbivory and carnivory, as determined by food abundance.

Several lines of evidence indicate that diet, and hence body size, should be more sensitive to variation in the abundance of arthropods than to variation in plant food abundance. First, plant material is less digestible than animal food and may produce substantially slower growth, even in herbivorous lizards (Pough 1973). In *T. pacificus* plant food is also bulkier than animal food: a given dry weight of plant matter visibly filled a greater volume of the stomach than an equal weight of arthropods. Second, plants are often sufficiently abundant that satiation is possible (see earlier). There was no

Tab. 6. Correlations between body size (SVL) and the mass of plant and animal food in the stomach (log-transformed data). NS refers to P>0.10.

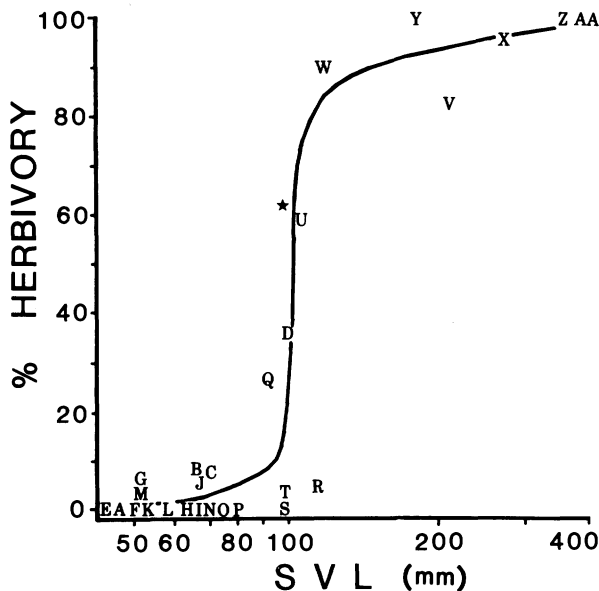| Site | Month | Animal | | Plant | |
		r	significance	r	significance
1	Feb	–0.08	NS	0.51	P=0.05
1	Nov	–0.09	NS	0.36	NS
5	Feb	0.24	NS	0.78	P<0.05
5	Nov	–0.23	NS	–0.11	NS

Fig. 3. Herbivory as a function of body size in the Iguanidae. % herbivory is the mean percentage of adult diet, by weight or by volume, comprised of plant material. The curve was fitted by eye. Diet data are from A) *Anolis limifrons,* B) *A. aeneus,* C) *A. roquet,* D) *A. richardi* (Schoener and Gorman 1968); E) *A. distichus,* F) *A. opalinus,* G) *A. sagrei,* H) *A. grahami,* I) *A. carolinensis,* J) *A. lineatopus* (Lister 1976a); K) *Urosaurus ornatus,* L) *Sceloporus merriami* (Dunham 1978); M) *Uta stansburiana* (Parker and Pianka 1975); N) *Phrynosoma douglassi,* O) *P. platyrhinos* (Pianka and Parker 1975); P) *Sceloporus occidentalis* (Johnson 1965); Q) *S. poinsetti* (Smith and Milstead 1971); R) *S. magister* (Parker and Pianka 1973); S) *Crotaphytus collaris* (Blair and Blair 1941); T) *C. wislizeni* (Parker and Pianka 1976); U) *Uma scoparia* (Minnich and Shoemaker 1972); V) *Basiliscus basiliscus* (Fleet and Fitch 1974); W) *Dipsosaurus dorsalis* (Minnich and Shoemaker 1970); X) *Cyclura carinata* (Iverson 1979); Y) *Sauromalus obesus* (Berry 1974); Z) *Conolophus subcristatus* (Carpenter 1969); AA) *Amblyrhynchus cristatus* (Carpenter 1966). Body size data are for males, occasionally from additional sources. SVL's for Lister's (1976a) anolines were estimated from head lengths (1976b) using allometric relations in Schoener and Gorman (1968). The star indicates *T. pacificus* from this study.

evidence that the amount of animal food in the diet of *T. pacificus* was ever limited by gut storage capacity, suggesting that arthropods were in relatively short supply in all situations. Finally, even herbivorous lizards will consume animal food when given the opportunity. This led Pough (1973) to suggest that large lizards consume plants primarily because they cannot satisfy metabolic demands on a carnivorous diet. Observations on *Tropidurus* (e.g., Werner 1978) suggest that individuals prefer arthropods when both this food and plants are available.

Relative benefits of herbivory to a *Tropidurus* population should therefore be strongly determined by the abundance of arthropods: only when arthropod abundance is low should plant consumption be high. The herbivory hypothesis thus predicts an inverse relation-

ship between body size in *Tropidurus* and the abundance of arthropods on Galápagos islands. Such a relationship is shown in Tab. 5. Values are from the dry season, but revisits to some of these islands indicate that wet season values are correlated. As predicted, body size tends to be greatest on islands where arthropod abundance is lowest (r=–0.93, P<0.05).

Dietary information provides additional corroboration for the herbivory hypothesis. There is indication that the largest *Tropidurus,* on Española, is almost entirely herbivorous in the dry season. Twenty fecal remains collected in two sites were filled with *Prosopis juliflora* leaves, and arthropod remains were virtually absent. No quantitative diet data are available for the other *Tropidurus* populations (Tab. 5), but the small *T. albemarlensis* on Santa Cruz (modal SVL=85, Carpenter 1970) is almost entirely insectivorous, at least in the wet season (Stebbins et al. 1967, R. Reynolds, pers. comm.).

4. General discussion

Models for optimal body size in predators generally assume that size is adjusted to characteristics of food (e.g., Schoener 1969), yet this has rarely been tested. This study of *Tropidurus* body size in relation to diet and food supply supports a food hypothesis. In particular the data provide evidence that body size on islands is adapted to a diet of plant and animal foods, the herbivory ratio depending primarily upon the availability of arthropods. Body size does not appear to be adapted to available arthropod prey size.

Several observations suggest that degree of herbivory is more important than prey size. Body size and prey size were only weakly related in *T. pacificus,* an apparent consequence of a large size relative to the most common prey sizes. Balanced-diet effects did not appear to influence this relationship. Quantity of arthropod food in the stomach did not increase with increasing *T. pacificus* size, despite increasing total metabolic requirements (Bennett and Dawson 1976). This suggests that feeding efficiency on arthropod prey may have been compromised by large size. *Tropidurus* body size on several Galápagos islands was unrelated to mean arthropod prey size there. However, degree of herbivory in individual *T. pacificus* was often a function of their size. Mean body size in this population is approximately the size predicted for an iguanid consuming both plant and animal foods. *Tropidurus* body size on different Galápagos islands varied inversely with arthropod abundance, and some data indicate that degree of herbivory varied in correspondence.

This does not mean that actual body size in *Tropidurus* is entirely an evolutionary response to food; other factors may certainly be operating. Territory defense, sexual selection and other reproductive factors may be influential. For example these factors may have contributed to sexual size dimorphism in *Tropidurus* (Tab. 1).

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However, it does not seem likely that these factors could by themselves have determined a particular size; rather their influence has most likely been to adjust size relative to an optimum determined by growth and survival-related factors such as food (Price 1984). In this way food may still be mainly responsible for inter-island variation in body size.

One assumption of these tests for the evolution of *Tropidurus* body size is that size has a substantial genetic component. Habitat variation in adult size on Pinta is related to variation in local food supplies (R. J. Brooks unpubl.), and the same effect may occur across islands. However island differences in size are unlikely to be mainly environmental since they have been quite stable over time. Also, a nongenetic response to food would predict the largest lizards on islands where food is most abundant, yet the reverse is true (Tab. 5).

Predation may also be important, but *Tropidurus* body size is unrelated to the presence or absence of predators. Snakes are present on two of the five islands compared, San Salvador and Española; these islands include both the largest and one of the smallest lizard species (Tab. 5). Hawks are abundant on all five islands.

Finally, climatic variation among islands may be important. General climate patterns were similar across islands studied, though subtle variation in temperature and shade properties may be present and significant. It would be difficult to predict the effects of such factors on body size without more quantitative data. This matter requires further investigation.

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