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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

THE ONTOGENY OF DIET IN THE MEXICAN SPINY-TAILED IGUANA, *CTENOSAURA PECTINATA*: PHYSIOLOGICAL MECHANISMS AND ECOLOGICAL CONSEQUENCES

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

By

RICHARD D. DURTSCHE

Norman, Oklahoma

1999

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THE ONTOGENY OF DIET IN THE MEXICAN SPINY-TAILED IGUANA, *CTENOSAURA PECTINATA*: PHYSIOLOGICAL MECHANISMS AND ECOLOGICAL CONSEQUENCES

A Dissertation APPROVED for the
DEPARTMENT OF ZOOLOGY

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PREFACE

This dissertation has been prepared as three chapters. Each chapter has been or will be submitted to a refereed journal for publication. The first chapter has been submitted to *Oecologia*. The second chapter will be submitted to *Ecology*. The third chapter will be submitted to *Physiological and Biochemical Zoology*. The format of each chapter is appropriate for the respective journals.

ACKNOWLEDGMENTS

This dissertation represents, at least in part, the culmination of seven years of studies, grant writing, research abroad, and laboratory analyses at the University of Oklahoma. When I began the graduate program, I had ideas about testing the ecological, behavioral, and physiological components of ontogenetic diet shifts in herbivorous lizards. I searched for study populations in Nicaragua and Texas before finding a population of lizards in Mexico large enough to collect adequate data over several years. Had it not been for the assistance, guidance, and support of many people, I could not have completed this dissertation. The trials and tribulations of research and graduate school in general have been buffered by my dear family, friends, colleagues, and mentors.

I have the good fortune of coming from a loving family that has been supportive throughout my life and in all stages of my doctoral program. My parents and my brothers have always been there when I needed them and they have encouraged my studies and my research. My parents, Allen and Irene, are role models for me both as a parent and as a person. They taught me diligence and hard work among other things and I truly appreciate their endless love. I have always held my brothers Dave and Tim in high esteem. Their advice and dedication to life and their families has always been an inspiration for me. My aunt and uncle, Phyllis and Sheldon, and my uncle Dean have also been supportive throughout my life and I am grateful for their love and assistance through the time it has taken me to complete this degree.

My committee has had several changes through my tenure as a doctoral student and I thank all members that have helped me to reach these final stages. Gregg Mitman enlightened me to many of the historical components of ecology. Stan Fox is a great ecologist and herpetologist and was instrumental in informing me of research opportunities in Mexico. Howard Haines taught me a great deal of physiology and was an excellent role model for teaching physiology. Bill Matthews is also a great ecologist and gave me excellent instruction for teaching field ecology. Chuck Peterson has been a good friend since he joined my committee. He has had insightful ideas on structuring my research and its presentation, and I am grateful to him for letting me use his semi-micro oxygen bombs so that I could complete my diet analyses. I have had fruitful discussions on volatile fatty acid production and use by iguanas with my outside member, Mike McInerney. Hopefully these discussions will blossom into future collaborations. Vic Hutchison has always been there when I have had questions or ideas about some physiological angle. He was, in essence, my surrogate advisor when Laurie was in the field and I am indebted to him for putting up with me and for the many things he has taught me. I hold a great debt of gratitude for my advisor, Laurie Vitt, who was a friend long before I even started the doctoral program. He has taught me many aspects of lizard biology and writing for publication. His comments on the chapters within this dissertation have greatly improved their presentation and helped to crystallize many of my random and sometimes disjunct thought patterns. His research has been an inspiration to me throughout and he has been instrumental in making sure I had the skills to succeed as a scientist and researcher. Thanks Laurie.

As the lions' share of my research took place in Mexico, I could not have made it without the logistical and personal support of many people from the Centro de Investigaciones Biologicas at la Universidad Autonoma del Estado de Morelos. They were kind enough to let me use their camper and Zodiac™ boat and motor throughout my study. Rubén Castro-Franco and Guadalupe Bustos-Zagal opened their home to me on many occasions and helped me get my research program off the ground. Topiltzen Contreras-MacBeth, Humberto Mejia-Mojica, Alfredo Chavez-Martinez, Cesar Jimenez-Piedragil, and Elimelec Anzures-Vazquez were all great friends and not only helped me with many logistical nightmares but were integral contributors as field assistants. A special thanks to Elimelec who spent more time assisting me in the field than anyone. Alvaro Flores-Castorena, Gustavo Soria-Rocha, and Maria Salazar-Avelar helped in plant identification. Eduardo Aranda-Escobar and Laura Lina graciously cultivated insect larvae on a daily basis so I had enough food to keep 20 lizards happy for three weeks. Aurelio Ramirez-Bautista was a great help in the field and was kind enough to help me secure permits for my research.

Many people from OU, both undergraduate and graduate, helped me to make this dissertation a reality. I was able to take several people to my study site, either individually or as a group, as field assistants. These include: Alisha Holloway, Elisabeth Kroese, Lars Hillström, Pedro do Amaral, Shawn Sartorius, Bill and Deb Lutterschmidt, and Randy Nydam. I appreciate all the help I received from everyone. Paul Gier, Karla Feist, Bill Lutterschmidt, Deb Lutterschmidt, Mark Pyron, Pedro do Amaral, and Shawn Sartorius were all sounding boards for me to vent my frustrations, uncertainties, and ideas

and I am grateful for their patience and support. I also benefited from fruitful discussions about research and many other things with Mike Fuller and Chris Tracy. Many of these people also took time out to read and make constructive comments on my manuscripts. Thanks guys.

Partial funding for this research was provided by research grants from the University of Oklahoma Department of Zoology, Graduate Student Senate, and Graduate College; Sigma Xi Grants-in-Aid of Research; the Hach Company, and the American Museum of Natural History Theodore Roosevelt Fund. A special thanks to Dr. Thompson, Paula Montague, and Wendal Porter of the Zoology Department for logistical and equipment support through many aspects of this study. Coral McCallister did a wonderful illustrative cartoon of these lizards that I have included at the end of the abstract.

Finally, I come to my most staunch supporters, those whom have been through thick and thin with me and have not complained once. To my family, my wife Åsa, and my children Kristina and Erik, I owe everything. You made it all worth while and gave me love every minute of the way. Kristina and Erik were my reality check with the world outside of academia and Åsa gave me the inspiration to keep going when it did not always seem worth it. With love, I dedicate this thesis to you.

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ABSTRACT

A natural size-structured population of iguanid lizards (*Ctenosaura pectinata*) with two subadult cohorts (juvenile and immature) and both adult sexes was studied through two wet and two dry seasons in a tropical deciduous thorn forest in central Mexico. This study aimed to examine the physiological mechanisms and ecological consequences of foraging and diet in this lizard through ontogeny. *Ctenosaura pectinata* shift their diet ontogenetically, with insects constituting 86.5% (by volume) of the food eaten by the smallest (< 10 g) juveniles and plants dominating the diet of adults. Dietary niche breadths based on both volumetric and numeric data were widest in subadult age classes and much narrower in adults. Opportunistic feeding on temporally available insect foods resulted in a broad diet for subadults that help juvenile and immature lizards through high predation-risk growth periods by reducing searching costs, increasing nutritional and energetic gains due to associative effects, and increasing exposure to new food. Despite differences in diet, the capacity (both volume and length) of digestive tract organs did not differ among age classes based on size-free comparisons. All age classes had the basic digestive tract architecture of an herbivorous iguanid lizard.

By selecting different habitats, the different age classes appear to gain in individual fitness based on their body size and feeding strategy. Rock habitats (outcrops and cliffs) had few food resources but offered lizards the highest temperatures ($\bar{T}$ = 44.7° C) and were dominated by large adult lizards in elevated positions ($\bar{x}$ = 7.6 m). The predominance of basking in these habitats by adult *C. pectinata* supports effective

digestion of plants by maintaining body temperatures ($\bar{T}_b$ = 34.8° ± 0.57° C) within the thermal performance range (33° - 38° C) for maximum digestion over the longest period of the day. The large body size of adults facilitated the use of open rock habitats through reduced predation risks and territorial dominance over immature lizards. The predominantly herbivorous immatures lizards were restricted to lower elevations in rock habitats by dominant adults, but compensated by using a wide range of habitats. Juveniles were found only in lower elevation plant habitats ($\bar{x}$ juvenile elevation in shrubs = 1.3 m) where insect foods were abundant and juvenile coloration was cryptic in the vegetation. Small size and low thermal inertia allowed juveniles to maintain mean body temperatures similar to adults in habitats with little direct sunlight.

The use of different foods by different age classes suggests that the net nutritional gain from foods depends on the feeding strategy employed by the different sized lizards. Digestive efficiencies for six different natural foods were tested in field-based pure diet experiments to determine if the maximization of nutrient and energy extraction correspond to the ontogeny of the natural diet shift. Extraction of energy and nutrients in insect larvae were maximized by juvenile lizards. Calcium, phosphorus, and energy were readily assimilated from flowers and fruit by immature and adult lizards. Magnesium levels were highest in leaves and were extracted by immature and adult lizards, but xenobiotic effects of at least one plant leaf (*Croton suberosus*), eaten by adults, killed juvenile lizards. Although juvenile *C. pectinata* ate some flowers (*Senna wislizenii*) naturally, they were less efficient at digesting cell walls from these plant parts were older lizards. On average, most immature and adult ctenosaurs assimilated 50 – 70% of plant fiber from the different

plant foods. Ontogenetic differences in ctenosaur digestive physiology when fed natural diets suggest that these foods were not selected based on tradeoffs involving costs of consumption efficiency, but rather, each age class preferred a diet that maximized its physiological benefit.


CHOMP!

ONTOGENETIC PLASTICITY OF FOOD HABITS IN THE MEXICAN SPINY-TAILED IGUANA, CTENOSAURA PECTINATA

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Running header: Ontogeny of diet in Ctenosaura pectinata

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Abstract

Ontogenetic shifts from insect consumption by juveniles to plant consumption by adults are rare in the herbivorous lizard family Iguanidae. My investigations on diet and digestive tract anatomy of the iguanid lizard Ctenosaura pectinata show that this species has an ontogenetic diet shift. Insects were rare in adult diets but constituted 86.5% (by volume) of the food eaten by the smallest juveniles. All age classes ate some plant parts from a range of plant types, but flowers and leaves of legumes were a primarily food source. Non-adult lizards had the widest food niche breadths. Arthropods in the diet of juveniles and immatures covaried seasonally with the decline of arthropod abundance.

Several alternative hypotheses could explain this ontogenetic plasticity in diet including: i) juveniles are constrained to an arthropod diet because their gut structure is more insectivore-like than herbivore-like, ii) juveniles can eat plants (assuming they have the proper gut structure) but do not because insects provide a greater nutritional gain than do plants, or iii) insect consumption is accidental because they are associated with plants juveniles select.

I rejected the first and third hypotheses respectively, because i) size-adjusted gut morphology and capacity was similar between non-adults and herbivorous adults, and ii) no food plants sampled had an excessive density of arthropods. The second hypothesis was supported because: i) an herbivore gut capacity and structure existed in all size classes, and ii) herbivore capacity and structure can increase digestive efficiency of juveniles through the associative effects of mixed arthropod and plant diets, through

reduced foraging frequency (i.e. predator exposure), and increased digestion rates (reduced number of colic valves).

Insect foods can compensate for size-related nutritional needs (energy and protein) and digestive limitations in juveniles. Opportunistic feeding on temporally available insect foods resulted in a broad diet that might help juvenile and immature lizards through high predation-risk growth periods by reducing searching costs, increasing nutritional and energetic gains due to associative effects, and increasing new food exposure.

Key-words: Diet shift, food availability, gut structure, herbivory, reptiles

Introduction

Herbivory occurs in adults of relatively few ectothermic vertebrates including chelonian and squamate reptiles (Bjorndal 1997; King 1996; Troyer 1991), fish (Horn 1989), and a frog (Das 1996). Digestion of plant materials by reptiles is aided by colic microbial fermentation with the assimilation efficiencies of some species near those of ruminant mammals (Bjorndal 1997; Troyer 1991; Zimmerman and Tracy 1989). Body size, gut retention time, and fiber content all are important in determining the efficiency of plant digestion by herbivores. The higher the proportion of plant fiber in the diet, the longer the retention period required for effective microbial breakdown (Hungate 1966; Stevens and Hume 1995). This retention time relates proportionately to allometric increases in the capacity of the digestive tract in some animals (Horn 1989). Herbivorous lizards often have an enlarged colon (i.e., fermentation chamber), where valves that partition the colon can decrease passage rates. The number of valves correlates directly with body size, resulting in a slower passage rate in larger lizards possessing more valves (Iverson 1982). The size of the fermentation region must be sufficient to support digestive breakdown of plant fiber to maintain energy balance on an herbivorous diet (Parra 1978; Bjorndal and Bolten 1990).

Pough (1973) suggested that large body size and the energetic cost of pursuit facilitate herbivorous food habits in adult lizards inept at capturing small, fast-moving prey, and preclude all but small individuals (less than 50 grams) from an insectivorous diet. The energetic demands of lizards provide support for this hypothesis, because

metabolic rates (R) scale to body mass (M_b) as $R = M_b^{0.8}$ (Nagy 1982). Under the assumption that these energetic demands were related to the size of the lizard, Pough (1973) suggested that small lizards should feed on insects, that only relatively large lizards could meet their nutritional and energetic requirements with a high-fiber plant diet, and that small juveniles of these large herbivorous lizard species should shift from insect to plant diets as they grow to adult size.

Iguanidae (sensu lato: Frost and Ethridge 1989; Sites et al. 1996) are unique among lizards because all are entirely herbivorous as adults. Most studies of iguanid foraging reject Pough's (1973) hypothesis of size-specific diet shifts because herbivory is maintained throughout all age and size classes (Auffenberg 1982; Christian et al. 1984; Mautz and Nagy 1987; Troyer 1984a; Wikelski et al. 1993). Juvenile iguanids studied by these authors compensated for reduced digestive efficiencies for high fiber plants by eating plant parts with relatively low fiber, high energy, and high protein. High passage rates of these foods also allowed increased food consumption. However, one iguanid, Ctenosaura similis, has been reported to undergo an ontogenetic shift from juveniles consuming insects to adults eating plants (Montanucci 1968; Van Devender 1982).

The genus Ctenosaura (spiny-tailed iguanas) is widely distributed in semi-humid lowlands from central Mexico to Panama (Ethridge 1982). Despite the high visibility of these lizards, few studies have focused on their ecology, natural history, or foraging biology (Evans 1951; Henderson 1973; Van Devender 1982). Ctenosaura similis is the only iguanid reported to shift from insectivory to herbivory with age. Assuming such a shift is real, several alternative hypotheses may explain why this ontogenetic change takes

place including: 1) juveniles are constrained to eat insects, perhaps because of an ontogenetic change in gut morphology from insectivore-like to herbivore-like; therefore juveniles cannot eat plants, 2) juveniles can eat plants (provided they have the requisite gut morphology) but do not because insects are better, containing easily digestible energy, protein, and other nutrients in neat little packages, or 3) the observed shift is "accidental": i.e., juveniles actually are herbivorous, but accidentally ingest more insects than adults (because they select particular plants or plant parts different from adults or possibly juveniles are naive to different foods). To confirm that an ontogenetic diet shift exists and to determine if any of these hypotheses supports this shift, I studied the feeding ecology and digestive anatomy of a common congener to C. similis, the Mexican spiny-tailed iguana (C. pectinata). Ctenosaura pectinata ranges across central and western Mexico at elevations below 1500 m, from Sinaloa south to the Isthmus of Tehuantepec and is one of the largest and most abundant lizards within its range. I describe the diet and digestive tract anatomy of this species and document the relative abundance of arthropod and plant foods during the wet and dry seasons.

Methods

Study site

I studied C. pectinata in two dry and two wet seasons, from January 1995 to August 1997, in canyon areas associated with the Rio Garzas in the state of Morelos in Central Mexico (18° 36' N, 98° 43' W, elevation 1100 m). Many lizards from all age

classes could be observed and collected. Natural vegetation along the canyon walls, where the lizards were found, contained an array of food resources. This habitat was a tropical caudicifolia forest with drought-deciduous trees, which lost their leaves and often flowered in the dry season (December to May). The wet season began with summer rains in early to mid-June, resulting in emergence of herbaceous vegetation and the appearance of new leaves on the shrubs and trees. Several trees and shrubs in the family Fabaceae were major flower and fruit producers at the site in both the dry season (Haematoxylon campechianum and Coursetia glaudulifera) and the wet season (Senna wislizenii). Ctenosaura pectinata were active on canyon walls, rocky outcrops, and in natural vegetation of the areas surrounding these canyons.

Diet

I collected iguanas using baited live traps (Tomahawk Live Trap Co., WI, USA), by noosing, shooting with an air rifle, or by hand. I obtained stomach contents within three hours of collection by stomach flushing (juveniles, immatures, and small adults) following the technique outlined in Durtsche (1995). The bolus was often flushed indicating that stomach contents had been extracted in their entirety. Seven juveniles and three immature lizards were killed after flushing to verify the effectiveness of this technique. All but one had completely empty stomachs; the one exception had only two small leaflets adhering to the wall of the stomach. The enlarged musculature of the jaw and pharyngeal region in large adult C. pectinata prevented successful stomach flushing.

For these individuals, I collected stomach contents by dissection. Food items from stomach samples were separated, counted, identified to the lowest possible taxonomic category (usually family), weighed "fresh" to 0.001g with an electronic balance (PC 440, Mettler Instrument Corp., NJ, USA), and length and width measured using digital calipers. I separated plant foods by type and counted individual leaf, flower, and fruit parts within each taxonomic category. I then formed taxonomically similar leaves, flowers, and fruit into the shape of a prolate spheroid before measuring length and width. Volumes were then calculated using the formula for a prolate spheroid:

$$\text{Volume} = 4/3\ \pi\ (L/2)\ (W/2)^2$$

where L = food length, and W = food width. Volumes of individual plant parts were then calculated by dividing the number of parts in the spheroid. Volumes of insects were calculated on an individual basis using the same formula.

The diet analysis program BugRun 1.6 (Vitt and Zani 1996) was used to analyze all diet data. Results of these analyses include proportional utilizations (p_i) of each food taxon for numerical and volumetric data (see Pianka 1973, 1986), and the frequency of use for each food item (i.e., the number of lizards containing a given taxon). These analyses also produced mean values of prey number, length, width, volume, and total stomach volume for individual lizards. Individual means were then combined with lizard size and sex data to create a matrix for age-class and food-size comparisons.

Eighty-eight taxonomic food categories were identified. In the first analysis I used 18 major food taxa that comprised 86% and 92% of the diet by number and volume,

respectively. In the second analysis I used 5 structural food categories (flowers, fruits, leaves, insects, and other) as they may be perceived by lizards. I combined prey types into broad categories because: 1) many of the taxa were rare in the diet, only occurring in one or a few lizard stomachs, and 2) most prey types were found in low frequencies, typically less than 5 in any age group.

Niche breadths were calculated for both numeric and volumetric food data using the inverse of Simpson's (1949) index:

$$B = 1 \Big/ \sum_{i=1}^{n} p_i^2$$

where p_i is the proportional utilization of resource i, and n is the total number of food resources (see Pianka 1986). Niche breadth values from 1 (100% utilization of a single food category) to n (equal use of all categories). Diet similarity in the food eaten by different age classes or adult sexes was evaluated using a symmetric overlap equation (Pianka 1986):

$$\phi_{jk} = \frac{\sum_{i=1}^{n} p_{ij}\, p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}}$$

where *j* and *k* represent the different age or sex classes under consideration. Overlap values vary from 0 (total dissimilarity) to 1 (identical diets). These overlaps are not intended to make any predictions of the environmental food resource base.

I analyzed food data for differences between size-based age groups (juvenile, immature, and adult), and between sexes in adult lizards. Juveniles were < 100 mm SVL and < 30g, immatures were 100 - 200 mm SVL and 30 - 200 g, and adults were > 200 mm SVL and > 200 g (Fig. 1). Juveniles were distinguished from immatures by their color pattern and habitat use (Durtsche unpub. data). Lizards up to four months in age were considered to be juveniles. They represent a cohort of lizards one year younger than the immatures. Adults were sexually mature and had enlarged testes with sperm (males) or enlarged vitellogenic follicles (females) in the reproductive (dry) season. To compare the use of foods between groups, I used a principal components analysis (PCA) on numeric, mass, and volumetric data from the structural food groupings to locate patterns among series of data. Factor loadings (weights) for the variables (food groupings) were used in subsequent analyses. The scores from these analyses were used to construct bivariate plots of the relationships between the diets of individual lizards. Positive or negative factor loadings indicate which food types influenced the positioning of individual lizards along each axis. Using single factor analysis of variance on the PCA scores, I examined diet similarity among groups. Post-hoc multiple comparison procedures were used for all pair-wise comparisons to determine which groups differed. To determine the effect of lizard size on prey size, I used regression analyses on the log-transformed variables with SVL as the independent variable for all groups combined. Using residuals from these

common regressions to remove the effect of body size (see Miles 1994), I then compared prey size among lizard categories using a one-way ANOVA and a Tukey-Kramer HSD multiple comparison procedure for all pair-wise comparisons (Toothaker 1993).

Food availability

To determine the availability and relative abundance of arthropods as a potential food resource, I haphazardly sampled the study using diurnal bush beating and sticky traps (Southwood 1978) in natural vegetation during each three day sampling period. Four sampling periods of three days each were made in each season (wet and dry). Each daily sample consisted of insects collected on a transect of 50 sticky traps and from 10 haphazardly chosen plants (shrubs or trees) for bush beating. Arthropod sampling took place when C. pectinata were active. I collected data during both the wet and dry seasons to determine the degree of seasonal fluctuation in arthropod availability.

Relative cover, relative density, and relative frequency of plants were also collected on the plants at the study site. I used a line-intercept method to sample trees and shrubs for collection of plant parameters (Brower and Zar 1984) and used these parameters to calculate a relative importance index for the plant community. The importance value is the sum total of the relative density, relative frequency, and relative cover for all species measured on these line-intercept transects. Importance values range from 0 to 3.0 with a proportional maximum contribution of 1.0 for each of the three relative measure (density, frequency, cover). These data were collected in both the wet

and dry seasons to determine seasonal fluctuation in the importance of plants in the plant community (i.e., their contribution of relative cover, density, and frequency to the community).

Digestive organ capacities

Forty-eight of 241 iguanas used for morphological measurements were killed to measure the organs in the gastrointestinal tract. Length, width, and organ wall thickness of the esophagus, stomach, small intestine, colon, and rectum were measured. Volumes of the esophagus, small intestine, and rectum were calculated using the equation of a cylinder:

$$\text{Volume} = \pi (W/2)^2 \cdot L$$

where W = inner width and L = organ length. Inner width of the organ was calculated as the outer (measured) diameter minus two times the organ wall thickness. An average of three measures taken at the anterior, medial, and posterior portion of the small intestine was used to characterize the outer diameters of that organ. Volumes of both the stomach and colon were calculated using the equation for a prolate spheroid ($V = 4/3\ \pi\ (L/2)\ (W/2)^2$), because this shape better defined their volumes than did a cylinder. Because the colon is wider than it is thick, thickness and width measures were averaged for use as the outer width measure in volume calculations. Digestive tract measurements were made with a digital caliper (0.01 mm) and flexible measuring tape (1 mm). Stomach pH values were recorded from fresh specimens using wide range pH test paper. All specimens killed

for digestive tract and stomach contents measurements were preserved in 10% formalin, and deposited at the Centro de Investigaciones Biologicas at the Universidad Autonoma del Estado de Morelos.

Statistics

All data were analyzed with either Statview (Abacus 1996) or JMP (SAS 1995) statistical software for Macintosh. Log (base 10)-transformed data were used for analyses to normalize distributions and to increase additivity and homogeneity (Kirk 1982). All tests were considered two-tailed. Means are presented $\pm$ 1 standard error unless otherwise noted. F value subscripts represent degrees of freedom of the model and error. For smaller sample sizes or unequal variances, a Welch's ANOVA was substituted for a single factor ANOVA (SAS 1995). Results were considered significant at a level of $\alpha = 0.05$.

Results

Ctenosaura pectinata undergoes a more than 300-fold increase in body mass, and greater than a seven-fold increase in body length as it matures from hatchling to maximum adult size (Fig. 1). Log-log transformed body mass and body length (measured as snout-vent length [SVL]) were highly correlated ($R^2 = 0.994$, $P < 0.0001$) and both yielded

similar results when used as size parameters in regression analyses. Immatures and adults were found during both the wet and dry seasons, and juveniles were only present during the wet season.

Diet and foraging ecology

Eighty-eight different food categories (9061 items) were identified in the stomach contents of 95 C. pectinata (Table 1). Most food items were identifiable to at least the family level. Two lizards had no food items and were excluded from analyses. Plants dominated the diet constituting 95.3% of the food items and 97.9% of the food volume. Most plant species consumed were in the families Fabaceae, Asteraceae, Bombacaceae, Convolvulaceae, and Euphorbiaceae. Taxonomic composition of plant foods varied seasonally. Trees and shrubs in the family Fabaceae maintain flowering phenologies that provided C. pectinata with a constant supply of floral foods throughout the year.

During the dry season Haematoxylon campechianum and Coursetia glaudulifera flowered in alternating patterns with new blossoms appearing about every two weeks. These flowers remained on the trees for two to three weeks before seed pods began to develop. Few leaves were present in the dry season, leaving flowers and some fruits as the main food resources. The few herbaceous materials available in the dry season were consumed by adult and immature lizards. Croton suberosus (Euphorbiaceae), a shrub, produced leaves throughout the year. Small herbaceous plants (e.g., Gnaphalium sp. -

Asteraceae) that grew on or near rocky cliffs and dried grasses (Poaceae) also were consumed during the dry season.

Foliage was primarily consumed in the wet season when new leaves and herbaceous plants were abundant. Flowers also constituted much of the wet season diet. Both flowers and leaves from the most conspicuously flowering wet season shrub, Senna wislizenii, were eaten by these lizards. Clumped, pinnately compound leaf structure in these shrubs facilitated the consumption of large quantities in a single bite by adults, and the small size of each leaflet may explain its occurrence in the diet of juveniles. Leaves were often found intact but folded in a bolus, suggesting they may be manipulated by these lizards for increased consumption capacity. Other material was separated into what appeared to be fecal material and inorganic clay, pebble, and stone. Although insects constituted a minor fraction of the sum of foods consumed, they constituted a major portion of the juvenile diet.

The mean number of food items per stomach was 97.4 ± 14.3 (Table 2) and the average stomach content volume and mass was 15,000.7 ± 3834.0 mm^3 and 9.1 ± 1.6 g, respectively. Although most stomachs approached the estimated maximum stomach capacity when collected, several individuals from all age classes had partially filled stomachs (Fig. 2). Often the lizards collected earliest in the morning or those having just emerged from burrows had the least material in their stomachs. Results of a regression analysis between the mass of stomach contents and body mass indicated that stomach contents made up an average of 4% of the body mass in C. pectinata ($Y = 0.04X - 0.839$, $R^2 = 0.626$). This proportion that stomach contents contribute to body mass was

consistent throughout all age and sex classes based on an ANOVA of regression residuals ($F_{3,38} = 0.042$, $P = 0.989$). Differences in the number and size of food items consumed by different age classes reflects primarily the allometric differences associated with body size (Fig. 3). When residuals were compared (to adjust for the effects of body size), no significant differences were found among any of the age classes or between adult sexes for either the number of food items consumed ($F_{3, 42.72} = 2.7479$, $P = 0.0545$) or for the size of individual food items eaten ($F_{3,89} = 0.5995$, $P = 0.617$); therefore, lizards in each size class consumed foods of proportionately equal number and size.

Ontogenetic differences existed in the major types of foods eaten (Fig. 4). Juvenile C. pectinata consumed 41 different food taxa, of which insects constituted 62% by volume. Insect larvae were the main animal food consumed by both juvenile and immature C. pectinata. Juveniles also consumed leaf beetles (Chrysomelidae) and grasshoppers (Acrididae). Immatures had the widest diet niche breadth, eating a wide diversity of food items (Fig. 4). Scarabaeiform (beetle) larvae were common arthropod foods in the immature lizard diet. This food source is often subterranean and immatures could have taken them while in burrows. Adults were strictly herbivorous, consuming leaves and flowers. Flowers and leaves of the shrub S. wislizenii (Fabaceae) were eaten by all age and sex classes in the wet season except for males that rarely ate the leaves. In the dry season, females ate flowers from Coursetia glaudulifera whereas males and immatures ate flowers from Haematoxylon campechianum. Males ate more foliage than flowers. These foods were primarily from herbaceous asters and leaves of Ceiba parvifolia, Croton suberosus, and Ipomoea sp. Croton suberosus was eaten by all groups

except juveniles. Inorganic materials and feces were found most frequently in the diets of juveniles and immatures. The reduced set of food categories (Fig. 4) did not change the distribution of foods in the diet other than to slightly increase the proportional importance of S. wislizenii flowers as a food source.

The greatest difference in diet existed between juveniles and adult males (Table 3), as juveniles ate a preponderance of insects and the plant S. wislizenii. Immatures had greater diet overlap with adults. Leaf (e.g., S. wislizenii between immatures and adult females) and flower (e.g., H. campechianum between immatures and adult males) consumption from the same plant taxa contributed to these diet similarities.

The ontogenetic diet switch from insects to plants takes place between the size classes of juveniles and immatures (Fig. 5). Juveniles < 10 g or 75 mm SVL mostly ate insects, 86.52% by volume, but adult C. pectinata (> ~200 mm SVL) rarely ate them.

A principal components analysis on the food groupings from stomach content data verified diet differences between adults and non-adults (Fig. 6). PC1 (Table 4) accounted for 18.6% of the variance and described a gradient between the amount of insect matter and the amount of leaf matter in the diet. PC2 described a gradient between insect foods (loading negatively) and flowers (loading positively). The first two axes explained 35.9% of the total variance. Juveniles and immatures clustered from the center to the negative end of each axis, where insects are weighted factors. Adults ordinated along the positive portion of both axes, on PC1 weighted by leaves, and on PC2 weighted by flowers. Clustering of points near null values on both axes confirms the diverse diet of these lizards (Gauch 1982). Results of a single factor ANOVA test on the scores from

both PC1 and PC2 demonstrated significant differences among age classes (PC1 - $F_{3,90}$ = 6.55, P = 0.0005; PC2 - $F_{3,90}$ = 4.309, P = 0.0069), but not between seasons ($F_{1,92}$ = 0.646, P = 0.424). Multiple comparison procedures on PC1 scores indicated differences in diet between both adult sexes and juveniles, and between adult males and immatures (P < 0.0035). On PC2 scores, post-hoc tests only revealed differences between adult females and juveniles (P = 0.0016).

Relative food abundance

Based on 12 trap days in each season, arthropods were 2.3 times as abundant by number (t = -4.038, P = 0.0007) and 6 times as abundant by volume (t = -5.826, P < 0.0001) in the wet season as in the dry season (Fig. 7). Arthropod abundance in the diet of C. pectinata showed similar significant differences between seasons (t_{number} = -2.541, P = 0.0142, t_{volume} = -3.30, P = 0.0019). Ninety-five different arthropod taxa were collected in the wet season, versus only 53 in the dry season (Durtsche unpub. data). Mean volumes of individual arthropods were over 2.5 times greater in the wet season ($\bar{x}$ = 20.74 ± 1.34 mm^3, range 0.06 - 1248.33 mm^3) than in the dry season ($\bar{x}$ = 7.93 ± 0.65 mm^3, range 0.04 - 262.2 mm^3). Some arthropod taxa were abundant in the dry season (e.g., spiders, ants, and crickets), where others were more abundant in the wet season (e.g., beetles, larvae, and grasshoppers). Although flies were abundant during both seasons, C. pectinata did not eat them (Table 1).

Plant diversity and abundance also decreased between the wet and dry seasons (Durtsche unpub. data). The number of species measured in line-intercept transect sampling decreased by 44% (32 to 18 species) from wet to dry season. From a linear cover index, the sum total of plants in the wet season covered 146.9% of the total transect sampled, indicating overlap in cover by plants. In the dry season, only 62.2% of the total transect sampled was covered with plants, which represented a cover reduction of 58%. Table 5 lists the ranking of major shrub and tree food plants in both the wet and dry seasons based on their importance value in the plant community. Except for Coursetia glaudulifera, food plants were not as common in the environment as other plants. This suggests that these plants or specific parts of these plants were selectively eaten by C. pectinata. Ranking plants by their relative cover values moves Croton suberosus from ninth (importance value rank) to fourth in the dry season, verifying that this plant was one of the main foliage plants available during the dry season.

Digestive tract anatomy

The volumetric capacity of digestive organs did not differ significantly between age groups or sexes of adults when the effect of body size was removed (Fig. 8). Test results of single factor ANOVA's on residuals from $\log_{10}$ transformed organ volumes and body size (SVL) regressions showed no statistical differences among juveniles, immatures, adult females, or adult males for any organ ($F_{esophagus:\ 3,\ 38} = 1.789$, $P = 0.1648$; $F_{stomach:\ 3,\ 38} = 0.492$, $P = 0.690$; $F_{sm.\ intestine;\ 3,38} = 2.35$, $P = 0.0868$; $F_{colon:\ 3,\ 38} = 1.117$, $P = 0.3536$;

$F_{rectum: 3, 38} = 0.367$, $P = 0.777$). Size-adjusted organ lengths also did not vary significantly among age classes or between adult sex groups ($F_{esophagus: 3, 40} = 1.846$, $P = 0.1543$; $F_{stomach: 3, 40} = 1.191$, $P = 0.3254$; $F_{sm. intestine: 3, 40} = 2.186$, $P = 0.1047$; $F_{colon: 3, 40} = 1.593$, $P = 0.2061$; $F_{rectum: 3, 39} = 1.351$, $P = 0.2718$). Gastrointestinal organ lengths and volumes were thus combined for all lizards.

With the effects of body size removed, significant differences existed in both capacity (volume, $F_{4, 231} = 92.781$, $P < 0.0001$) and length ($F_{4, 234} = 325.126$, $P < 0.0001$) among different alimentary organs. Colons, the site of cellulose digestion, had the largest volumetric capacity. The small intestine is the longest organ in the digestive tract, yet its volume did not exceed that of the stomach. There were ontogenetic differences in the number of transverse valves in the proximal colon of these lizards. Juveniles had 2 - 4 septa, immatures 2-5 septa, and adults 5 - 6 septa. Nematodes were observed in massive quantities in the colon of all age classes except juveniles, in which they were absent. Most stomachs were slightly acidic, with adults having a significantly lower pH ($\bar{x} = 4.96 \pm 0.29$) than non-adult lizards ($\bar{x} = 5.96 \pm 7$, $F_{1,33} = 6.406$, $P = 0.0163$).

Discussion

Diet and changes with ontogeny

Leaves and flowers of many different plants made up most of the diet of C. pectinata. Like C. pectinata, most other iguanids have a generalist diet that includes different parts from a wide range of plant foods (e.g., Cyclura carinata, Auffenberg 1982;

Sauromalus varius and S. hispidus, Sylber 1988; Dipsosaurus dorsalis, Mautz and Nagy 1987; Conolophus pallidus, Christian et al. 1984; Iguana iguana, Rand et al. 1990). Some iguanids appear to be diet specialists or selective in the plant parts they consume (e.g., Amblyrhynchus cristatus, Wikelski et al. 1993; Iguana iguana, Troyer 1984b). Ctenosaura pectinata appears opportunistic in its feeding habits, consuming flowers and some fruits as they appear during the dry season and newly flushed leaves from a variety of species in the wet season. The ranking of food plants below plants of more "community-wide" importance suggests that these foods were actively selected by C. pectinata. Higher ranked plants were not eaten suggesting they potentially were not beneficial for consumption. Senna wislizenii was a food reserve for these lizards during the wet season because it produced a plethora of flowers throughout the summer and maintained abundant leaves, small enough for juveniles and clumped in large quantities for adults. Similarly, Haematoxylon campechianum and Coursetia glaudulifera provided flowers and fruits in the dry season. All three of these major food plants are legumes (Fabaceae). Legumes often contain higher nitrogen content than other plants because of nitrogen-fixing bacteria associated with root nodules (Bidwell 1979). Consumption of these legumes provides a nitrogen resource for C. pectinata that can be incorporated into protein production for growth and reproductive production. Another plant species, Croton suberosus (Euphorbiaceae), maintained leaves throughout the year and was consumed by all age classes except juveniles. This shrub may have acted as a vegetative food source for these lizards when other foliage was unavailable.

My data indicate that C. pectinata have an ontogenetic diet shift from mostly insects as juveniles to almost exclusively plants as adults. Only one other iguanid, Ctenosaura similis, is known to exhibit a similar ontogenetic diet shift (Montanucii 1968; Van Devender 1982). While other iguanids may change diets as they mature, switches are from one plant type or plant part to another (Mautz and Nagy 1987; Troyer 1984b; Wikelski et al. 1993). Juveniles of these iguanids typically consume plant parts (e.g., flowers, young leaves) that contain lower fiber and higher protein. Lower fiber plant foods allow increased extraction of cytoplasmic energy and nutrients and faster digestive turnover rates. Consumption of higher protein foods can result in rapid juvenile growth that can push relatively small lizards more quickly through high predation periods. Insects, depending on their availability, can provide a more effective source of nutrients and protein for small juveniles than can plant foods.

Why shift diets?

Explanations for why these juveniles feed on insects while other iguanid juveniles eat plants may be related to the size of C. pectinata juveniles, the required growth rate needed to reach adult size, and to the abundance of arthropods in the environment. I reject the hypothesis that increased insect proportions in juvenile diets resulted from the accidental consumption of arthropods with selected plants eaten for the following reasons: 1) insect sampling revealed no plants with superabundant insect populations, 2) if insects were highly abundant on plants eaten by juveniles or immatures, then adults

eating those plants should also have higher proportions of arthropods in their diet, and 3) juvenile's stomach contents containing 100% insects could not happen by accident. The plant with the greatest association to juvenile or immature diets was Senna wislizenii which would qualify it as a plant suspect for carrying high insect abundance. If this were the case, both adult male and female C. pectinata that also consume similar parts of this plant would be expected to have high proportions of arthropods in their diet. They did not.

Ontogenetic shifts in diet also were not a reflection of an ontogenetic change in the digestive tract morphology from an insectivore-like gut structure (i.e., reduced colon size, lack of colic septa) in juveniles or immatures to an herbivore-like gut structure in adults. Measures of size-adjusted digestive tract organ lengths and volumes did not indicate morphological differences among age groups in C. pectinata, so I reject this hypothesis. There was an increase in the number of colic septa with age, but no lizards were found lacking septa.

Possession of an herbivore-type gut throughout all age classes lends support to the hypothesis that juveniles can eat plants but consume arthropods instead when they are available. The additional capacity provided by an enlarged colon does not appear to affect the digestive performance of an herbivorous lizard fed a diet of arthropods. Ruppert (1980) showed the herbivorous lizard (Sauromalus obesus, Iguanidae) can survive on an insect diet with assimilation efficiencies (60%) equal to that of a carnivorous lizard (Crotaphytus collaris, Crotaphytidae). Conversely, the carnivorous lizard was not able to digest plants with an efficiency (32.4%) that would permit survival.

Despite having gut morphology and capacity that does not differ significantly from adults based on size-free comparisons, the digestive ability of juveniles to handle and ferment plant fiber may be limited by the actual size of their colon (i.e., site of fermentation). Juveniles may also lack established microbes or nematodes in their colons, which are required for fermentation (McBee and McBee 1982; Iverson 1982). Fecal material did appear primarily in the stomach contents of juvenile and immature C. pectinata, which suggests the potential for inoculation of the gut with fermentative bacteria similar to those of I. iguana (Troyer 1982). Along with a lack of microbes, the reduced number of transverse septa in the colons of juveniles may not slow food passage rates enough for adequate fermentation to take place. This ontogenetic difference in valve number between juvenile and adult C. pectinata may be a true reflection of changes in diet because as Iverson (1982) points out, colon structure (valve size, number, type) is constant within iguanid species that are herbivorous throughout their lifetime.

Growth demands of juvenile C. pectinata may require them to be insectivorous or omnivorous. Based on energetic demand calculations, a 10 g lizard should only require half the dry food mass (75.7 mg/day) when feeding on insects than that required if feeding on plants (151.43 mg/day, Nagy 1982). Iguana iguana juveniles (mean SVL = 105 mm and mass = 37 g) consumed plant foods twice as fast as adults (Troyer 1984a). This suggested that small herbivorous lizards can compensate for low fiber digestive ability by passing plant foods at a faster rate and extracting more cytoplasmic nutrients. A C. pectinata of similar size to a juvenile I. iguana would already be in the immature size class and have a predominantly herbivorous diet suggesting that body size limitations reflect

the capacity to digest foliage diets. Conversely, juvenile Dipsosaurus dorsalis (mean mass 3.8 g) primarily consume flowers (Mautz and Nagy 1987). Flowers, in this case, offered a low fiber high energy food that was also passed by juveniles at a rate almost double that of adult plant digestion. Juvenile D. dorsalis had assimilation efficiencies on a flower diet that were much higher (54%) than adults fed a natural and assumed highly fibrous vegetation diet (29%). When fed this adult diet, the juveniles did not have the capacities for efficient digestion of the plant fiber (assimilation efficiency = 19%). Despite a smaller body size in juveniles D. dorsalis, the nutritional demand for growth may not be as great as experienced by C. pectinata. Dipsosaurus only undergo a 12-fold increase to reach an adult size (Mautz and Nagy 1987), whereas C. pectinata can undergo up to a 300-fold increase.

Nitrogen as protein is also a major nutritional component required for growing animals (Stevens and Hume 1995) and may be another possible reason for arthropod consumption by juvenile C. pectinata. Growth, the gain in body mass through synthesis and deposition of protein, is energetically costly with bond synthesis of proteins accounting for the largest proportion of biochemical costs (Jorgensen 1988; Wieser 1994). Herbivores are especially susceptible to plant nitrogen levels and may suffer reduced growth rates when feeding on nutrient-impoverished plants or plant parts which may be spatially or temporally distributed (Mattson 1980). Herbivorous reptiles are frequently nitrogen limited and require higher nitrogen content foods for protein synthesis (Peterson 1996). Young leaves of certain plants yield a higher source of protein than older leaves and these young leaves make up a larger proportion of the hatchling diet than is found in

the adult diet of green iguanas (Troyer 1984a). Insects offer a source of easily digestible food that contains a much greater per gram proportion of protein content than plants and more energy (Donoghue 1995; Golley 1961). The relative volumetric abundance of insects in the wet season was up to six times greater than what was found in the dry season. As arthropods were abundant during the period when hatchling C. pectinata emerged, they provided a food source that could supply both energy and nitrogen for protein synthesis and growth. As opportunists, C. pectinata juveniles consumed insects when they were abundant. Despite their abundance, insects are small and their consumption may be energetically inefficient for adults (Pough 1973). Adult ctenosaurs are known to be opportunistic predators if superabundant food sources (e.g., bird eggs, chicks at seabird nesting sites) are encountered (Rodriguez-Juarez and Osorno-Cepeda 1998).

Diet selection of non-adult C. pectinata also may be affected by the associative effects among the different types of foods eaten. More energy or nutrients may be assimilated when eating a mixed diet than when using a single food type. In an omnivorous turtle ≈ 70% more energy and 20% more nitrogen could be extracted from plant food when eaten with some insect food than when eaten alone (Bjorndal 1991). The diet of juvenile and immature C. pectinata contained both plant and arthropod foods, suggesting that there may be a nutritional or energetic gain from this mixed diet. Dietary niche breadths also were larger for both juveniles and immatures than for adults. Varied diets as indicated by larger niche breadths may be important to non-adult lizards for several reasons: 1) lizards can conserve search costs by feeding on locally aggregated foods, 2) they can take advantage of optimal food sources as they become available, 3)

they can sample new food types, and 4) they can maintain a balanced diet of nutrients (energy and especially protein) necessary for growth (Westoby 1978).

Moreover, having a gut capacity proportionately similar to the herbivorous adult C. pectinata can reduce the required frequency of daily foraging activity by juveniles. Depending on the energetic demands of the lizard and the risk of predation, increased gut capacity would allow a single large feeding to replace several smaller feedings. Having an herbivore-like gut can also be beneficial to handle the digestion of small portions of plant materials as in the case of a mixed diet or when insects are not available.

Based on this study, C. pectinata is atypical within the family Iguanidae, with an ontogenetic diet shift with juveniles eating primarily insects and switching to plant consumption by the time they are adults. Retention of an herbivore gut structure throughout life may facilitate juvenile growth rates by allowing increased food consumption, decreased passage rates (i.e., increased assimilation efficiencies), and reduced predation risk through reducing the frequency of foraging bouts. This gut structure may also serve to facilitate the digestion of the plant material that is consumed enabling a wider variety of food selection. Furthermore, the mixed diet of insects and plants maintained by non-adults can contribute to growth through reduction of searching costs, increasing energy and nutrient assimilation, increasing the diversity of foods eaten, and maintaining a balance of required nutrients. As opportunist feeders, this species samples from a diverse set of potential foods and takes advantage of high quality foods (e.g., flowers, insects) when they are temporally available.

Acknowledgments

I thank E. Anzures-Vázquez, R. Castro-Franco, L. Hillström, A. Holloway, E. Kroese, and H. Mejia-Mojica for field assistance throughout portions of this study. I am greatly indebted to my colleagues in the Centro de Investigacion at the Universidad Autonoma del Estado de Morelos for their logistic support and friendship throughout my stay in Morelos. I thank W. Lutterschmidt, M. Pyron, and S. Sartorius for comments on earlier versions of this manuscript. A special thanks to my advisor L. Vitt and committee members V. Hutchison, W. Matthews, M. McInerney, and C. Peterson for support and constructive editorial suggestions. This research was conducted under the research permits granted to the Centro de Investigacion at the Universidad Autonoma del Estado de Morelos. Partial funding for this research was provided by research grants from the Univ. of Oklahoma Dept. of Zoology, Graduate Student Senate, and Graduate College; Sigma Xi Grants-in-Aid of Research; and the American Museum of Natural History Theodore Roosevelt Fund. This research was submitted in partial fulfillment of a Ph.D. in Zoology at the University of Oklahoma.

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Table 1. Diet summary of Ctenosaura pectinata from central Mexico. Percent by number (%NO.) and volume (%VOL.) indicate the individual value divided by the sum of all numbers and volumes multiplied by 100. The frequency value (FREQ.) represents the number of lizard containing a given food taxon. Plant foods are identified by plant part (f = flower, fr = fruit, l = leaf). The season in which each food type was found in stomach contents is identified with D = dry season, and W = wet season. Single individuals found with a food normally consumed in the opposite season are represented in parentheses.

Food Type	*NO.*	*%NO.*	*VOL. (mm^3)*	*%VOL*	*FREQ*	*SEASON*
Plant Foods						
Acanthaceae						
Justicia sp. (f)	4	0.04	575.95	0.04	1	D
Justicia sp. (l)	67	0.74	5180.24	0.37	4	D
Asteraceae (l)	412	4.55	271214.66	19.44	5	W
Artemisa sp. (l)	9	0.1	2804.11	0.2	1	W
Gnaphalium sp. (l)	352	3.88	18638.77	1.34	9	D, W
Sauvitalia procumbeus (l)	70	0.77	4896.73	0.35	7	W
Bombacaceae						
Ceiba aesculifolia (l)	143	1.58	88186.24	6.32	3	W
Ceiba parvifolia (l)	777	8.58	65531.38	4.7	6	D, W

Boraginaceae						
Lithospermum sp. (l)	137	1.51	17063.35	1.22	4	W
Commelinaceae (l)	1	0.01	221.56	0.02	1	W
Commelina sp. (l)	5	0.06	1567.84	0.11	1	W
Convolvulaceae						
Exogonium conzattii (f)	37	0.41	293.33	0.02	2	D
Ipomoea sp. (l)	249	2.75	93045.5	6.67	14	W, D(1)
Calycobolus nutans (l)	53	0.58	7068.43	0.51	1	W
Calycobolus sp. (l)	31	0.34	6861.17	0.49	1	W
Euphorbiaceae						
Croton suberosus (l)	506	5.58	78801.42	5.65	18	D, W
Ricinus comunis (l)	9	0.1	6576.72	0.47	1	W
Fabaceae						
Acacia pennatula (fr)	3	0.03	3004.34	0.22	1	D
Acacia pennatula (l)	7	0.08	4.76	0	2	W
Chamaecrrista nictitans (l)	68	0.75	881.95	0.06	7	W
Coursetia glaudulifera (f)	453	5	40222.4	2.88	8	D
Coursetia glaudulifera (fr)	24	0.26	1394.22	0.1	4	D
Coursetia glaudulifera (l)	273	3.01	21483.77	1.54	9	D, W
Haematoxylon campechianum (f)	1205	13.3	63293.77	4.54	9	D
Haematoxylon campechianum (l)	3	0.03	14.15	0	1	D

Indigofera suffruticosa (f)	2	0.02	69.86	0.01	1	W
Indigofera suffruticosa (l)	1	0.01	20.99	0	1	W
Nissolia fruticosa (f)	338	3.73	64479.6	4.62	4	W
Senna wislizenii (f)	1523	16.81	399598.91	28.64	21	W
Senna wislizenii (fr)	6	0.07	188.76	0.01	2	W
Senna wislizenii (l)	978	10.79	32649.74	2.34	9	W
Loganiaceae						
Buddleia sessiliflora (f)	45	0.5	2842.84	0.2	1	D
Buddleia sessiliflora (l)	5	0.06	3982.13	0.29	1	D
Loranthaceae						
Cladocolea sp. (fr)	142	1.57	122.64	0.01	2	D
Malphigiaceae						
Buuchosia canescens (l)	45	0.5	3544.1	0.25	3	D, W
Moraceae						
Ficus sp. (l)	31	0.34	5597.95	0.4	4	W
Poaceae (l)	33	0.36	754.37	0.05	9	D, W
Rubiaceae						
Crusea sp. (l)	21	0.23	878.59	0.06	3	D, W
Sapindaceae						
Serjania triquetra (l)	1	0.01	362.79	0.03	1	D
Scarpholareaceae (l)	57	0.63	2097.06	0.15	1	D

Solanaceae						
Solanum americanum (fr)	11	0.12	144.51	0.01	1	W
Verbanaceae						
Lantana camera (fr)	82	0.9	2034.63	0.15	3	W
Lantana camera (l)	72	0.79	18379.95	1.32	7	W
Lantana sp. (f)	9	0.1	1600.23	0.11	3	W
Lantana sp. (l)	46	0.51	2716.05	0.19	4	W, D(1)
other (f)	260	2.87	22020.11	1.58	6	W, D
other (l)	28	0.31	2802.8	0.2	3	W
Animal Foods						
Arthropods						
Blattaria						
Blattidae	1	0.01	1647.93	0.12	1	W
Coleoptera						
Carabidae	3	0.03	219.98	0.02	2	W
Chrysomelidae	24	0.26	1394.86	0.1	12	W
Coccinellidae	1	0.01	21.78	0	1	W
Curculionidae	9	0.1	205.89	0.01	7	W
Dermestidae	1	0.01	7.57	0	1	W
Scarabaeidae	2	0.02	14.05	0	2	W
Tenebrionidae	3	0.03	125.08	0.01	1	W

Dermatera	1	0.01	79.83	0.01	1	W
Hemiptera						
Coreidae	1	0.01	231.89	0.02	1	W
Cydnidae	1	0.01	46.78	0	1	W
Lygaeidae	2	0.02	15.73	0	1	W
Reduviidae	3	0.03	284.19	0.02	3	W
Scutelleridae	1	0.01	129.48	0.01	1	W
Hymenoptera						
Apidae						
Apis melifera	2	0.02	168.42	0.01	1	D
Anthrophoridae						
Ceratina sp.	1	0.01	974.14	0.07	1	W
Formicidae	2	0.02	34.28	0	2	D, W
Halictidae	1	0.01	27.87	0	1	W
Hesperiidae	1	0.01	468.78	0.03	1	W
Leptidoptera	1	0.01	27.14	0	1	W
Noctuidae	1	0.01	18.06	0	1	W
Nymphalidae	1	0.01	208.7	0.01	1	W
Satyridae	4	0.04	923.86	0.07	2	W
Neuroptera						
Myrmeleontidae	1	0.01	169.08	0.01	1	W

Odonata	1	0.01	362.61	0.03	1	W
Orthoptera						
Acrididae	13	0.14	3070.98	0.22	11	W
Gryllidae	1	0.01	116.36	0.01	1	W
Thysanoptera	69	0.77	8.45	0	3	D
Larvae						
Eruciform	110	1.21	3264.59	0.23	22	W
Scarabaeiform	114	1.26	4557.73	0.33	3	W
Vermiform	6	0.07	202.28	0.01	4	W
unidentified insect	1	0.01	8.42	0	1	W
Other Arthropods						
Araneae	17	0.18	504.89	0.03	9	W
Chilopoda	2	0.02	66.8	0	2	W
Other Invertebrates						
Gastopoda	1	0.01	281.47	0.02	1	W
inorganic	13	0.14	6093.95	0.44	13	W, D(1)
inorganic (feces)	6	0.07	1703.71	0.12	6	W, D(1)
skin shed	4	0.04	1636.5	0.12	4	W
SUMS	9061	100	1395067.07	100		
Niche breadths		12.55		7.12		

Table 2. Descriptive statistics for individual food items consumed by the different age classes and both adult sexes in C. pectinata.

Variable	*Count*	*Mean ± SE*	*Min. - Max.*
Food Length (mm)			
juvenile	28	7.50 ± 0.26	1.39 - 30.31
Immature	29	8.44 ± 0.10	1.19 - 49.3
adult female	17	13.71 ± 0.16	0.01 - 52.23
adult male	19	11.52 ± 0.10	1.32 - 49.05
all lizards	93	11.22 ± 0. 07	0.01 - 52.23
Food Width (mm)			
juvenile	28	2.41 ± 0.07	0.44 - 6.71
Immature	29	2.95 ± 0.03	0.40 - 15.00
adult female	17	3.81 ± 0.03	0.28 - 18.00
adult male	19	4.82 ± 0.04	0.22 - 11.00
all lizards	93	3.88 ± 0.02	0.22 - 18.00
Number of Food Items			
juvenile	28	11.32 ± 2.28	2 - 48
Immature	29	87.76 ± 16.50	2 - 335
adult female	17	172.00 ± 36.49	19 - 490

adult male	19	172.37 ± 46.31	2 - 651
all lizards	93	97.43 ± 14.23	2 - 651
Food Mass (g)			
juvenile	28	0.071 ± 0.009	0.002 - 0.73
Immature	26	0.194 ± 0.037	0.008 - 3.63
adult female	15	0.200 ± 0.049	0.025 - 2.20
adult male	17	0.234 ± 0.089	0.017 - 4.77
all lizards	86	0.154 ± 0.020	0.002 - 4.77
Food Volume (mm^3)			
juvenile	28	39.18 ± 3.74	0.31 - 494.99
Immature	29	79.09 ± 4.00	0.14 - 4442.60
adult female	17	165.82 ± 6.34	0.00 - 8860.76
adult male	19	212.68 ± 4.19	0.03 - 1001.45
all lizards	93	153.96 ± 2.85	0.00 - 8860.76

Table 3. Diet similarity between age and sex classes of C. pectinata based on symmetrical overlap values. Values in boldface above the diagonal are numerical overlaps and values below the diagonal are volumetric overlaps.

age/sex class	*juvenile*	*immature*	*adult female*	*adult male*
juvenile	-------	**0.320**	**0.351**	**0.099**
immature	0.610	-------	**0.426**	**0.574**
adult female	0.688	0.715	-------	**0.281**
adult male	0.295	0.440	0.390	-------

Table 4. Loadings greater than 0.30 from the first two axes in a principal components analysis of stomach content in an ontogenetic series of Ctenosaura pectinata. Numerical, volumetric, and gravimetric measures of ecological food groupings were analyzed within stomach contents. The last row is the percent of total variance explained by each of the principal components.

Variable	*PC1*	*PC2*
Number flower		0.820
Number insect	-0.389	-0.376
Number leaf	0.830	
Volume flower		0.831
Volume insect	-0.396	-0.406
Volume leaf	0.839	
Mass flower		0.911
Mass insect	-0.441	-0.416
Mass leaf	0.912	
% of total variance explained	18.6	17.3

Table 5. Rank of selected major food plants (shrubs and trees) in the plant community based on importance values from line-intercept transect sampling (Durtsche unpub. data). Ranks are given for both the wet and dry seasons.

Food Plant	*wet season*	*dry season*
Bombacaceae		
Ceiba aescalifolia	10	
Ceiba parvifolia	29	
Convolvulaceae		
Ipomoea sp.	11	14
Euphorbiaceae		
Croton suberosus	9	9
Fabaceae		
Coursetia glaudulifera	1	1
Haematoxylon campechianum	15	15
Senna wislizenii	8	11

Figure Legends

Fig. 1. Size distribution of each age class and both adult sexes based on snout-vent length in Ctenosaura pectinata. Arrows indicate means

Fig. 2. Log transformed data showing how full C. pectinata stomachs were at time of capture. Line on the outer edge of the data points represents the maximum volumetric stomach capacity.

Fig. 3. Regression analysis of log transformed data showing the relationships between body size of Ctenosaura pectinata (SVL) and **A)** the number of food items in the stomach contents (log number of food items = -2.06 + 1.64 * log SVL, $R^2 = 0.38$, $F_{1,91} = 54.6$, $P < 0.0001$), and **B)** the mean volume of each food item consumed (log food volume = 0.19 + 0.74 * log SVL, $R^2 = 0.11$, $F_{1,91} = 11.3$, $P = 0.0011$).

Fig. 4. Main foods from the diet of Ctenosaura pectinata based on their volumetric percentage in the stomach contents. The diet is divided by age class and adult sex and by food groupings (e.g., leaf, flower). n.b. represents niche breadth.

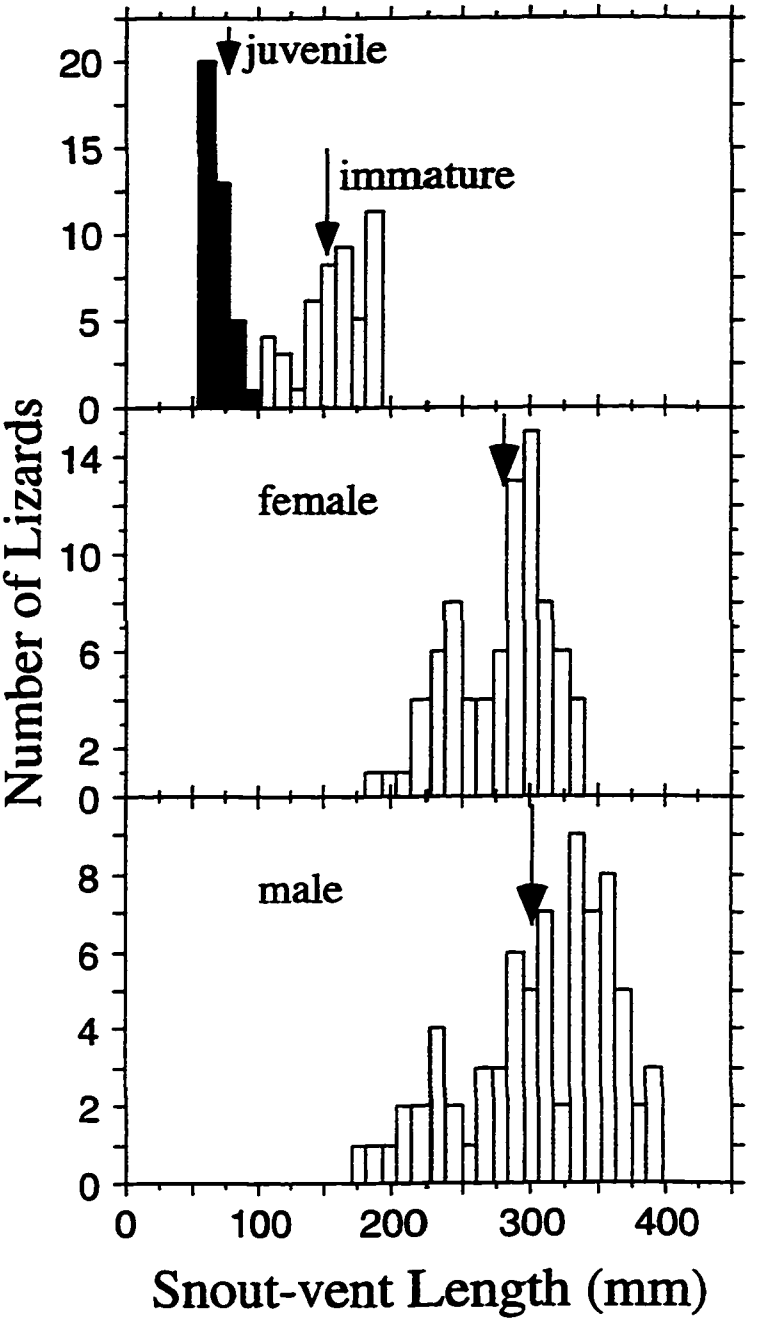
Fig. 5. Relationship between the percent of insects and the percent of plants in the diet of juvenile and immature Ctenosaura pectinata. Circles represent the % insect volume in the diet, and squares represent the % plant volume in the diet. Plants replaced insects in the diet as lizards increased in body size, with dietary insect proportions having a significant negative relationship to lizard body size ($Y = -0.006X + 0.999$, $R^2 = 0.517$, $F_{1,47} = 50.4$, $P < 0.0001$) and dietary plant

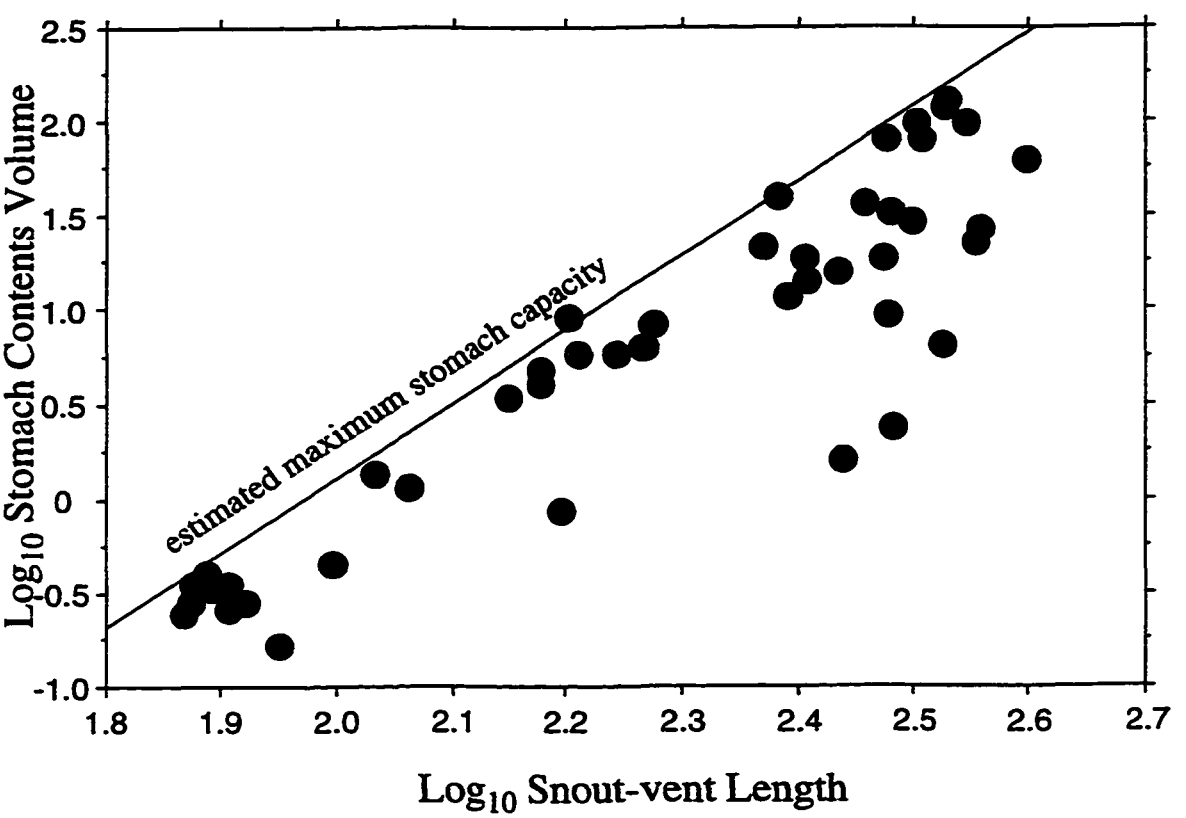
proportions having a significant positive relationship to lizard body size ($Y = 0.006X - 0.086$, $R^2 = 0.504$, $F_{1,47} = 47.8$, $P < 0.0001$).

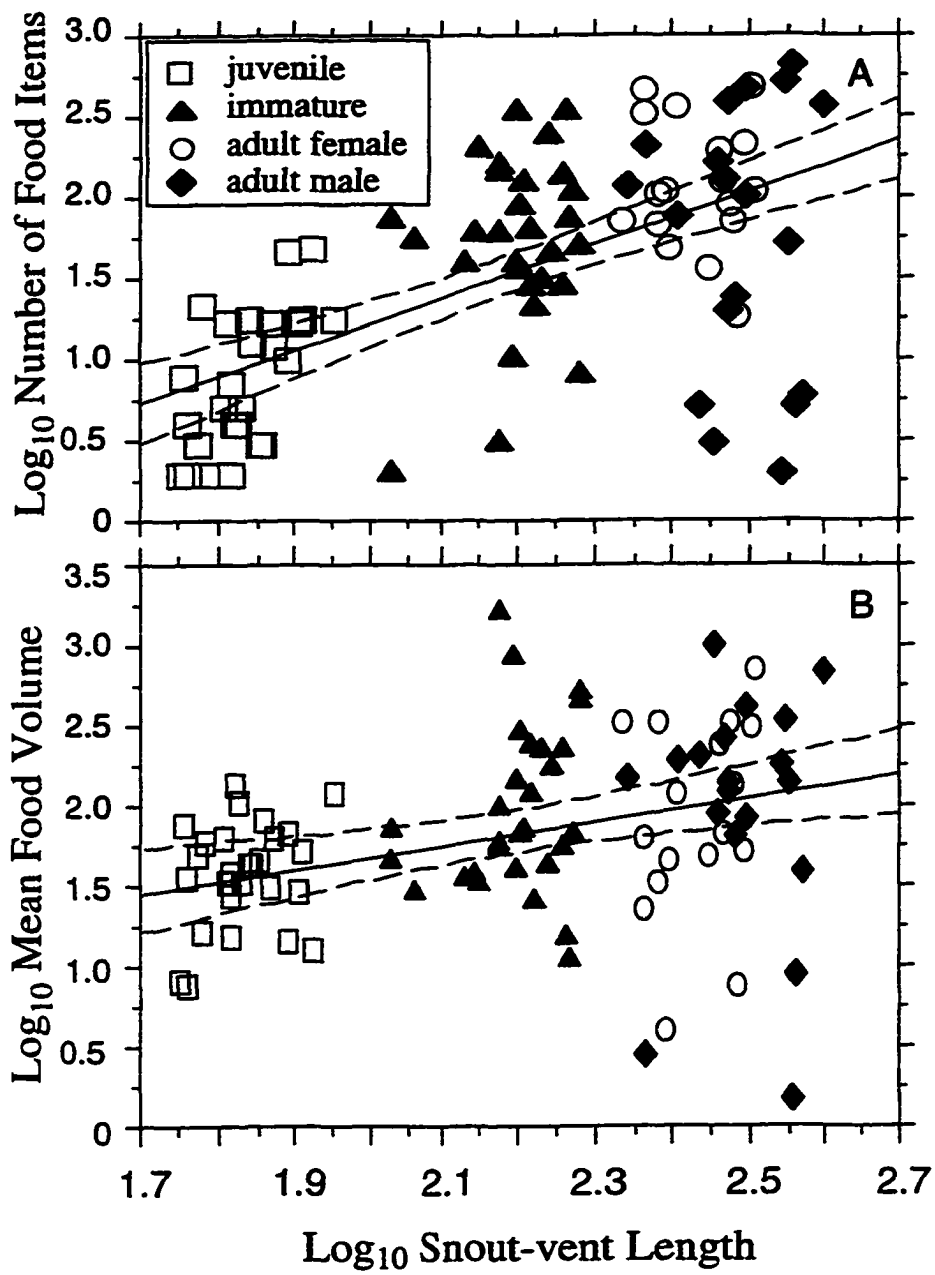
Fig. 6. Principal components analysis of food mass data in the diet of Ctenosaura pectinata. The position of juveniles, immatures, adult females, and adult males in dietary space is defined by the first two principal component axes.

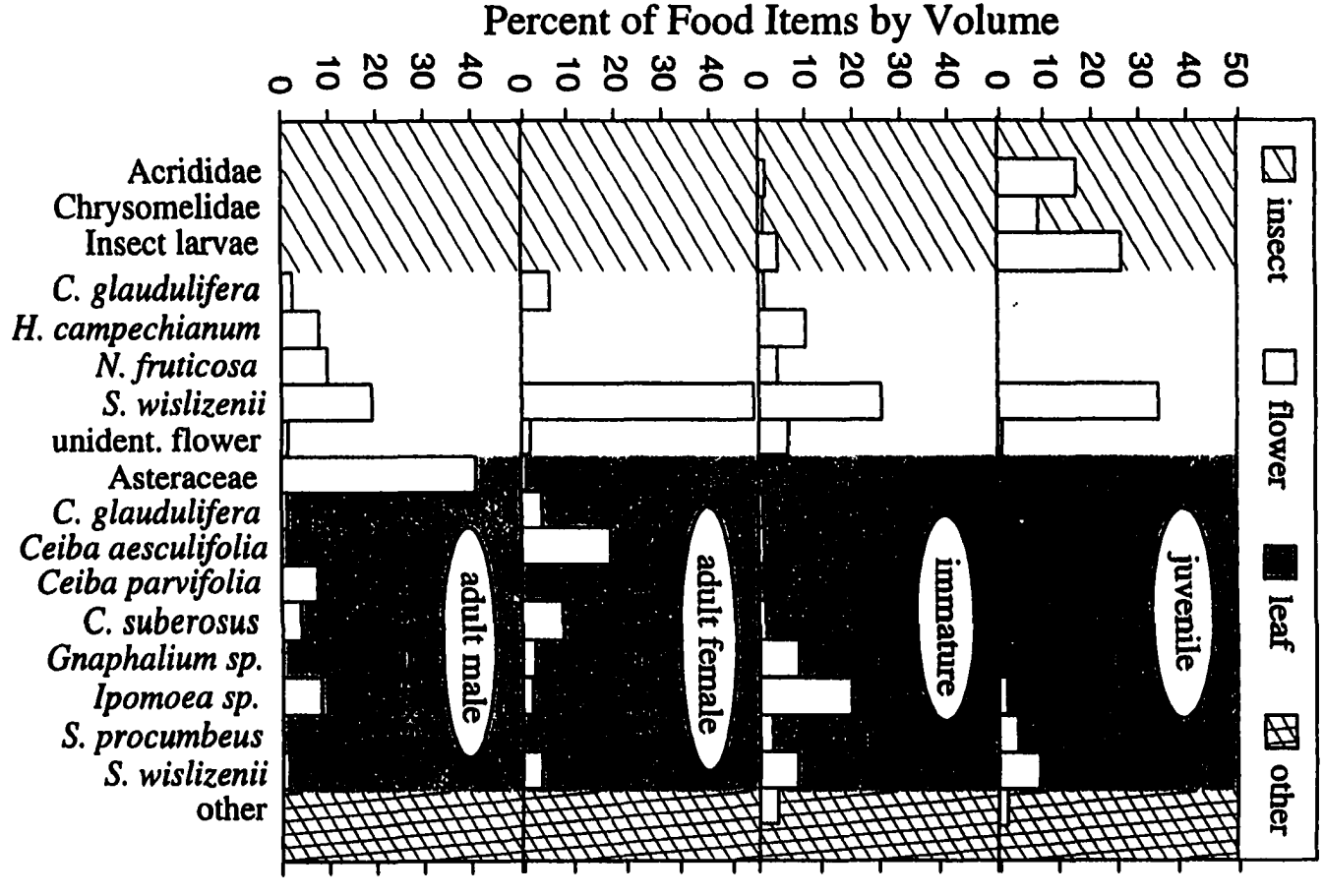
Fig. 7. Seasonal variation in the relative abundance of arthropods (numerically and volumetrically) in the environment. Seasonal arthropods differences are also represented by the percent of arthropods (numerically and volumetrically) found in the diet of Ctenosaura pectinata (= juveniles and immatures combined). Open bars represent dry season samples, striped bars represent wet season samples.

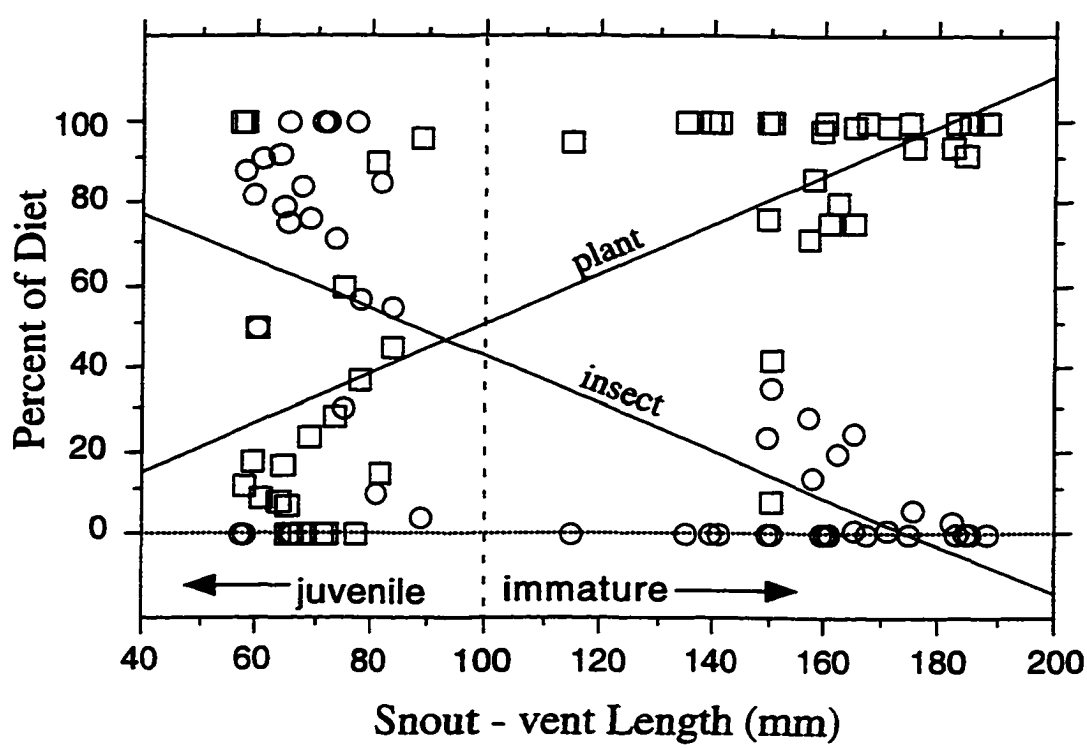
Fig. 8. Comparison of size-adjusted digestive organ volumes for size and sexes (adults only) of Ctenosaura pectinata.

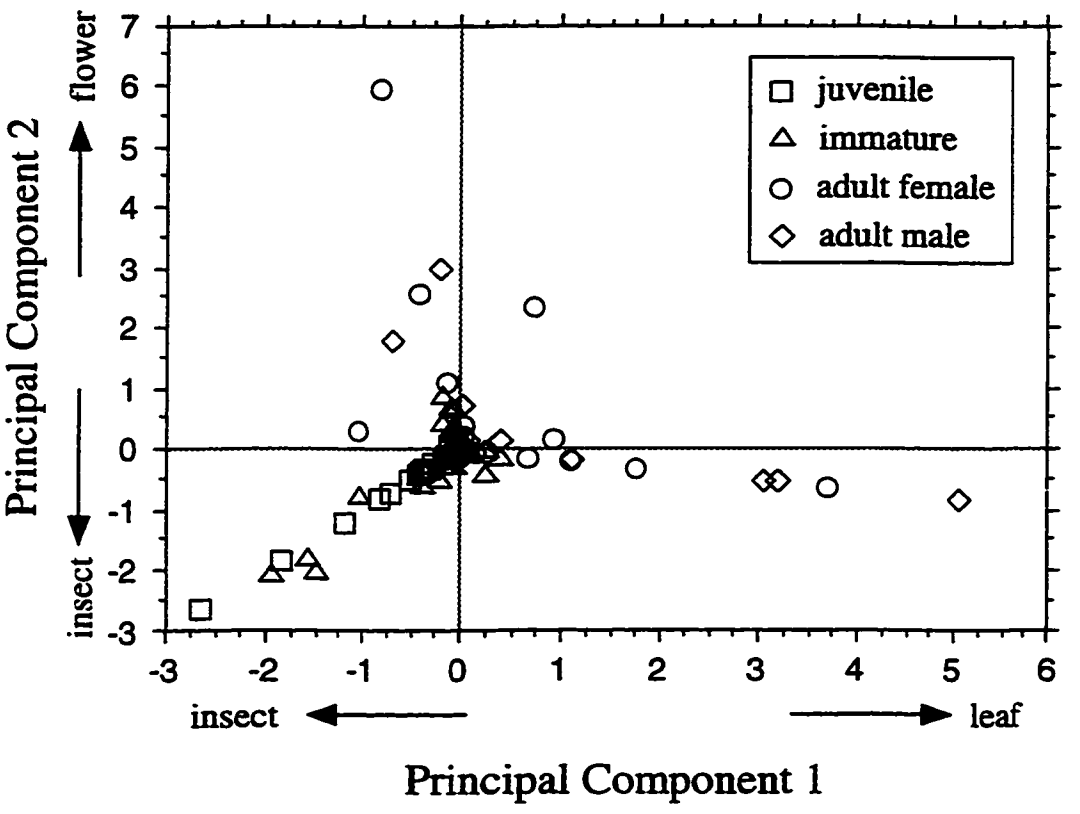

juvenile
immature
female
male
Number of Lizards
Snout-vent Length (mm)
0
5
10
15
20
2
6
14
4
8
100
200
300
400

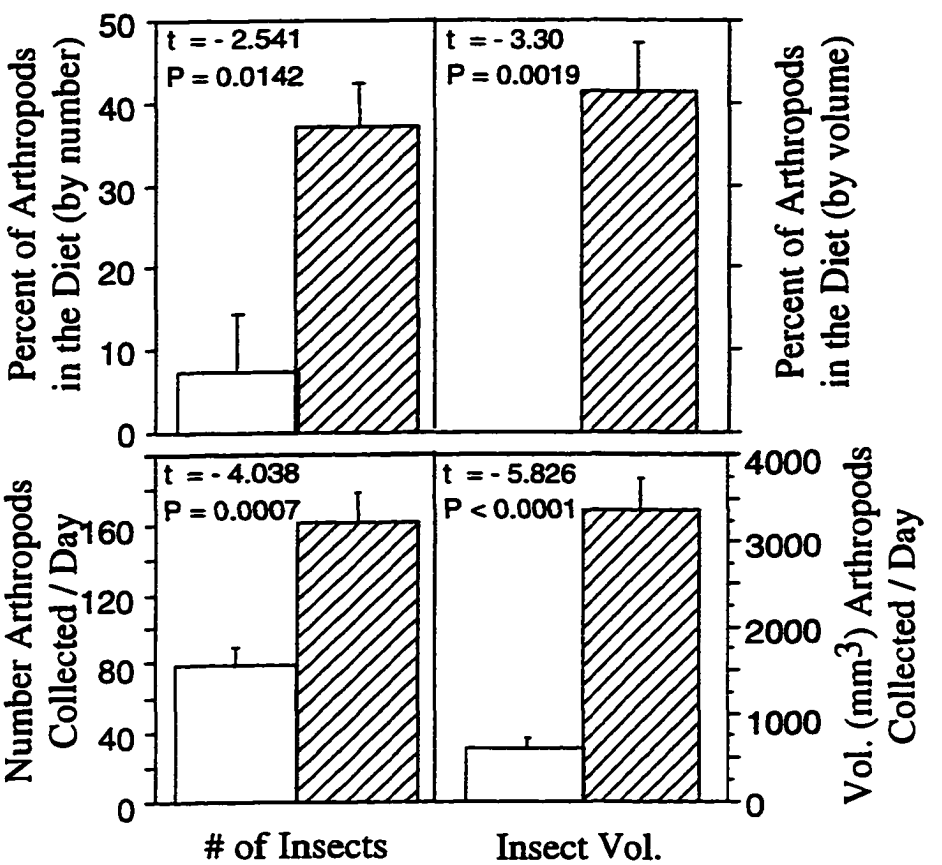

2.5
2.0
1.5
1.0
0.5
0
-0.5
-1.0
1.8
1.9
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7
Log10 Stomach Contents Volume
Log10 Snout-vent Length
estimated maximum stomach capacity

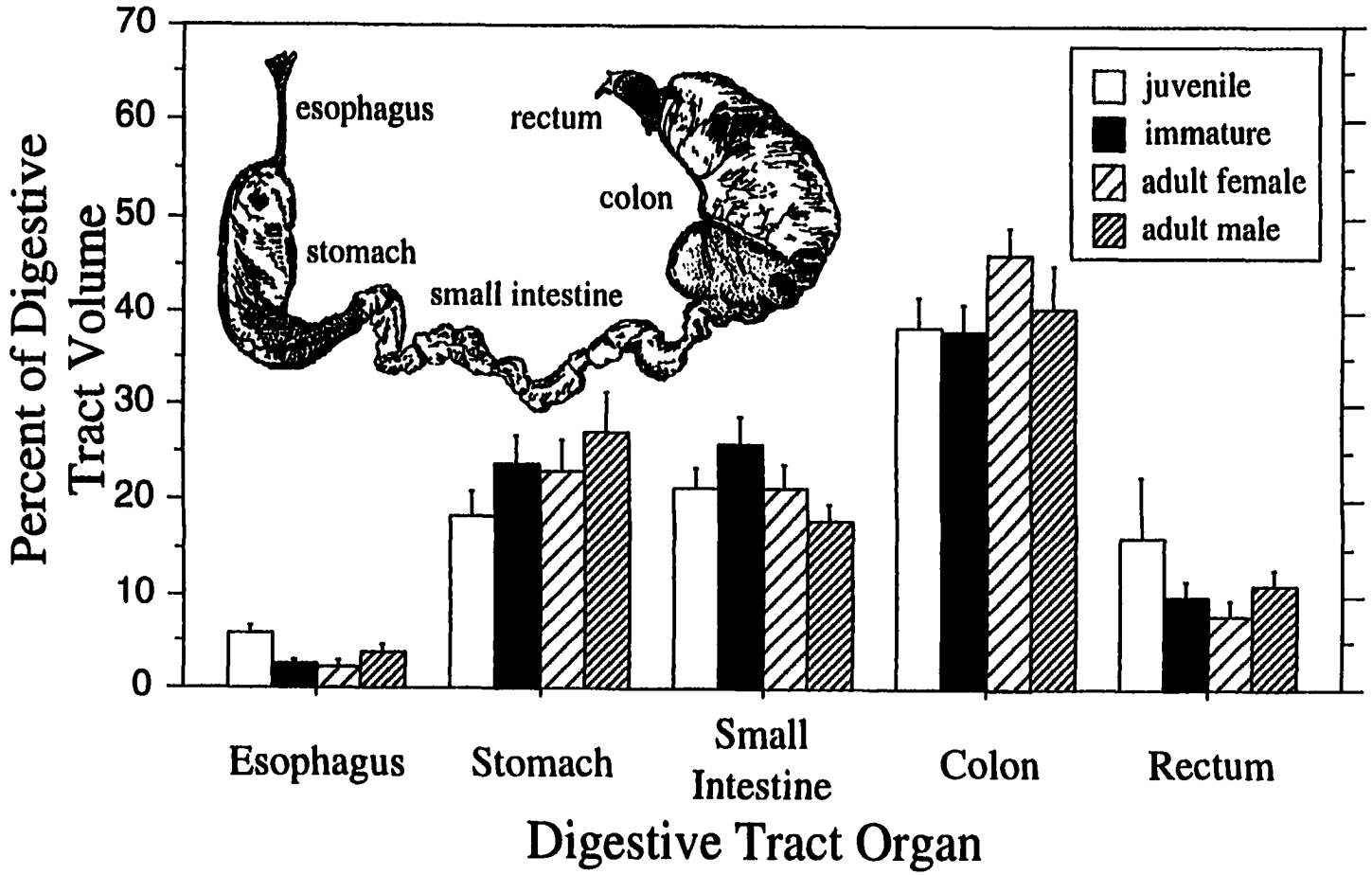

juvenile
immature
adult female
adult male
A
B
Log10 Number of Food Items
Log10 Mean Food Volume
Log10 Snout-vent Length
3.0
2.5
2.0
1.5
1.0
0.5
0
3.5
1.7
1.9
2.1
2.3
2.5
2.7


Percent of Food Items by Volume
0
10
20
30
40
50
Acrididae
Chrysomelidae
Insect larvae
C. glaudulifera
H. campechianum
N. fruticosa
S. wislizenii
unident. flower
Asteraceae
C. glaudulifera
Ceiba aesculifolia
Ceiba parvifolia
C. suberosus
Gnaphalium sp.
Ipomoea sp.
S. procumbeus
S. wislizenii
other
adult male
adult female
immature
juvenile
insect
flower
leaf
other


Percent of Diet
100
80
60
40
20
0
plant
insect
juvenile
immature
40
60
80
100
120
140
160
180
200
Snout - vent Length (mm)


Principal Component 2
flower
insect
7
6
5
4
3
2
1
0
-1
-2
-3
juvenile
immature
adult female
adult male
-3
-2
-1
0
1
2
3
4
5
6
insect
leaf
Principal Component 1


t = - 2.541
P = 0.0142
t = - 3.30
P = 0.0019
Percent of Arthropods in the Diet (by number)
Percent of Arthropods in the Diet (by volume)
50
40
30
20
10
0
t = - 4.038
P = 0.0007
t = - 5.826
P < 0.0001
Number Arthropods Collected / Day
Vol. (mm3) Arthropods Collected / Day
160
120
80
40
0
4000
3000
2000
1000
0
# of Insects
Insect Vol.


Percent of Digestive Tract Volume
70
60
50
40
30
20
10
0
esophagus
rectum
colon
stomach
small intestine
juvenile
immature
adult female
adult male
Esophagus
Stomach
Small Intestine
Colon
Rectum
Digestive Tract Organ

Habitat Selection in Ectotherms of Different Size: Ontogenetic Maintenance of Body Temperature and Variation in Feeding Strategies in an Iguanid Lizard

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Running header: Habitat selection in ectotherms of different size

Abstract

I studied patterns of habitat selection and thermal ecology in the iguanid lizard (Ctenosaura pectinata), a tropical lizard that shifts ontogenetically from insectivory to herbivory. Determinants of habitat selection varied based on body size and feeding strategy. The population was size-structured including two sub-adult cohorts and adults, and ranging in body size from 56 - 397 mm snout-vent length. Five different habitats were used by this population. Rock habitat (outcrops and cliffs) offered lizards the highest temperatures ($\bar{T}$ = 44.7° C) but the least cover against predation. Vegetation habitats (herbaceous plants, shrubs, trees) offered elevational variation and cover against predation. Burrow habitats provided lizards refuge against temperature extremes and predation. Adult lizards dominated the warmest habitat in elevated positions ($\bar{x}$ = 7.6 m) on cliffs and rocky outcrops where food was scarce, maintaining these basking sites through social status. Juveniles were found only in lower elevation plant habitats ($\bar{x}$ juvenile elevation in shrubs = 1.4 m) where insect foods were abundant and juvenile coloration matched the color of the vegetation. Small size and low thermal inertia allowed juveniles to maintain mean body temperatures similar to adults in habitats with little direct sunlight. Immature lizards used a wide range of habitats, but on cliff habitats they were restricted to lower elevations by dominant adults. The predominance of basking activity on cliff and rock outcrops by adult C. pectinata supports effective digestion of plants by keeping body temperatures ($\bar{T}_b$ = 34.8° ± 0.57° C) within the thermal performance range (33° - 38° C) for maximum digestion most of the day. Large adult body

size reduced predation risks and facilitated territorial dominance over immature lizards. Small body size and cryptic coloration allowed juveniles to use shrub and vegetation habitats for feeding and for protection from predators. Their low thermal inertia and shuttling in a thermal mosaic allowed them to elevate body temperatures to maintain growth rates in cooler microclimates.

Key words: habitat selection, model, ectothermic herbivore, lizard, temperature, Ctenosaura pectinata, reptile.

Introduction

The distribution of animals in the environment and selection of habitats by individuals can be affected by resource availability (Riechert and Tracy 1975, Orians and Wittenberger 1991), intra and interspecific interactions (Ebenman 1988, Werner and Hall 1988, Rosenzweig 1991), and biophysical factors (Dunham et al. 1989, Huey 1991). Ectotherms are particularly influenced by biophysical factors because they rely on environmental temperatures (T_e) to elevate their body temperatures (T_b) to an operating activity range (Huey 1982). Ectotherms seek areas with environmental temperatures that maximize physiological and behavioral performance (Huey and Stevenson 1979, Stevenson et al. 1985). Defining which temperatures are "optimal," however, becomes complicated because optimal T_b (i.e., maximizing physiological performance) of an ectotherm can vary depending on its activity (Huey 1982, Stevenson et al. 1985). The thermal optima of individual activities may vary, each requiring different thermal regimes and thus, different habitats. Activities influencing individual fitness that are presumably affected by habitat choice include: 1) physiological survival, 2) reproduction, 3) predator avoidance, 4) foraging, and 5) digestion.

In thermally stressful habitats, the lack of access to suitable or tolerable T_es may lead to time constraints on ectotherms, because they are forced to limit their activity (Karasov and Anderson 1984, Grant and Dunham 1988, Adolph and Porter 1993). Thus, time-consuming activities such as feeding and courtship must be accomplished in narrow time windows (Collier and Johnson 1990). The resulting trade-offs ultimately can lead to

decreased survival via reduced foraging success or to reduced fitness via missed mating opportunities. Alternatively, activities can be carried out at sub-optimal temperatures, but ectotherms would suffer decreased physiological performance under these conditions (Grant 1990).

Forested areas, with only shade and filtered sun, represent habitats of sub-optimal temperatures if an ectotherm can not reach preferred T_b due to large body size (and consequent high thermal inertia) or the inability to reach sun patches for thermoregulation (Huey 1974). However, if small individuals (juveniles) can shuttle in and out of forest sunlight patches, they can use their low thermal inertia (i.e., resistance to heat transfer) to maintain elevated T_b in these habitats (Hillman 1969, Claussen and Art 1981, Bauwens et al. 1996). A forest mosaic of filtered sun would typically be insufficient for large individuals (adults) to maintain similar body temperatures. Therefore, the preferred habitat of an ectotherm should have a microclimate that allows extended periods of activity, and may depend in turn on body size.

The relative importance of an activity for an ectotherm can vary with its life history stage. Juveniles often experience selective pressures for maximizing food consumption under high risk of predation (Werner and Gilliam 1984); acquired energy is then used for maintenance and growth. Increased growth rates can lessen time spent under normally high size-based predation pressures. By increasing body size, an individual can essentially decrease its pool of potential predators and invade new habitats (Werner and Hall 1988, Mittelbach and Osenberg 1993). In adults, activity trade-offs may exist between foraging, reproduction, predator avoidance, and defense of thermoregulatory

basking sites. These trade-offs often depend on the individual's current energy reserves, its dominance within the population, and the availability of environmental resources (food and basking sites). Relative status in a dominance hierarchy may determine whether an individual will reproduce or invest energy into growth and storage.

Nutritional gains for ectotherms are often under a series of proximate constraints, including food availability, foraging success, digestive limitations, and risk of predation (Congdon 1989). Response to these constraints depends on which is most limiting to the animal. Habitat use by animals often reflects relief from these constraints. Food patches can be used differently by individuals depending on their foraging strategy (MacArthur 1972, Pianka 1974, Durtsche 1992). Foraging efficiency within a patch depends on how easy food is to detect, capture, and consume. Competition for available resources can affect foraging success and lead to a density-dependent population distribution within the environment as a result of differences in resource use by animals of different dominance levels (Fretwell and Lucas 1970, Rosenzweig 1991). Further limitations of harvesting rate can be experienced by ectotherms when food supplies (both plant and animal) vary seasonally (Durtsche 1995, Peterson 1996). These limitations can be magnified for insectivores and carnivores if prey activity is restricted by biophysical factors (Dunham 1978). Ectothermic herbivores, especially generalist herbivores, are not often food limited because plant foods are in greater abundance than are prey for carnivores. These herbivores rely on the rate of processing to increase their nutritional assimilation (Zimmerman and Tracy 1989, van Marken Lichtenbelt 1992). Performance of digestion in

ectothermic herbivores increases with an increase in the duration of time that an ectotherm spends at optimal temperatures (Troyer 1987, Wikelski et al. 1993).

All else being equal, habitat selection in ectotherms should vary as a function of the individual's ability to maintain T_b where performance is maximized. Assuming that most ectotherms have a temperature dependent performance curve (Huey 1982), choosing habitats for the maintenance of optimal T_b (i.e., maximum physiological performance) may be among the most critical selection factors for those individuals. The herbivorous iguanid Conolophus pallidus selected habitats that allowed the maintenance of a constant T_b for the longest portion of the day regardless of seasonal changes in T_e (Christian et al. 1983). While maintaining a constant T_b, the size or life history stage of an ectotherm should dictate which ecological, behavioral, and physiological processes are most important to the individual. Lizards that feed on fibrous plant foods tend to have a large body size (Pough 1973, Auffenberg 1982, Christian et al. 1984, Rand et al. 1990, R. D. Durtsche *unpublished data*) and therefore large herbivorous lizards should be restricted to open areas where extended periods of solar exposure are available to maintain optimal T_b for digestion. Smaller herbivorous lizards and insectivorous species may use other habitats (e.g., forested areas) that offer protective cover against predation and abundant food resources. Low thermal inertia associated with small body size provides individuals the option to elevate and maintain T_b to an optimal range for activity with restricted solar exposure. Large (e.g., herbivorous) lizards should thus be more constrained than smaller (usually insectivorous) lizards in selecting habitats to maximize digestive efficiency.

My intention was to investigate patterns of habitat use in ectotherms to determine how individuals of different body size maintain T_b, yet also invest energy into processes important within a life history stage. I used the Mexican spiny-tailed iguana (Ctenosaura pectinata - Iguanidae) as a model organism to study these patterns during both the wet and dry seasons in a tropical thorn forest ecosystem. These lizards differ from most others in the extreme differences in size between adults and offspring, where adults are large and offspring are small (Andrews 1982, Van Devender 1982, Durtsche et al. 1997). They are also atypical among iguanids because they shift their diet ontogenetically, from juveniles eating primarily insects to adults eating plants (R. D. Durtsche *unpublished data*). Consequently, they provide the opportunity to examine this question independent from inherent problems with interspecific comparisons (Garland and Adolph 1994). Laboratory studies suggest that adult C. pectinata seek elevated temperatures (T_b range 30 - 42 °C, $\bar{T}_b$ = 37 °C) for their daytime activity (Throckmorton 1973). I describe the ecology of this population of lizards emphasizing polymorphism among age classes, space and time use, social interactions, and field active temperatures with relation to habitat use.

Methods

Study site

I studied C. pectinata in two dry seasons and two wet seasons from January 1995 to August 1997 in Central Mexico. The study site was near Los Carros dam, in

Axochiapan Co., Morelos, Mexico (18° 36' N, 98° 43' W) along the border with the state of Puebla, elevation 1100 m. This site was chosen because C. pectinata were abundant and relatively undisturbed by humans. Natural vegetation existed in patches near the canyons where the lizards were found. The habitat was a seasonal tropical forest with deciduous trees and shrubs that often flowered in the dry season, and can be categorized as a semi-humid thorn forest with several species of columnar "cardon" cactus. The dry season extended from December to May. Several shrub and tree species in the family Fabaceae were major flower and fruit producers in both seasons of this study, and were a major source of food for all age classes throughout the year (R. D. Durtsche, *unpublished data*). The population of C. pectinata in this study used rocky outcrops, the canyon walls of the rivers "Las Garzas" and "Rio Grande," and forest fragments surrounding these canyons.

Morphological characteristics

Ctenosaura pectinata were collected using Tomahawk™ live traps, by noosing, by shooting with an air rifle, and by hand. Snout-vent length (SVL) was recorded for each lizard as the distance from the tip of the snout to the opening of the cloaca with a digital caliper to 0.01 mm or a flexible tape measure to 1 mm accuracy.

Habitat use

I used spot samples to quantify habitat use, activity, and sun exposure in the population of lizards along a canyon transect of the river "Las Garzas." Spot samples were the observations of each lizard active at a station. This transect had ten stations that

ranged in area from 0.48 - 1.25 ha and represented the complete diversity of habitats found at the study site. All stations could be visited by boat and all spot samples recorded within one hour, allowing hourly samples to be taken from sunrise to sunset. Spot samples, which were made on all C. pectinata that were visible, included the following information: 1) age class or adult sex, 2) activity (moving, basking, feeding, or social interaction [head bobbing, chases, fights], reproduction), 3) distance moved during activity (m), 4) exposure (sun, filtered sun, shade, or overcast), 5) habitat (grass or herbaceous plant, shrub, tree, rock or cliff, or burrow), 6) elevation - above ground or water, and 7) foraging - success, location (habitat), and food type. Burrows were identified as holes and crevices in the canyon walls in addition to excavated refuges in the soil in forested area near these canyons. Each lizard was observed for approximately 15 seconds to note any change in activity. If a lizard was in a movement activity, the spot sample was concluded when the movement stopped for at least 10 seconds. Furthermore, the time of each activity involving movement was recorded. These data were pooled by age, adult sex, time of day, and season to give frequency results for the population. I did not collect lizards from this transect to avoid interference with their behavior.

I used haphazard observations as an additional means of spot sampling for forested areas associated with the canyons that were not easily observed by boat. I made haphazard walks through the forests at different times during the day and I used the same protocol for recording observations as in the transect samples.

Time-activity budget

I used focal sample observations of individual lizards in the population to create a time budget and quantify daily behavioral activities. I used binoculars and a micro-cassette tape recorder to document events, using the same behavioral categories that were incorporated into the spot sampling protocol. Focal sample duration was set to at least two times the length of the longest activity. Focal sample periods ranged from 15 minutes to four hours. On occasion, inactivity and relatively short movement bouts of adult C. pectinata made focal observations of up to three lizards per sampling period possible. Many of these focal samples were made from a boat anchored 10–15 m from the shore. This position provided a view of most habitats used by the lizards. I also used a blind to aid in some of my on-land observations. Several focal samples, particularly of juveniles and some immatures, were made during haphazard forest walks.

Environmental temperatures

I recorded environmental temperatures with a multi-channel Omega™ thermocouple data logger to determine thermal profiles of the habitats in which these animals were active. I recorded temperatures every 15 min from burrow, rock cliff face, grass (0 - 0.5 m), shrub (1 m), and tree (2 m) habitats in the wet season when all age classes were active. Habitat temperatures were obtained in the wet season to describe the effect foliage had on vegetation habitat temperatures. I also measured substrate temperatures with direct solar exposure (covered thermocouple) and air temperatures (at 2 cm with a shaded thermocouple) in the shade and with direct solar exposure in both the

wet and dry seasons to determine seasonal shifts in temperature regimes. Thermal data were recorded for three to seven days per run. Body temperatures of lizards that were noosed, shot, or hand-captured were recorded directly (within 30 sec) after collection with a Miller-Weber™ quick reading cloacal thermometer (0.1 °C). Substrate and air temperatures at 2 cm (shaded bulbs) were also recorded at the site where the lizard was first seen before capture.

Statistics

All data were processed with either Statview (Abacus 1996) or JMP (SAS 1997) statistical software for Macintosh. Data transformation (usually $\log_{10}$) was used to adjust for non-normality and to increase additivity and homogeneity (Kirk 1982). All test statistics were two-tailed. Means are presented ±1 standard error unless otherwise noted. A Welch's ANOVA was substituted for a single factor ANOVA (SAS 1997) when sample sizes were small and variances were unequal. Differences between age or adult sex classes were determined using a Tukey-Kramer HSD multiple comparisons procedure using all pair-wise comparisons (Toothaker 1993). Significance for all analyses was at $\alpha = 0.05$.

Results

Age class distinction

The population of Ctenosaura pectinata was size-structured (Fig. 1). More than a seven-fold difference in body length was measured between hatchling and maximum size adult lizards. Juveniles represented a smaller body-sized cohort of non-adults than immatures and were separated by one year in age. Ctenosaura pectinata had a single annual breeding season during the dry season (February–April) from which the juvenile cohort emerged in late June and early July. The separation between immatures and adults was set at 200 mm SVL based on the presence of sperm (in males) and enlarged vitellogenic follicles (in females) in the reproductive (dry) season (R. D. Durtsche, *unpublished data*). Adults were sexually dimorphic in head size. Head dimorphism was not observed in non-adult ctenosaurs. Moreover, tail spines and claws were less developed in non-adult ctenosaurs.

Age classes could be distinguished by coloration. Juvenile coloration was a brilliant emerald green, which closely matched the newly emerging foliage of the herbaceous plants and shrubs (e.g., several Acacia species). Immatures in the wet season were also bright green, but black mottling over all but the ventral surface added a disruptive coloration pattern. Immatures retained green coloration in the dry season but pattern brightness was reduced to a dark olive-brown. Adults were primarily a dark blue-gray to black, with small blotches of white or orange in some individuals. Males had a

deep sapphire coloration in the reproductive season that became less intense in the wet season.

Lizard activity

Ctenosaura pectinata maintained a unimodal activity period and relatively stable T_b throughout the day (Fig 2). The number of active lizards observed varied significantly with the hour of the day ($F_{11, 72} = 12.24$, $P < 0.0001$). These differences were in association with changing environmental temperatures, where the abundance of lizards active at any time followed the availability of sun exposure. This hourly pattern of lizard abundance did not vary between seasons ($P > 0.05$). Activity peaked at mid-day (1300 hrs) with significantly more lizards active than at mid-morning hours (0900–1000 hrs) based on Tukey HSD post-hoc tests. Early morning (0700–0900 hrs) and late evening (1800 hrs) were the periods with the fewest active lizards.

The mean lizard density (based on lizard counts at transect stations during peak activity [1300 hrs]) was 4.24 ± 0.56 (range 2.07 to 11.85) lizards per hectare (Table 1). Two stations (9 and 10) with the highest lizard densities differed in part from the other stations by having large open cliff faces with many crevices and a high degree of solar exposure throughout the day.

Time activity budgets from 98 focal samples showed that C. pectinata basked most of the time, with a total of 91.9 ± 1.6% of their activity period spent in non-moving activities (Table 2). A similar pattern of daily activity (e.g., mean percent of population basking = 72.84 ± 3.88%) was observed from spot samples (over 1550 observations).

With the exception of reproductive activity (dry season only), the time-activity budget pattern for these lizards (arcsin transformed) did not differ between dry and wet seasons, thus results from the two seasons were pooled for further analysis. Age classes did not differ in the percent time spent basking. Juveniles were unique among age classes in splitting the time they spent basking into more numerous but shorter duration bouts. I partitioned daily lizard activity into four periods (morning = 0700-1000 hr, mid-day = 1000-1300 hr, afternoon = 1300-1600 hr, evening = 1600-1900 hr) to consider broad temporal patterns of exposure. There was a pattern of no change in the basking activity among all ctenosaur age classes over the day.

Lizards were involved in non-basking activities approximately 8% of the time. Movement accounted for 51% of this non-basking time. Juveniles spent significantly more time moving, with a higher movement frequency than any other age class. Most movement by juveniles occurred before midday and decreased in the afternoon and evening hours. Movement bouts by immatures were the longest, and females' were the shortest. Ctenosaura pectinata moved on average slightly less than one meter during every move (Table 2). No seasonal differences were observed in the distances moved or the movement rates at any times of the day; thus movement data from both seasons were pooled for comparisons of age/sex classes. Adult males moved farther during each move than either adult females or juveniles ($F_{3, 610} = 5.921$, $P = 0.0006$), and also had a faster per move rate than did adult females. Adults in general moved faster than juveniles ($F_{3, 610} = 8.398$, $P < 0.0001$). Juveniles typically made many shorter moves more frequently. No differences were observed among any age or sex class based on the overall movement rate

or the rate of movement for the entire focal sampling period ($F_{3, 89} = 0.761$, $P = 0.519$). Only 10% of non-basking time was spent foraging in C. pectinata. This low proportion of time was primarily the result of the lack of time spent feeding by immature and adult lizards. The insectivorous juveniles spent significantly more time foraging than the older herbivorous ctenosaurs. Juveniles had the shortest feeding bouts while immature and adult lizards, especially adult females, had much longer consumption bouts (Table 2). Juveniles foraged from morning through midafternoon, and immatures and adults fed exclusively from midday through early evening.

Reproductive activities of adults accounted for 6% of the non-basking time and occurred between 1000 and 1500 hrs. Copulation in this species lasted on average 3.71 ± 0.84 minutes (range 1-7 min., n = 6 pair). Males that mated had a higher mating frequency than females (Table 2) suggesting a polygynous mating system similar to other iguanids (Dugan and Wiewandt 1982, Gier 1997). Aggressive or agonistic interactions (intraspecific chases, head bobs, etc.) typically were short in duration. Such behaviors were more common among males than among females. I observed few fights between equally sized males. One of these lasted 80 min., and involved the two males repeatedly falling off a cliff into the river as they grappled.

Habitat use

This area of central Mexico provided a mix of trees, shrubs, and low vegetation habitat types as well as rock habitats on outcrops and the walls of river-cut canyons. Overall, rock or cliff habitats were used most by the population of C. pectinata (all age

classes pooled; Fig. 3). Focal samples of individuals confirmed this finding because individual lizards spent more time (40.3 ± 4.42 %) active in rock habitats than any other habitat ($F_{4, 582} = 15.185$, $P < 0.0001$). Only juveniles used shrubs (Fig. 4). They also used the herb and grass habitat extensively. Adults and immatures used rocks more than did juveniles. Age classes also sorted by elevation or distance above the water, where canyon walls were used at the highest elevation among habitats (Fig. 5). At peak activity (midday-1300 hrs) adults occupied significantly higher places ($\bar{x}_{\text{adult males}} = 6.06 \pm 0.65$ m, $\bar{x}_{\text{adult females}} = 6.00 \pm 0.55$ m) than either immatures ($\bar{x} = 2.86 \pm 0.61$ m) or juveniles ($\bar{x} = 1.25 \pm 0.20$ m) among all habitats ($F_{3, 257} = 9.104$, $P < 0.0001$). These midday differences in elevation between adults and immatures were most pronounced in the cliff habitat ($F_{2, 139} = 3.22$, $P < 0.0428$), but were not observed when lizards were in trees. The vertical distribution of adults on the cliffs seemed related to behavioral dominance; larger individuals of both sexes defended their high perches from smaller individuals.

Trees and shrubs were used more by C. pectinata in the wet season than in the dry season (Welch's $t = 2.609$, $P = 0.013$, $df = 37.26$). Lizards were seen more often in burrow entrances in the dry season (Welch's $t = 2.169$, $P = 0.046$, $df = 37.26$). These two trends are also supported by focal samples (Fig 4), with a dry season to wet season increase of 13.23 % in tree use ($F_{1, 96} = 5.114$, $P = 0.026$) and a 28.29 % decrease in burrow use ($F_{1, 59} = 38.416$, $P < 0.0001$). Most lizards relied on the burrows as a nocturnal retreat, although a few used treetops (in the wet season) and some subadults used hollow cacti. These alternative retreats were not considered "burrows" in this study.

Flowering trees were used as food sources in the dry season by immature and adult lizards. Wet season vegetation increased the variety of leaves and flowers available to all age classes of lizard. Adults and immatures ate primarily leaves and flowers in the wet season, whereas juveniles foraged on insects and some flowers in shrubs and low vegetation (R. D. Durtsche, *unpublished data*).

Environmental and body temperatures

The various habitats used by C. pectinata functioned in part as thermoregulation sites where lizards gained or lost heat. The highest available T_es were found in rock and cliff habitats during all but the early morning hours (Fig. 6). Burrows remained at relatively constant low temperatures throughout the day, and the constant burrow temperatures may have served as a thermal retreat for lizards against the cooler nighttime and warmer daytime temperatures of other habitats. All vegetation habitats were similar to each other in temperature throughout the day, and collectively they were consistently lower than rock or cliff habitats.

Environmental temperatures within a habitat varied with the degree of radiation exposure and with season (Fig 2). Midday (1300 hrs) substrate temperatures under direct solar exposure were the warmest available to the lizards and were nearly twice as high as shade temperatures. Temperatures in the air under direct solar exposure were intermediate between substrate temperatures under similar conditions and shade temperatures. The dry season had significantly higher temperatures than the wet season ($P < 0.0001$) under all three exposure measures except during early morning hours (0700 – 0800 hrs).

The mean T_b of C. pectinata was 34.81 ± 0.57 °C (range 22.6 – 39.8 °C; Table 3) and varied little throughout the day (Fig. 2). No significant differences were observed in body temperatures among any of the age/sex classes ($F_{3,53} = 0.102$, $P = 0.959$), between seasons ($F_{1,55} = 1.04$, $P = 0.312$), or among times of day ($F_{10,46} = 1.01$, $P = 0.451$). Lizard T_bs were positively correlated with both substrate ($F_{1,44} = 56.616$, $P < 0.0001$, $R^2 = 0.563$; Fig. 7) and air ($F_{1,44} = 55.880$, $P < 0.0001$, $R^2 = 0.559$) temperatures. Divergence of the T_b regression away from a thermal isocline in Fig. 7 suggests a thermoregulatory capacity to maintain stable diurnal T_b (Fig. 2). T_es (Table 3) significantly lower than lizard body temperatures at capture locations (site of first lizard observation) supports this thermoregulatory behavior (paired t-test: $t_{air - body} = -9.152$, $P < 0.0001$; $t_{body - substrate} = 5.181$, $P < 0.0001$; $df = 45$).

Ctenosaura pectinata thermoregulated by shuttling among different sunlight exposures (Fig 8). I used spot sample data from each temporal period to analyze differences in the use of exposure throughout the day. Transect data from only one hour per activity period, each of which was separated by at least one hour (i.e., morning = 0800 hrs; mid-day = 1000 hrs; afternoon = 1300 hrs; and evening = 1600 hrs), were pooled with haphazard samples from each period for analysis. Proportions of mean lizard abundance in an exposure were arcsin transformed before statistical analyses. Most C. pectinata were first observed exposed either to sun ($\bar{x}_{spot} = 39.0 \pm 4.3$ %, $\bar{x}_{focal} = 37.0 \pm 3.9$ %) or to filtered sunlight ($\bar{x}_{spot} = 30.6 \pm 4.5$ %, $\bar{x}_{focal} = 34.2 \pm 4.0$ %). No significant differences were observed among age/sex groups (Table 2) so data were pooled for further analyses. I observed a greater proportion of the population active in sun exposure in the

dry season than in the wet season (t_{sun} = 2.493, P = 0.0144, df = 93) which may reflect the lack of foliage cover. However, focal samples indicated that individual lizards spent more of their total activity time active in the sun in the wet season than in the dry season (t_{sun} = -3.83, P = 0.0002, df = 86). Increased cover from wet season vegetation might have contributed to lower T_es (Fig. 2) and obligated lizards to spend more time in the sun for thermoregulation. Similarly, in the dry season when temperatures were very high (e.g., > 45 °C, Fig 2), lizards spent more time in the filtered sun and shade than in the wet season ($t_{filter\ sun}$ = 2.56, P = 0.012; t_{shade} = 3.61, P = 0.0005; df = 86; Table 2). Relatively constant diurnal T_bs were maintained by decreased use of sun exposure in the dry season and by moving among exposures in the wet season (Fig 8). No apparent temporal pattern exists for the diurnal use of exposures by the lizards in the wet season, with the exception of filtered sun in the afternoon.

Discussion

Data on C. pectinata from Central Mexico indicated a complex interaction between food resource and space use among the different age classes where relatively constant T_bs were maintained. Most of the population used rock and cliff habitats throughout the day in both seasons of study (Fig. 3). Burrow use was more extensive in the dry season when reproduction occurred, and plant habitats were occupied in the wet season when foliage was abundant. There were no changes in the daily temporal pattern of habitat use within either the wet season or the dry season. Juveniles were effectively a life history stage

only in the wet season for approximately the first 4 - 6 months post-hatching. These smaller insectivorous lizards spent the majority of time in low elevation shrub and herbaceous plant habitats. Herbivorous adults and immatures spent the majority of their time on rock outcrops or cliffs but were separated by elevation. Adults dominated the higher elevations and immatures were found at lower elevations. Immatures diversified their habitat use, spending time in trees and low elevation vegetation, in addition to time spent on rock cliffs. Spatial separation among age classes occurs in other iguanids, where the juveniles often occupy low elevation shrubs and adults live at higher elevations (Troyer 1982) or in open areas (Fitch and Henderson 1977). A variety of selective pressures ranging from biophysical factors to food resources to predation and social interactions could plausibly influence habitat selection of this ontogenetic series within this ectothermic population.

Biophysical factors - temperature

Body temperature in C. pectinata remained relatively constant under the different microclimate conditions of varied habitats. These T_bs were similar throughout the day, between seasons, and among all size classes (Fig. 2, Table 3). These field T_bs fell within the range of preferred T_bs selected by this species in the laboratory (Throckmorton 1973). The thermal performance breadth of ectotherms (Huey and Stevenson 1979, Huey 1982) contains the optimal T_bs for varied activities, and represents the relatively narrow range of T_bs where ectotherms are found active (Stevenson et al. 1985, Van Damme et al. 1991). Despite the inability of some ectotherms to maintain T_b for maximal performance

under field conditions, the optimal temperatures for these performance maxima (e.g., sprint speeds in lizards) appear to be evolutionarily conservative and do not change substantially among closely related species or ontogenetically within a species (Hertz et al. 1983, Van Damme et al. 1990). My study demonstrated that within a single lizard species, C. pectinata, very different sized juveniles and adults were able to maintain T_bs within the thermal performance breadth throughout the day through differences in habitat choice and associated differences in feeding strategies.

Temperature may have been the most influential factor in habitat choice by the herbivorous age classes. Adult and immature C. pectinata were strongly heliothermic and used the habitats where they could maintain elevated T_bs for the longest periods of the day. Elevated T_b facilitates fermentative breakdown and passage rates of plant materials in the colon of iguanid lizards and a decrease in this temperature often results in decreased food intake and digestive performance (Troyer 1987, Zimmerman and Tracy 1989, van Marken Lichtenbelt et al. 1997). The rock and cliff habitat had open exposure to solar radiation and was the only habitat that maintained T_es at or above the mean $\bar{T}_b$ of C. pectinata throughout the day (Fig. 6). Accordingly, this was the habitat used most extensively by the herbivorous adult and immature ctenosaurs.

A similar pattern was observed in a saxicolous population of Iguana iguana, individuals of which chose habitats that allowed them to maintain a relatively constant elevated T_b throughout the day (van Marken Lichtenbelt et al. 1997). The range of T_bs maintained by these iguanas were similar to C. pectinata T_bs (Table 3). In both studies the potential for elevating T_bs exceeded the actual field T_bs recorded (Fig. 6). The narrow

range of midday T_bs for both species (C. pectinata 32 ° – 37 °C, I. iguana 33 ° – 38 °C) contains the derived optimal T_b (36.5 °C for Iguana iguana) for maximum digestive capacity (van Marken Lichtenbelt et al. 1997).

Other iguanids exploit basking habitats (similar to the cliff habitats) with elevated temperatures where fermentative digestion is facilitated. Iguana iguana in other areas often are found in the upper canopy or on the outer branches of trees that extend into sunlight openings over rivers or lakes (Troyer 1984). Marine iguanas (Amblyrhynchus cristatus) perch on black lava after an algae meal to regain T_bs and promote digestion (Wikelski et al. 1993). Galapagos land iguanas (Conolophus pallidus) actively shift their T_b between seasons to maintain it in a constant range for the longest period of the day (Christian et al. 1983). These land iguanas shift their habitat use between cliff and plateau depending on the season or type of day (sunny vs. cloudy) to maintain these T_bs. Chuckwallas (Sauromalus obesus) in the Mojave Desert maintained constant T_bs (36 – 37° C) for the longest periods possible during both day and night by exploiting the warmest diel temperatures in the early portion of the activity season to enhance digestion when food was abundant (Zimmerman and Tracy 1989).

Selection of warmer thermal habitats by ctenosaurs extended into the night with their use of burrow habitats. Nighttime temperatures of burrows remained higher than all other habitat temperatures (Fig. 6). This suggests that the lizards gained not only protection from predation but could also increase digestive rates by using these refuges at night instead of other habitats.

Insectivorous juveniles inhabited the cooler vegetation habitats but their small size and low thermal inertia allowed them to thermoregulate actively and maintain elevated T_bs in a mosaic of sunlight patches. Elevated T_bs are required for insectivores to maximize performance of feeding and movement (Bennett 1980, Huey et al. 1984, Magnusson et al. 1985), and predator escape (Hertz et al. 1982). By increasing locomotor performance these juveniles had the potential to increase prey encounter rates and capture success. Movement rates (frequencies) and the percent of time spent moving were significantly greater in juveniles than in any other age class (Table 2). The frequency of feeding bouts did not differ between age classes, however, juveniles spent a greater percent of their time foraging than did immatures or adults. This increased foraging effort provided juveniles with more time to spend finding cryptic prey (e.g., caterpillars and other plant insects), while adults used less time consuming a plant food from a single food patch. Elevated T_bs and increased movement behavior (an index of foraging activity) in cooler vegetation habitats also were observed by Belliure and Carrascal (1996) in insectivorous lacertid lizards. They attributed these patterns of movement and thermal selection to the insectivorous feeding strategy of these lizards. Elevated T_bs of these forest dwelling lacertids were attained through frequent, short duration basking bouts on warmer substrates than those used by open habitat lacertids. Juvenile C. pectinata in vegetation followed patterns of basking frequency and duration and movement behavior similar to those of forest dwelling lacertids, but juveniles were not found in warmer microclimates than older ctenosaurs inhabiting open habitats (Table 3). Therefore, the ability to use

these habitats while maintaining T_bs comparable to herbivorous adults must have resulted from the lower thermal inertia associated with the small body size in juveniles.

Resource factors

Growth demands are highest in juveniles, and ctenosaurs have some of the highest growth rates for iguanids (Van Devender 1982, R. D. Durtsche, *unpublished data*). This smaller insectivorous age class used low elevation shrub and herbaceous plant habitats where both insect and plant food resources were available. Foraging on insects provided sources of high energy and protein that facilitated high growth rates. Moreover, juveniles are more efficient on insect foods than adults (R. D. Durtsche, *unpulished data*). Adults and immatures used rock outcrops or cliffs where plant foods were not abundant, suggesting that food resources were not a major factor in habitat choice by adults. Moreover, these rock and cliff habitats were the primary site of adult activity, even in the dry season when much of the forest was without foliage and food resources were primarily limited to a few flowering tree species. Adults foraged in plant habitats for significantly shorter periods of the day than did juveniles, yet most stomachs examined were full or nearly full (R. D. Durtsche, *unpublished data*) suggesting a reduction in time required to reach satiation on a plant diet. This corresponds with the bulk associated with plant materials. Quick satiation frees time for other activities (e.g., digestion) in these herbivores.

Social interaction and predation factors

The roles of intra- and interspecific interactions in habitat selection varies with life history stage in C. pectinata. Adults were affected during the dry season by activities associated with reproduction and nesting. Each of these activities could change habitat choice. Large adult males presumably select and defend territories that hold the most females during the reproductive season (Evans 1951, Gier 1997). Territorial defenses often were directed toward subordinate males that attempted sneak matings. Large males also engaged in extended fights during this season, suggesting competition for space, as no females were present during contests. The behavioral pattern of these fights was similar to those described for the congener C. similis by Gier (1997). The increased use of burrows by females in the dry season (Fig. 4) suggested that these habitats were potentially used as nesting sites. These burrows were also the main refuge against predators. Lizards quickly escaped to these refuges at the first sign of danger. Furthermore, the use of higher elevations on cliffs by adults may have reduced their risk of predation through increased vigilance and inaccessibility to terrestrial predators.

Ctenosaura pectinata had several predator avoidance mechanisms which could be linked to habitat selection. The ontogenetic color shift from green to black ensured that the body coloration matched habitats inhabited by different age groups, especially in sub-adults. Presumably, predation risks were higher in juvenile and immature age classes than for adults. This assumption was supported by Van Devender's (1982) findings that approximately two thirds of a C. similis population was lost in the first month after hatching, and that survivorship increased only slightly thereafter through the first nine

months. Adult C. pectinata had a battery of morphological defenses (Greene 1994) in addition to large size to reduce predation risk on rock and cliff habitats. These habitats were relatively open and predators often were associated with these habitats. I observed several species of raptors (e.g., Harris Hawk, Great Black Hawk, American Kestrel, Great Horned Owl, and Barn Owl) that flew close to these cliffs and could have taken smaller C. pectinata. Snakes (e.g., Drymarchon corais) and ringtails (Bassariscus astutus) often used both the cliffs and the crevices, but adult ctenosaurs were much too large for most of these cliff-associated predators. To escape capture, C. pectinata ran to burrows, cracks, or crevices in the rocks or cliffs where they wedged themselves in head first using claws and body, exposing only a tail of spines. Tail spines on adults were sharp and were used to deter predation. Additionally, adults moved faster than subadults (Table 2). The running capacity of lizards in general (endurance and maximum distance) increases allometrically (e.g., C. similis, Garland 1984).

Social dominance played at least a partial role in the distribution of individuals in the environment. I observed a size-based hierarchical structure in this population. Immature lizards used rock and cliff habitats when possible but often were chased from basking areas by dominant adults, both males and females. Social dominance is a common trait within the family Iguanidae (Carothers 1981, Dugan and Wiewandt 1982, Evans 1951, Gier 1997, Henderson and Fitch 1979, Ryan 1982, Werner 1982). The degree of dominance could contribute to density dependent effects experienced by C. pectinata immatures, resulting in their use of lower elevations in the rock and cliff habitats. These

lower elevation locations represented suboptimal basking sites because they received less solar radiation during the day due to shadows created by the high canyon walls.

A model of habitat selection

The selective advantages of choosing proper habitats for T_b to maximize performance and, ultimately, individual fitness can vary with body size or life history stage. The factors involved in habitat choice can vary depending on their influence on physiological performance, nutritional acquisition, and survival against predation. A suite of factors, from environmental influences to population demographic structure, can be modeled to indicate the complexities of habitat selection in different sized ectotherms (Fig. 9). Factor influence in habitat selection is variable depending on its affect on the life history stage of the animal. Ectotherms select habitats with microclimates that allow them to reach and maintain performance body temperatures for the longest period of daily activity (Christian et al. 1983, Zimmerman and Tracy 1989, Diaz 1997). Models of ectotherm habitat selection based on thermal profiles (Dunham et al. 1989, Huey 1991) assume behavioral thermoregulation to be the mechanism used to maintain optimal body temperatures. The model I present here (Fig. 9) has additional assumptions that: 1) small (juvenile) body size increases the range of microclimates available for thermoregulation, due to decreased thermal inertia; 2) large (adult) body size reduces the risk of predation in otherwise high risk habitats; and 3) foraging time decreases with an increase in the percentage of plant material in the diet.

Smaller individuals or juveniles of large adult species with high size-related energetic demands may have food and reduced risk of predation as the most influencial factors affecting their life history stage. The low thermal inertia of juvenile C. pectinata allowed them to maintain elevated T_bs in habitats (e.g., plants) with relatively low amounts of solar radiation or with small sun patches (model assumption 1). The vegetation and structure of plant habitats was important in providing cover to smaller individuals to avoid predation. Cryptic coloration of juveniles could also have aided in predator avoidance in these habitats (Greene 1994). Moreover, plant habitats harbor many arthropods that avoid open habitats. By consuming insects, the juveniles could meet their energetic and protein demands for maintenance and growth (Pough 1973, Nagy 1982). The mean size of insects (e.g., eruciform larvae vol. ≈ 29.7 mm^3) consumed tends to be much smaller than the size of plant foods (e.g., Senna wislizenii flower vol. ≈ 262.3 mm^3) eaten by C. pectinata (R. D. Durtsche, *unpublished data*). These differences in food size require a lizard to consume more insects to fill their gut than plants. Juveniles also extracted more energy and protein from these larvae than from the plant foods (R. D. Durtsche, *unpublished data*). Therefore, the selective pressures of predation and food resources would be reduced in plant habitat used by small insectivorous ectotherms, while low thermal inertia allows them to thermoregulate in a thermal mosaic.

Large body size places certain constraints on ectotherms while releasing others. Adult C. pectinata spent more time active than juveniles in open habitats where predation risk was high (model assumption 2). Presumably the morphological defenses and speed associated with large body size reduced predation pressures. Similar patterns where an

increased body size can reduce the effective pool of predators in a habitat have been observed in bluegill sunfish (Mittelbach and Osenberg 1993, Werner and Hall 1988).

Large ectotherms (adults) require habitats with solar exposure and T_es of sufficient duration to maintain T_bs for activity performance. Insects are probably not large enough or abundant enough for large ectotherms to consume efficiently; the cost of transport required to capture them would be too great (Pough 1973). Additionally, adult C. pectinata were less efficient at digesting an insect diet than were juveniles on the same diet (R. D. Durtsche, *unpublished data*). Herbivory allows large ectotherms to acquire energy and nutrients while minimizing costs of foraging. Larger body size in adult C. pectinata and other ectotherms allows efficient digestion of fibrous plant diets (Bjorndal 1997, R. D. Durtsche, *unpublished data*). Most habitats with vegetation provided adequate food for these ectotherms and the bulk of plant foods allowed the herbivorous age classes of C. pectinata to quickly to reach satiation (model assumption 3). This minimized the time needed for foraging so that other activities could be maximized. Digestive performance in iguanids can be optimized through elevated body temperatures, to speed the passage rates of plant foods (Zimmerman and Tracy 1989). Both Troyer (1987) and van Marken Lichtenbelt (1992) demonstrated this in Iguana iguana with increased digestive efficiencies resulting from prolonged periods of elevated body temperatures. A microclimate like that in the open habitat used by adult C. pectinata which allowed sustained body temperatures for digestive performance may define the types of habitats used by large herbivorous ectotherms. Therefore, habitat selection by

ecothermic herbivores should be influenced by the duration of time that optimal digestive temperature can be maintained.

In summary, ectotherms of very different body size select habitats where they can maintain T_b within their thermal performance breadth and still carry out all the processes important to each life history stage. Adult C. pectinata used cliff and rock habitats that had high T_es throughout the day. Behavioral thermoregulation between different solar exposures allowed these lizards to maintain body temperatures near optimum for digestive efficiency. It was assumed that digestive performance was a strong factor influencing habitat choice in these ectothermic herbivores. Large body size and related morphological features may reduce adult's risk of predation in these rock and cliff habitats, and dominance over immatures allows adults to hold these areas. Juvenile C. pectinata used shrub and vegetation habitats for insect food resources and predation protection. Low thermal inertia and the ability to shuttle in and out of sun patches allowed juveniles to maintain elevated T_bs in these habitats while sustaining periods of movement and foraging for maximum growth rates. The model presented here describes habitat selection for the maintenance of T_bs within the thermal performance breadth in ectotherms of very different body size and feeding strategy. Differences in feeding strategy and predator defense allow small insectivores to occupy low vegetation, maximizing foraging capacity and crypsis while large herbivores occupy high cliffs that maximize digestive performance and vantage positions.

Acknowledgments

I thank E. Anzures-Vázquez, R. Castro-Franco, L. Hillström, A. Holloway, E. Kroese, H. Mejia-Mojica, and A. Ramirez-Bautista for field assistance throughout portions of this study. I am greatly indebted to my colleagues in the Centro de Investigacion at the Universidad Autonoma del Estado de Morelos for their logistic support and friendship throughout my stay in Morelos. I thank J. P. do Amaral, P. Gier, and S. Sartorius for comments and fruitful discussions about earlier versions of this manuscript. I thank my committee members V. Hutchison, W. Matthews, M. McInerney, C. Peterson, and L. Vitt for support and constructive editorial suggestions. This research was conducted under the research permits granted to the Centro de Investigacion at the Universidad Autonoma del Estado de Morelos and I.N.E. DOO750.6824 to A. Ramirez-Bautista and R. D. D.. Partial funding for this research was provided by research grants from the Univ. of Oklahoma Dept. of Zoology, Graduate Student Senate, and Graduate College; Sigma Xi Grants-in-Aid of Research; and the American Museum of Natural History Theodore Roosevelt Fund. This research was submitted in partial fulfillment of a Ph.D. in Zoology at the University of Oklahoma.

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Table 1. Relative density of the Mexican spiny-tailed iguana (Ctenosaura pectinata) at 10 different stations in a transect along the river Las Garzas in the state of Morelos, Mexico at peak lizard activity (1300 hrs). These data represent 72 hourly transect surveys from 3 days (sunrise to sunset) each in both the wet season and the dry season. A cumulative mean density is given, as is the percent of surveys in which lizards were observed during this peak period. The range of lizard densities observed at each stations is also provided.

Transect Station	*% surveys with observed lizards*	*Mean Density ± SE (lizards/ha)*	*Min - Max Density (lizards/ha)*
Station 1	67%	2.07 ± 0.40	1.38 - 2.76
Station 2	100%	3.88 ± 1.02	1.66 - 8.32
Station 3	67%	2.44 ± 0.47	1.63 - 3.25
Station 4	83%	2.19 ± 0.34	1.37 - 2.74
Station 5	83%	2.57 ± 0.80	1.07 - 5.35
Station 6	100%	3.42 ± 0.75	1.58 - 6.32
Station 7	67%	3.63 ± 0.95	1.12 - 5.58
Station 8	33%	2.07 ± 0.00	2.07 - 2.07
Station 9	100%	11.85 ± 2.35	6.91 - 21.72
Station 10	100%	4.65 ± 0.93	1.59 - 7.97
Means	80%	4.23 ± 0.56	1.07 - 21.72

Table 2. Behavioral activities for Ctenosaura pectinata are represented as the percent of time (%) spent in each activity, the frequency of that activity (no./min.), and the duration (sec.) of each activity bout based on focal observations. The percent of time (%) spent under different degrees of solar exposure is included. Movement rate (m s^{-1}) and distance moved (m) were corrected for each movement bout. Means are presented ± 1 SE. Superscript letters (a, b) represent significantly different age/sex class means, Tukey-Kramer HSD multiple comparisons and ANOVA at $P < 0.05$.

Category	*adult male (n = 31)*	*adult female (n = 44)*	*immature (n = 9)*	*juvenile (n = 14)*	*total (n = 98)*
Behavior					
basking(%)	88.5 ± 4.4	94.8 ± 1.0	96.9 ± 0.9	87.2 ± 3.7	91.9 ± 1.6
(frequency)	0.07 ± 0.01^{a}	0.06 ± 0.01^{a}	0.08 ± 0.02^{a}	0.18 ± 0.02^{b}	0.08 ± 0.01
(duration)	1601.7 ± 234.5^{a}	1717.9 ± 227.5^{a}	1767.2 ± 532.5^{a}	332.6 ± 69.0^{b}	1461.0 ± 136.4
moving (%)	2.7 ± 0.5^{a}	3.3 ± 0.6^{a}	3.0 ± 0.8^{a}	10.7 ± 3.1^{b}	4.1 ± 0.6
(frequency)	0.14 ± 0.02^{a}	0.14 ± 0.02^{a}	0.17 ± 0.05^{a}	0.44 ± 0.11^{b}	0.18 ± 0.02
(duration)	12.9 ± 1.4^{ab}	11.6 ± 1.0^{a}	19.3 ± 3.0^{b}	17.3 ± 1.9^{ab}	13.5 ± 0.7
feeding (%)	0.3 ± 0.2^{a}	0.9 ± 0.6^{a}	0.1 ± 0.1^{a}	2.1 ± 0.8^{b}	0.8 ± 0.3
(frequency)	0.03 ± 0.01	0.07 ± 0.03	0.01 ± 0.0	0.17 ± 0.05	0.10 ± 0.03
(duration)	36.3 ± 7.3^{ab}	78.7 ± 19.1^{a}	43.3 ± 28.3^{ab}	16.8 ± 4.2^{b}	44.7 ± 8.5
reproduction (%)	0.8 ± 0.7	0.5 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.3
(frequency)	0.027 ± 0.002	0.016 ± 0.004			0.022 ± 0.003
(duration)	222.6 ± 50.4	222.6 ± 50.4			222.6 ± 50.4
social interaction (%)	7.7 ± 4.4	0.5 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	2.7 ± 1.4

(frequency)	0.10 ± 0.02[a]	0.03 ± 0.01[b]			0.06 ± 0.1
(duration)	25.5 ± 7.4	18.1 ± 3.9			23.0 ± 5.1
Exposure					
sun (%)	35.1 ± 6.7	30.2 ± 5.5	54.7 ± 15.4	47.7 ± 11.0	36.5 ± 3.9
shade (%)	19.5 ± 6.8	25.1 ± 6.1	12.2 ± 8.7	10.7 ± 7.0	20.1 ± 3.7
filtered sun (%)	37.6 ± 7.3	30.0 ± 6.0	32.7 ± 14.3	38.7 ± 9.7	33.9 ± 4.0
under clouds (%)	9.9 ± 4.6	12.8 ± 4.4	0.0 ± 0.0	1.6 ± 1.6	9.1 ± 2.5
Movement					
movement rate	0.094 ± 0.011	0.061 ± 0.006	0.055 ± 0.009	0.027 ± 0.006	0.069 ± 0.005
distance moved	1.24 ± 0.18	0.77 ± 0.08	1.58 ± 0.45	0.29 ± 0.05	0.96 ± 0.09

Table 3. Mean body temperatures for three different age classes of Ctenosaura pectinata and for all classes combined (Total). Substrate temperatures and air temperatures (at 2 cm, shaded bulb) were recorded from the location where the lizard was first observed before capture. Mean temperatures are given ± SE. Temperature ranges of active lizards are presented within parentheses.

	Body Temperature	*Substrate Temperature*	*Air Temperature*
Juvenile	34.11 ± 1.06	30.58 ± 1.16	29.91 ± 0.96
	(22.6 - 39.8)	(19.8 - 44.0)	(19.8 - 41.1)
Immature	35.19 ± 0.78	33.07 ± 0.84	31.44 ± 0.65
	(29.8 - 39.1)	(28.3 - 36.9)	(27.9 - 35.0)
Adult	35.62 ± 0.76	33.50 ± 2.01	31.37 ± 1.67
	(31.2 - 39.0)	(24.1 - 42.6)	(23.5 - 39.9)
Total	34.81 ± 0.57	31.98 ± 0.78	30.69 ± 0.63
	(22.6 - 39.8)	(19.8 - 44.0)	(19.8 - 41.1)

FIGURE LEGENDS

Figure 1. The distribution of body size (snout-vent length) within a population of Ctenosaura pectinata. Mean sizes are indicated for two subadult age cohorts (shaded) and for both adult sexes (unshaded).

Figure 2. Hourly environmental temperatures, body temperatures, and frequency of activity in Ctenosaura pectinata during both the wet and dry seasons. Lizard activity was not significantly different between seasons ($P>0.05$), therefore hourly sample data were pooled.

Figure 3. Habitat use by Ctenosaura pectinata (all sizes) recorded during hourly censuses along the canyon transect.

Figure 4. Percent of time spent in each of five habitats by all age classes and both adult sexes in the dry and wet seasons based on focal observations.

Figure 5. Daytime variation in the use of elevations by all age classes and both adult sexes of Ctenosaura pectinata and their elevational distribution in five different habitats based on spot samples.

Figure 6. Mean habitat temperatures recorded with a datalogger at 15 minute intervals during hours of lizard activity from five different habitats in the wet season. Recording periods lasted from three to seven days each.

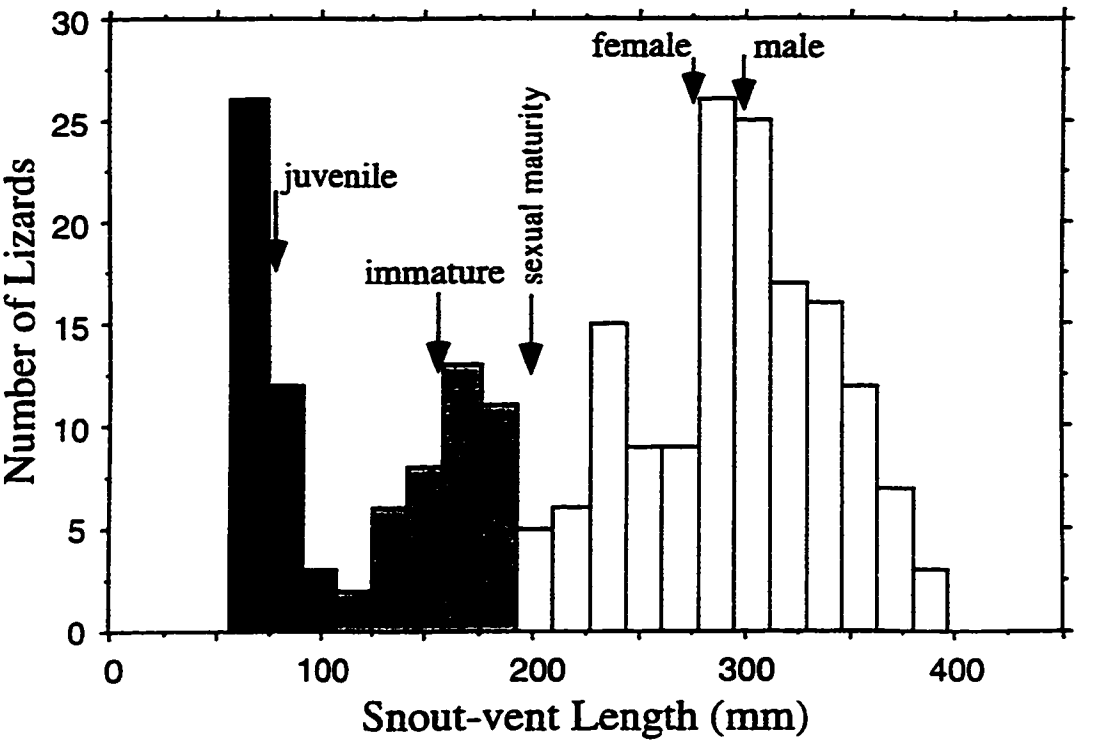
Figure 7. Regression of Ctenosaura pectinata body temperatures (from haphazard samples) against environmental substrate temperatures where lizards were first

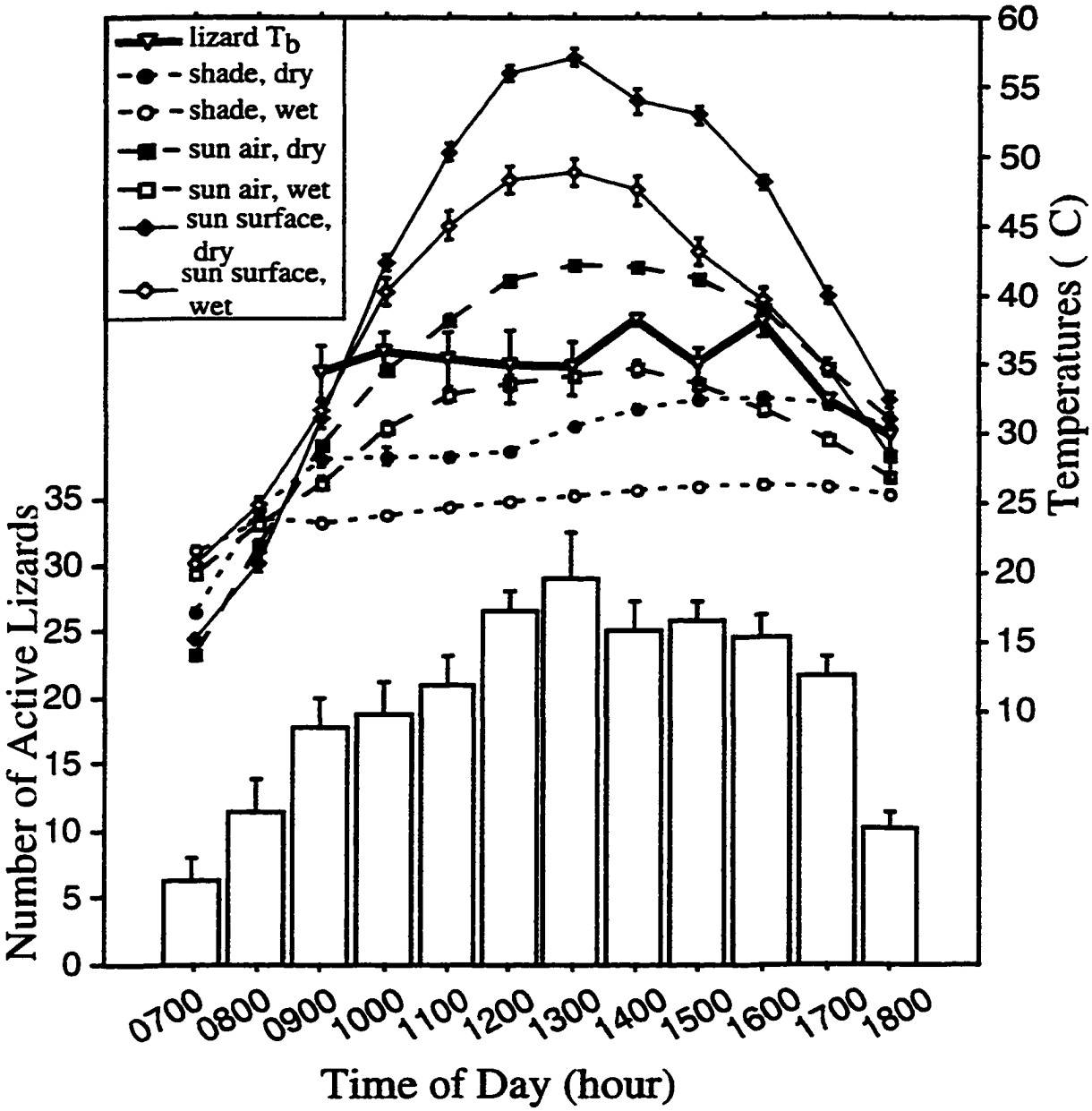
observed shows non-conformity to the slope of the isotherm, suggesting that these lizards actively thermoregulate.

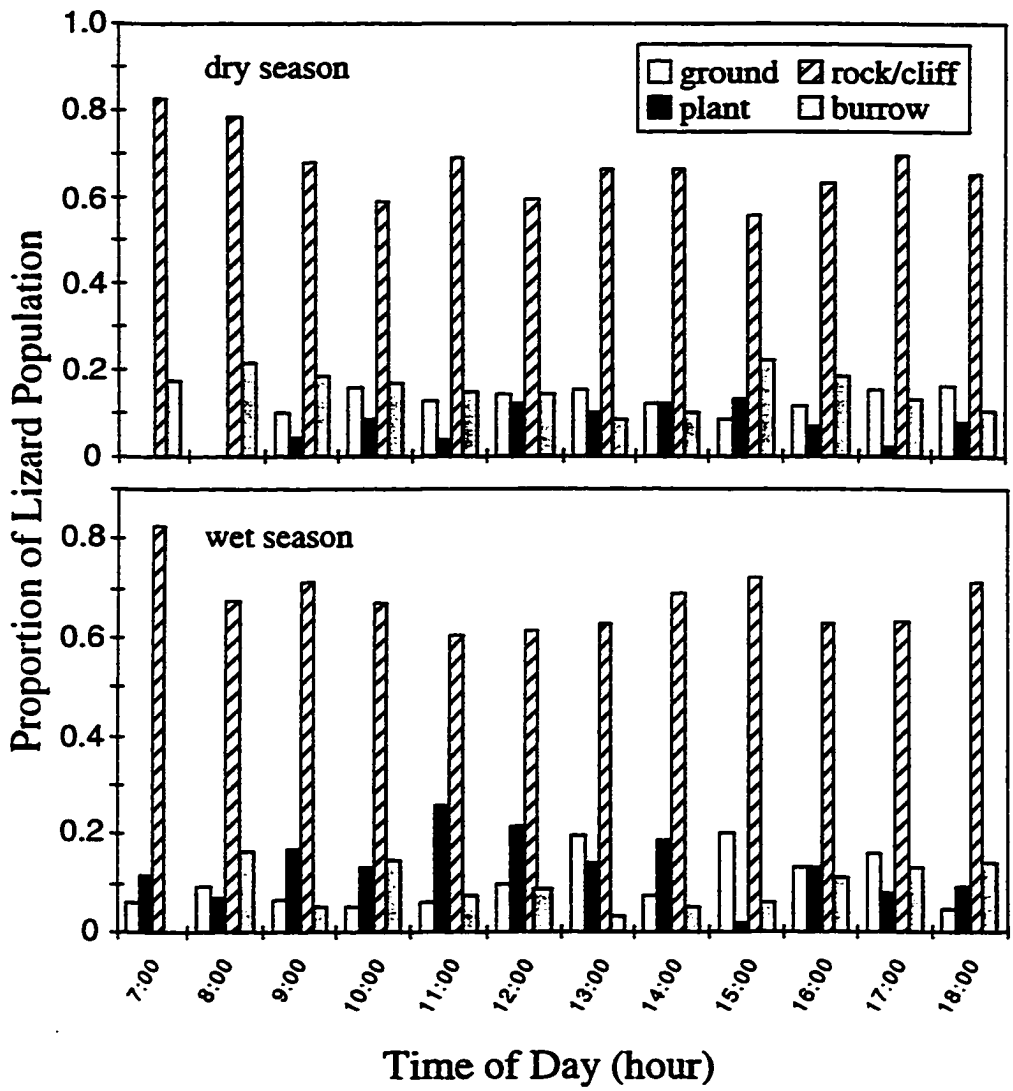
Figure 8. Percent of Ctenosaura pectinata population observed from spot samples in four different solar exposures during different periods of the day in both the dry and wet seasons. Each daytime period consists of a three hour block of time from 0700 to 1900 hours.

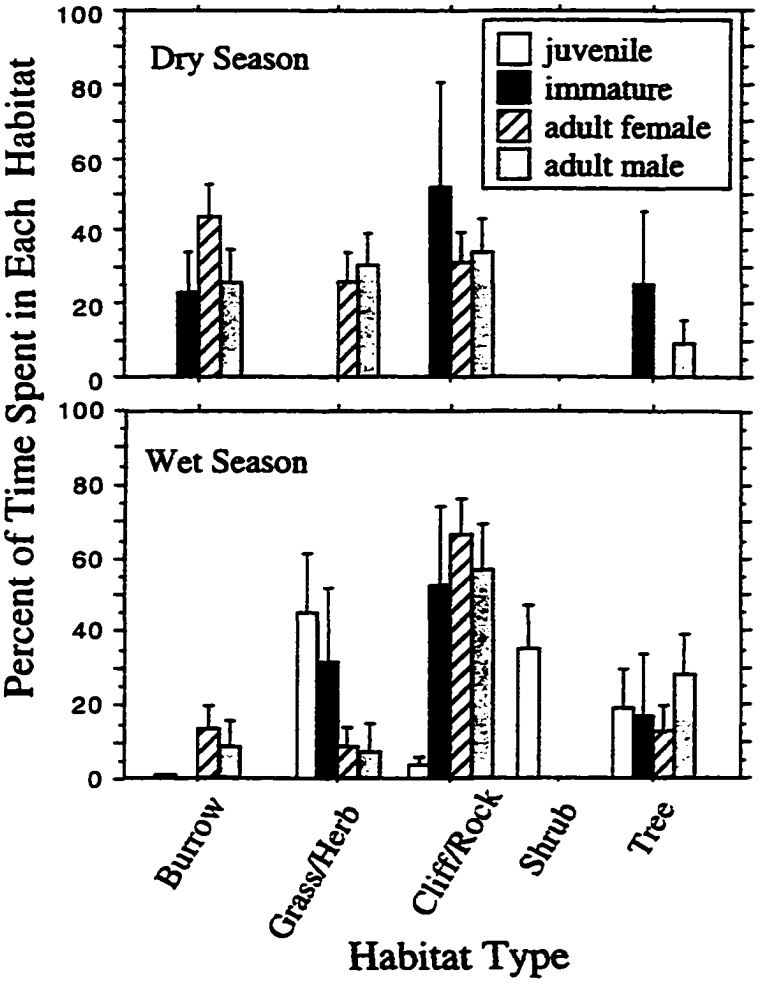
Figure 9. Model of variables proposed to influence habitat selection for optimal body temperature (Tb) in different sized ectotherms. Arrows represent either growth direction (i.e., small juvenile to large adult) or decisions (i.e., habitat choice or feeding strategy) which can lead to the optimal body condition (i.e., juvenile = increased growth rates, adults = increased reproductive success). Small individuals use plant habitats where they can maintain optimal T_b through low thermal inertia and shuttling in a thermal mosaic. Vegetation also offers cover against predators and a source of insect foods. Insectivory and increased foraging time allows small individuals to increase in body size. With an increased body size, large individuals may not be able to reach and maintain optimal T_b in plant habitats and may be restricted to open habitats where they can easily gain heat. Accessibility of heat and increased body size allows large individuals to do well as herbivores where increased basking would maximize digestive performance and lead to an increased body condition . Plant habitats could be used by large individuals for food sources just as open habitat could be used by small individuals for thermoregulation.

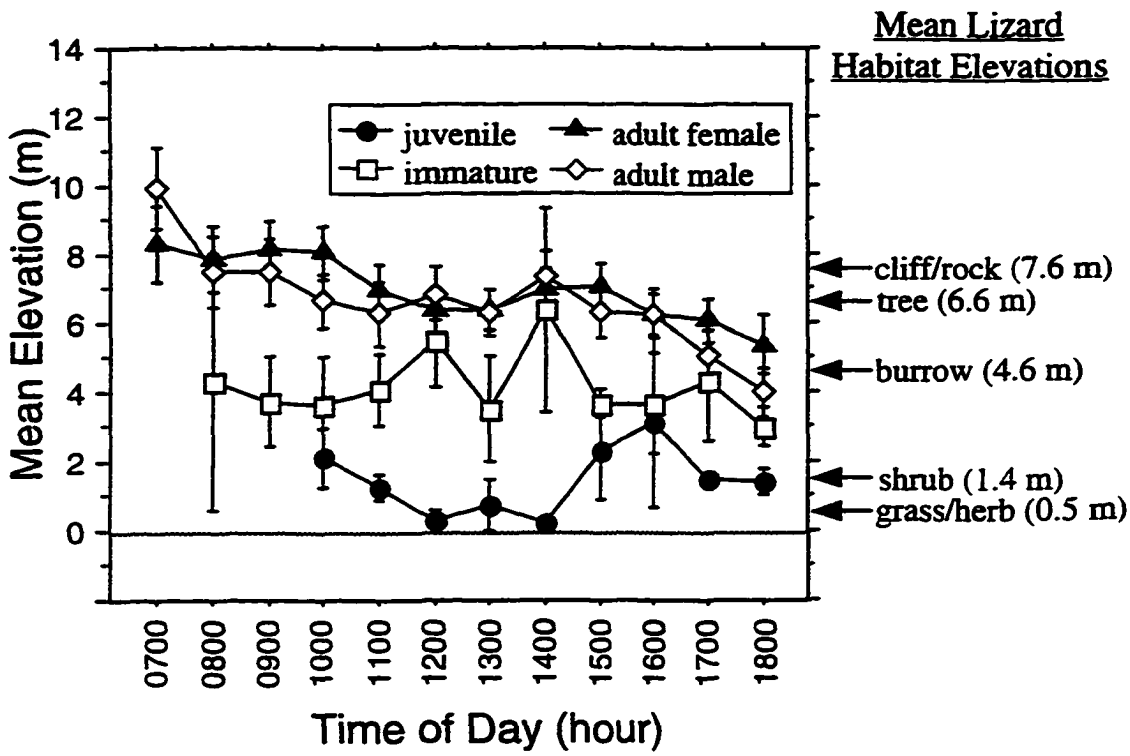
Similarly, juveniles could feed on plants if insects are scarce and adults could feed on insects if they are common. (See discussion for the assumptions of this model)

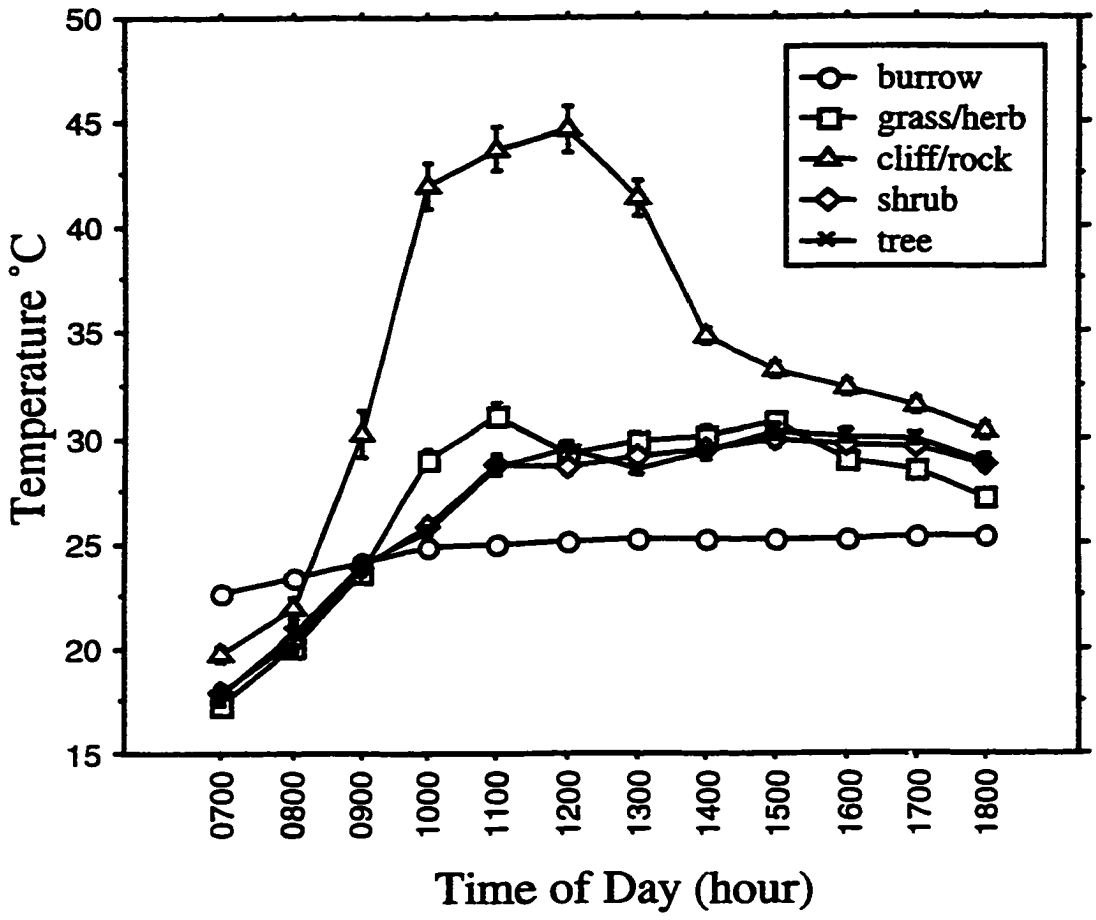

30
25
20
15
10
5
0
Number of Lizards
female
male
juvenile
immature
sexual maturity
0
100
200
300
400
Snout-vent Length (mm)

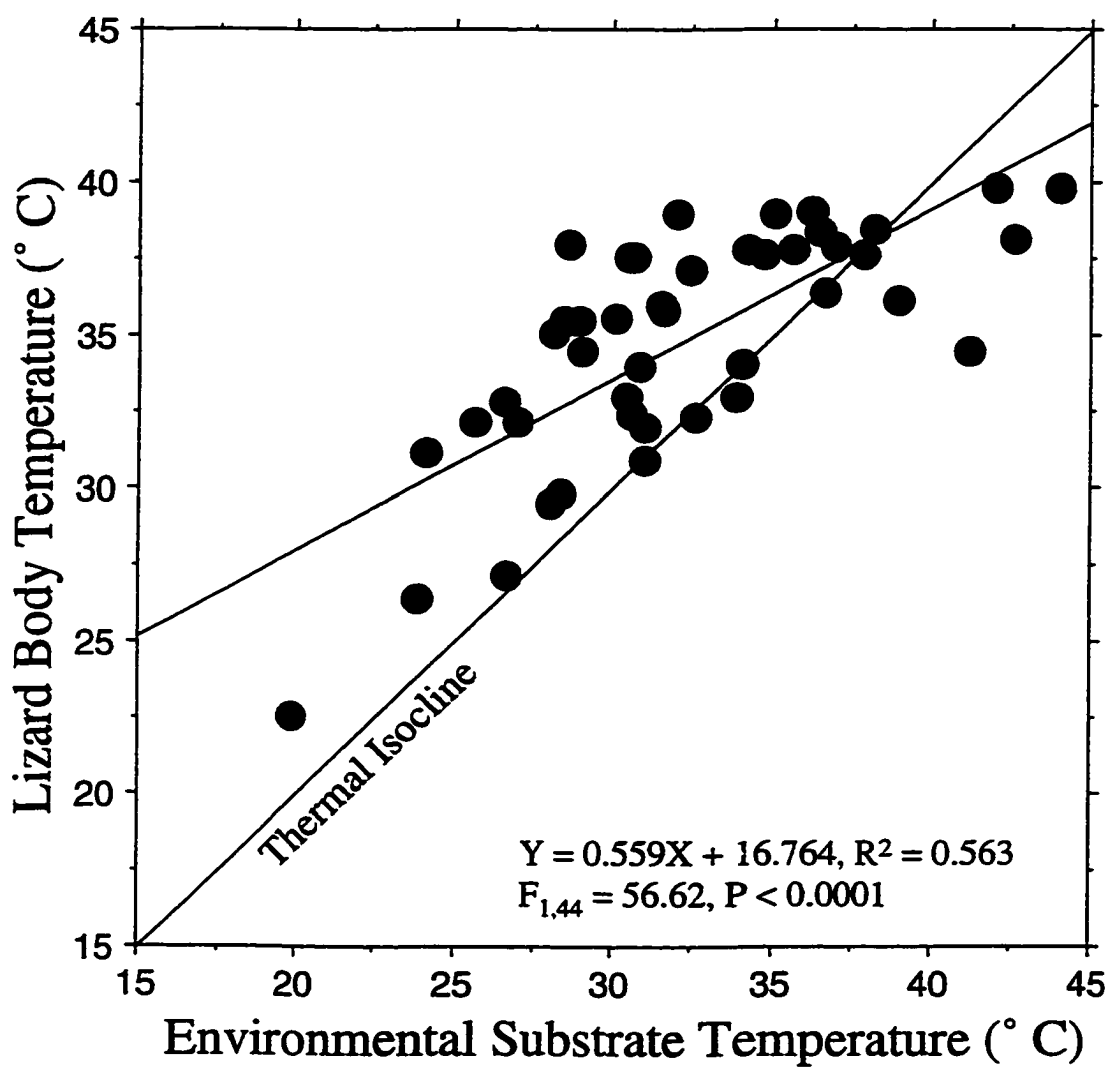

lizard T_b
shade, dry
shade, wet
sun air, dry
sun air, wet
sun surface, dry
sun surface, wet
Number of Active Lizards
Temperatures (C)
Time of Day (hour)
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800

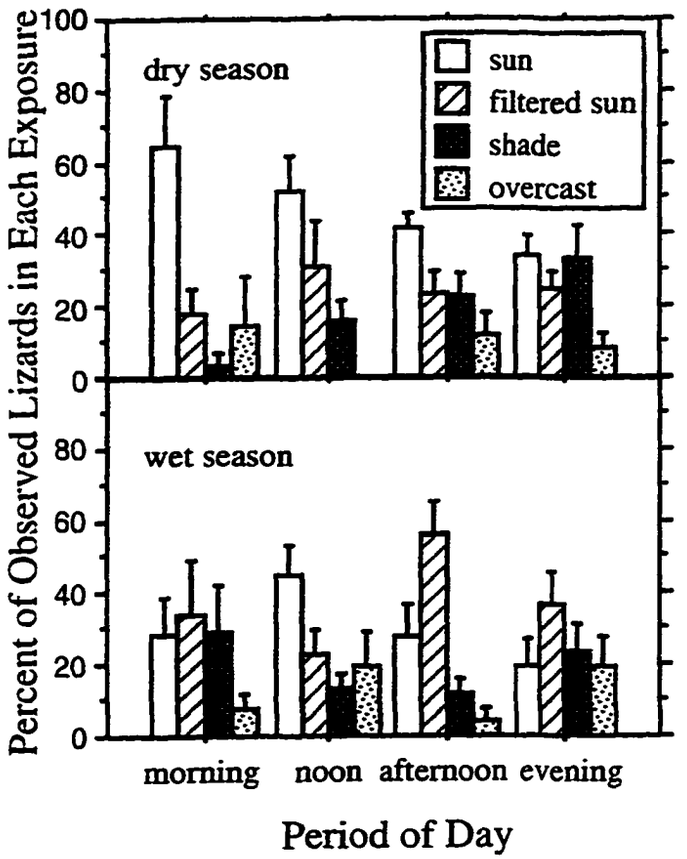

dry season
wet season
ground
rock/cliff
plant
burrow
1.0
0.8
0.6
0.4
0.2
0
Proportion of Lizard Population
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
Time of Day (hour)

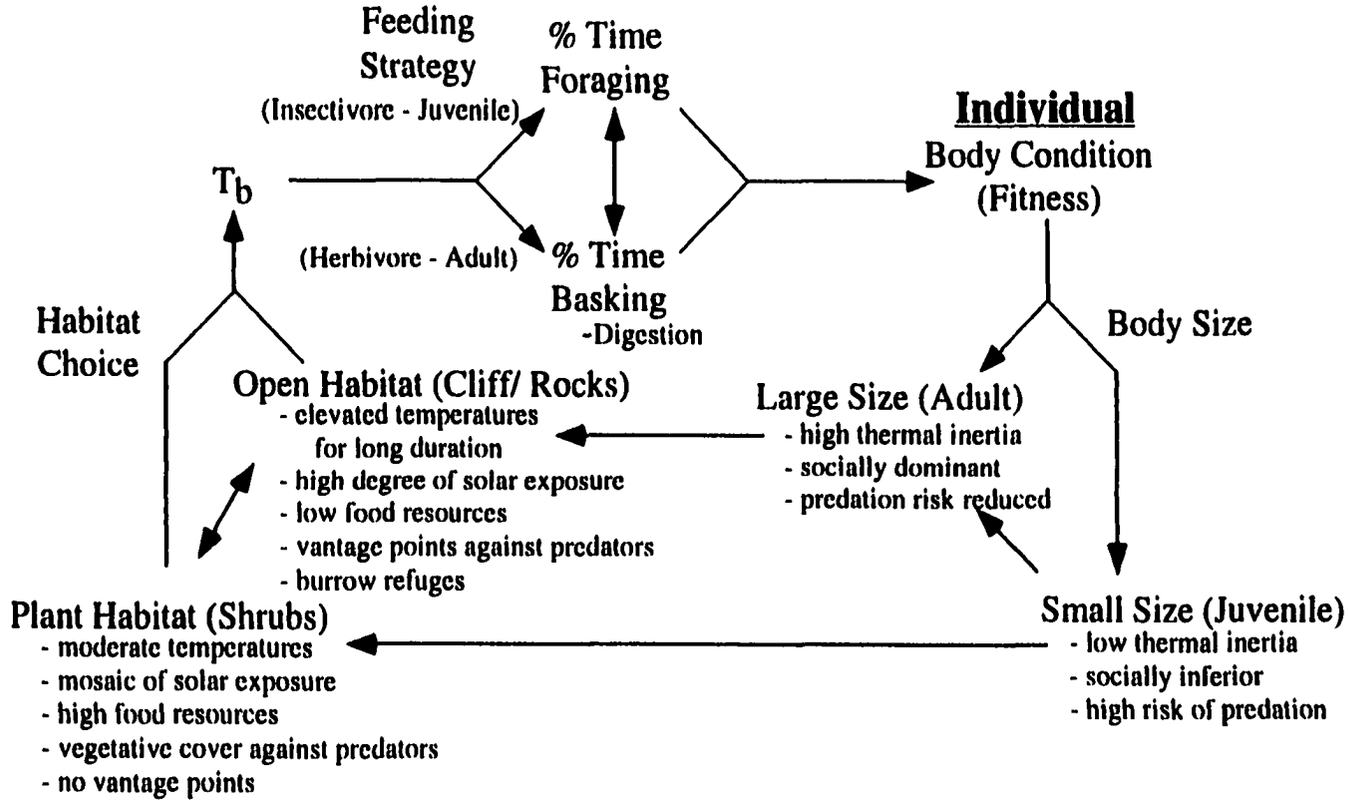

Dry Season
Wet Season
juvenile
immature
adult female
adult male
Percent of Time Spent in Each Habitat
100
80
60
40
20
0
Burrow
Grass/Herb
Cliff/Rock
Shrub
Tree
Habitat Type


Mean Lizard Habitat Elevations
juvenile
adult female
immature
adult male
Mean Elevation (m)
14
12
10
8
6
4
2
0
cliff/rock (7.6 m)
tree (6.6 m)
burrow (4.6 m)
shrub (1.4 m)
grass/herb (0.5 m)
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800
Time of Day (hour)


burrow
grass/herb
cliff/rock
shrub
tree
Temperature °C
50
45
40
35
30
25
20
15
0700
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
1800
Time of Day (hour)


Lizard Body Temperature (° C)
Environmental Substrate Temperature (° C)
Thermal Isocline
Y = 0.559X + 16.764, R2 = 0.563
F1,44 = 56.62, P < 0.0001
15
20
25
30
35
40
45


Percent of Observed Lizards in Each Exposure
100
80
60
40
20
0
dry season
sun
filtered sun
shade
overcast
wet season
morning
noon
afternoon
evening
Period of Day


Feeding
Strategy
(Insectivore - Juvenile)
% Time
Foraging
Individual
Body Condition
(Fitness)
T_b
(Herbivore - Adult)
% Time
Basking
-Digestion
Habitat
Choice
Body Size
Open Habitat (Cliff/ Rocks)
- elevated temperatures
for long duration
- high degree of solar exposure
- low food resources
- vantage points against predators
- burrow refuges
Large Size (Adult)
- high thermal inertia
- socially dominant
- predation risk reduced
Plant Habitat (Shrubs)
- moderate temperatures
- mosaic of solar exposure
- high food resources
- vegetative cover against predators
- no vantage points
Small Size (Juvenile)
- low thermal inertia
- socially inferior
- high risk of predation

Ontogenetic Variation in Digestion of Various Diets in an Herbivorous Lizard (*Ctenosaura pectinata*)

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Running header: Ontogeny of digestion in an herbivorous lizard

ABSTRACT

I tested the hypothesis that in an animal with an ontogenetic diet shift, the digestive efficiencies of different foods correspond to this diet shift, so nutrient and energy extraction are maximized. The iguanid lizard Ctenosaura pectinata undergoes an ontogenetic diet shift from eating insects as juveniles to plants as adults. When fed six different pure foods from the natural diets of different age classes, the assimilation of nutrients and energy by C. pectinata differed depending on food type and age class of lizard. Extraction of energy and nutrients in insect larvae were maximized by juvenile lizards. Calcium, phosphorus, and energy were readily assimilated from flowers and fruit by immature and adult lizards. Magnesium levels were highest in leaves and were extracted by immature and adult lizards, but xenobiotic effects of one plant leaf (Croton suberosus), eaten by adults, killed juvenile lizards. Although juvenile C. pectinata ate some flowers (Senna wislizenii) naturally, they were less efficient at digesting cell walls from these plant parts than were older lizards. Ontogenetic changes in ctenosaur digestive physiology were not the result of a tradeoff involving ecological costs of foraging efficiency, but rather, each age class preferred a diet that maximized its physiological benefit.

Introduction

Increasing attention has been focused on the nutritional ecology of herbivorous ectothermic vertebrates and their ability to procure and digest plant foods (Horn 1989; Troyer 1991; Bjorndal 1997). Endothermic herbivores (mammals and birds) digest plant fiber by fermentation, with the aid of microbes housed either anterior or posterior to the main site of gastric digestion (foregut and hindgut fermenters, respectively). Herbivory in reptiles is confined to a few turtles and lizards, which employ hindgut fermentation (but see Bjorndal and Bolten 1990). Despite potential limitations of physiological performance associated with ectothermy, some of these reptiles achieve digestive efficiencies similar to those of ruminant mammals (Bjorndal 1979; Troyer 1984; Karasov et al. 1986).

The family Iguanidae is unique among lizards because all species are herbivorous as adults. Fermentative breakdown of plant fiber occurs in the proximal hindgut (colon) in these lizards. The enlarged colon accommodates fermentation and is modified by transverse septa to facilitate plant fiber digestion by slowing passage rates of digesta (Iverson 1982). Microbes and protozoans in the colon break down plant fiber, and thin colon walls uptake end products of fermentation, like short-chain fatty acids (McBee and McBee 1982; Troyer 1991; Bjorndal 1997). Nematodes are abundant at the site of fermentation and likely participate in digestion (Nagy 1977, Iverson 1982; Bjorndal 1997).

The nutritional content extracted from plant materials by ectothermic vertebrates is often dependent on the temperature at which digestion takes place, size of food

particles eaten, degree of plant fiber in plant parts, and body size of the herbivore. Increased body temperatures decreased food passage rate in iguanid lizards (Zimmerman and Tracy 1989; van Marken Lichtenbelt 1992) or increased assimilation efficiency (Troyer 1987). Both effects, whether functioning independently or in concert, yield increased rates of nutritional gain with increased body temperature. Plant parts and plant species vary in their percentage of plant fiber. Nutrients can be extracted from cell contents, but unless fermentation of plant fiber takes place the carbohydrate energy locked in cell walls will pass through the system without being extracted.

Proteins, crucial for growth, tend to be limiting in herbivorous diets because of their low abundance in plant compared to animal tissue (Mattson 1980). The crude protein available in plants is assimilated by herbivorous lizards in direct proportion to its occurrence in the plant food (van Marken Lichtenbelt 1992). Under the demands of growth, juvenile herbivorous lizards compensate for lower plant nitrogen levels by eating the parts of a plant that contain the most protein (Troyer 1984).

Large–bodied lizards have been thought to be obligate herbivores because energy balance can not be maintained foraging on small arthropod prey (Pough 1973). Although it was predicted that smaller lizard species or juveniles of large herbivorous species should not eat plants, many studies document that herbivory extends well into the small body size range of many lizards, including most juveniles of large herbivorous iguanids (examples cited below).

Efficient extraction of energy from plant fiber depends on fermentation, including an extended retention time of plant fiber and a chamber for microbes that break down

cellulose. Fermentation of food particles increases with a decrease in the particle size and rate of particle passage through the region of fermentation. Larger individuals have larger colons where much plant fiber can be broken down via fermentation. Smaller species and juveniles of larger species may not have the volumetric capacities required for processing a plant diet. Yet most juvenile iguanid lizards and several other small lizards are herbivorous (Auffenberg 1982; Troyer 1984; Mautz and Nagy 1987; Schall and Ressel 1991; Troyer 1991; Wikelski et al. 1993; Durtsche 1995). These lizards may not rely heavily on fermentation of plant fiber but may, instead, extract nutrients and cell contents by consuming low-fiber plant foods and by passing these foods at a faster rate than larger individuals. Several components contribute to the value of a plant food (either by species or plant part), including: 1) protein and energy contents, 2) proportion of plant fiber, 3) consumer's capacity for fermentative fiber digestion, 4) availability of the food item in the environment, and 5) assimilation and utilization potential for the food. The value of a particular food item may change with size of the herbivore, its nutritional needs for growth, and its capacity for fermentative digestion of plant fiber.

Two species of Ctenosaura are atypical iguanid foragers because they consume insects as juveniles and switch to plant foods as adults (Van Devender 1982; Durtsche unpublished data). This ontogenetic diet change presents several questions about factors affecting food selection based on the digestive capacity of different size classes and nutritional requirements for growth. In these animals with an ontogenetic diet shift, do digestive efficiencies of different foods correspond to this diet shift such that nutrients (e.g., protein, macrominerals) and energy assimilation are maximized? Are ctenosaurs

under nutrient (e.g., macromineral) constraints or does the ratio of nutrients in the diet regulate nutrient uptake? With plants as the adult diet, do these lizards have resistance to plant toxins? I examined digestibilities, nutritional uptake, and transit times of several different food classes (flowers, fruit, leaves, and insects) by three different age (size) classes of Ctenosaura pectinata. I selected dominant foods from the diets of all age classes from both the wet and dry season diets. Leaves and insects were not abundant (environmentally or in the diet) in the dry season, so those were fed as wet season foods. Insects were also the dominant food of the juvenile age class and juveniles were only represented as an age class in the wet season. The main flower eaten in each season was used as a test food. Also, to complete the broad category of plant foods eaten by these lizards, a fruit pod consumed in the dry season was included in feeding trials. Gut capacity scales in direct proportion to body size in this species (Durtsche unpublished data). Therefore, a null hypothesis of "no difference" in assimilation efficiencies (both energetic and nutritive) would be predicted. An exception on an energetic basis would be if increased absolute gut capacity increases the potential for fermentation. I assumed that all individuals had established gut microbes for fermentation.

Material and Methods

Feeding studies

Ctenosaura pectinata used in these feeding studies were captured by hand, noose, or live trap (Tomahawk ™) from a population in the state of Morelos in Central Mexico (18°

36' N, 98° 43' W). Captured lizards were weighed with Pesola™ spring balances to the nearest 0.5 g if under 100 g, 1.0 g if under 1000 g, and 10.0 g if over 1000 g. Lizards were housed individually in plastic containers. Three containers sizes (5.6 liter, 11.3 liter, 28.3 liter) were used for juvenile, immature and small adult, and large adult ctenosaurs, respectively. A screen false bottom was installed in each container so that feces and urates could be collected. Mosquito screen covered air vents to prevent dung-eating insects from entering. Water was provided ad libitum. Foods used in feeding trials were major components of natural ctenosaur diets (R. D. Durtsche, unpublished data), fed as pure diets. These foods included: Senna wislizenii flower (wet season), Coursetia glaudulifera fruit (dry season), Coursetia glaudulifera leaf (wet season), Haematoxylon campechianum flower (dry season), Croton suberosus leaf (wet and dry season, fed in wet season), and eruciform insect larvae (Lepidoptera: Noctuidae: Spodoptera frugiperda) (wet season). These foods were fed to two subadult cohorts (juveniles and immatures) and adult lizards. Juvenile and immature cohorts were defined by body size ranges of 4.5 - 28 g and 35 g to 200 g, respectively, and adults were greater than 200 g (R. D. Durtsche, unpublished data). Juveniles were only present as an age class in the wet season.

Lizards were force fed these pure diets, allowing an accurate measure of food consumption rates. The size dimensions of food given to the lizards were adjusted to mimic that found in the natural diet within each age class. Leaves and fruit were torn or broken to approximate bite size pieces. Pure diets (wet mass) were weighed, moistened in water, and inserted into the esophagus of the lizard with long forceps. A syringe (range 10

- 60 cc) with the end cut off was used as a delivery tube to transfer the foods to the esophagus while the mouth was held open.

Food intake levels were calculated from a modified version of Nagy's (1982) required food intake rates for field active herbivorous and insectivorous lizards based on lizard mass where:

mg of dry plant food ingested/day = 24 $g^{0.8}$

and

mg of dry insect food ingested/day = 12 $g^{0.8}$

where g = lizard body mass in grams. These rates are based on the assumptions that on average, plants contain 17 kJ/g dry mass and insects contain 23 kJ/g dry mass. Assuming that an herbivorous lizard metabolizes approximately 55% of a plant diet, plant foods represent an effective 9.4 kJ/g dry mass (Nagy 1982). Similarly, to the average insectivorous lizard that metabolizes about 80% of an insect diet, insect foods represent an effective 18.4 kJ/g dry mass (Nagy 1982). Diets were scaled down slightly because Nagy's calculations were based on field active lizards and ctenosaurs in these feeding experiments were primarily sedentary in containers. Lizard body mass was monitored throughout the experiment and adjustments were made to food level so that body mass did not change more than ±1% per day.

Feces and urates (uric acid) separated by the false bottoms of the housing containers were collected daily and air dried in a cloth covered container exposed to the sun. Fecal and urate samples were later dried to a constant mass (24 h minimum) in a drying oven at 60° C.

Unlike other nutritional studies in which lizards were maintained at constant temperatures in artificial conditions, these feeding experiments were carried out under field conditions. Containers were kept under shade and filtered sun exposures during the day. Daily minimum and maximum temperatures were measured at random throughout the different containers during the experimental feeding periods.

Food Passage Rates

Food passage rate was determined using foods marked with chromium (Cr^{-3}) that binds to indigestible plant fiber (Uden et al. 1980) or a non-digestible fluorescent powder (polyacrylamide beads - Waldschmidt et al. 1986). Both markers were assumed to move at the same rate as structural components of the diet. Soluble material was removed from plant fiber by washing with sodium lauryl sulphate and thoroughly rinsing with water before forming a complex with chromium. The plant fiber mordant was prepared by cooking the plant fiber in a solution of 14% hexavalent chromium ($Na_2Cr_2O_7$) to fiber weight at 100° C for 24 h. Fiber mordant was then rinsed in water, soaked in an ascorbic acid solution (one-half fiber weight) for at least 1 h, and rinsed again. Soaking in ascorbic acid reduces toxic hexavalent chromium to non-toxic trivalent chromium. The fluorescent powder was injected into the insect larvae with a 5 cc syringe and used with some of the plant foods. Marked foods were fed to individual lizards one to two days after feeding began with unmarked pure diets. Presence of chromium in feces was determined by spectophometric analysis after fecal subsamples had been digested (described below). Trivalent chromium in aliquots (25 ml) from fecal digest were first oxidized to hexavalent

chromium in the presence of potassium permanganate and heat before reacting with diphenylcarbazide to produce a reddish purple color (Taras et al. 1971). Chromium concentration from fecal samples was then determined by comparison against a standards calibration curve (5 to 400 µg / l Cr) using a Hach™ DR2000 spectrophotometer at 540 nm wavelength and a 1 cm flow-through cell. Fluorescent powder in feces was easily detected with a dissecting microscope. Mean transit time was determined by the peak occurrence of chromium in the feces or the average time between first and last appearance of fluorescent powder in the feces. Feeding trials lasted a minimum of 8 days (mean = 12 days) with the exception of Croton suberosus leaves in the case of juvenile lizards (see Results).

Nutritional Analyses

Food, feces, and uric acid samples from pure diet feeding trials were separated for energetic and nutrient analyses. Samples were redried before analyses at 60° C. Food and feces were ground to a small particle size (ca. 1mm) and homogenized in a Waring™ blender/grinder. Small fecal samples and uric acid samples were pulverized separately in a mortar and pestle. Mass of samples and subsamples was determined on a Sartorius™ electronic balance at 0.001g accuracy. Dry matter component of pure diets were determined as percent of wet mass. Moisture remaining in samples beyond air-drying was extracted through oven-drying at 135° C for 2 hrs. Percent organic matter in samples was determined by ashing a subsample of homogenized material in a muffle furnace at 550° C for a minimum of three hours. Plant fiber determination was made with both neutral

detergent-fiber (NDF = percent cell wall constituents) and acid detergent-fiber (ADF = lignocellulose) analyses from fecal and plant food subsamples. Procedures of detergent-fiber analysis followed the Van Soest technique (Goering and Van Soest 1970) as modified according to Hach (1990). Energy content of food, feces, and urates was determined using bomb calorimetry with a Parr® (Moline, IL) semimicro oxygen bomb calorimeter. Subsamples (0.25 g) of food and feces were digested in a Hach™ (Loveland, CO) Digestahl® digestion apparatus at 440° C for four minutes using concentrated sulfuric acid followed by the addition of hydrogen peroxide (50%) and distilled water. Total digest time was approximately 10 min per sample. The resultant digests were used in a battery of nutrient analyses.

Chemical analysis of digests were used to determine nutrient composition of individual samples (Hach 1990). A Hach™ (Loveland, CO) DR2000 spectrophotometer with a pour-thru cell system was used in all chemical nutrient determinations. Calibration for each nutrient was established with a set of standard solutions. Total Kjeldahl nitrogen was determined using a Nessler test and crude protein in the sample was calculated as:

$$\% CP = \%N \times 6.25$$

where CP = crude protein and N = nitrogen. Accuracy of the protein analysis and the digestion procedure was established by digesting three different primary standard compounds of varying digestion resistance. The resistance of these nitrogen containing compounds varied from ammonium p-toluene sulfonate (no digestion required) to glycine p-toluene sulfonate (moderately easy to digest) to nicotinic acid p-toluene sulfonate (difficult to digest). Digests of these primary standards were subsequently 100%, 98%,

and 89% accurate, respectively. Digestion time in sulfuric acid was adjusted to 4.5 min. to increase extraction accuracy for difficult nutrients. The additional nutrient analyses of the percent phosphorus, calcium, magnesium, and potassium in digest samples followed the Hach™ procedures for feed and forage analysis (Hach 1990). These nutrients were chosen for analysis because they represent the mineral elements or macrominerals essential in the largest quantity to the diet of many animals (Pond et al. 1995). Both calcium (Ca) and phosphorus (P) are required as structural components for the maintenance and production of skeletal material. The ratio of Ca–P must remain in balance for animals to retain each of these elements as structural components (Frye 1997). Magnesium (Mg) is used in skeletal structure and for enzymatic activity. Potassium (K) has many functions in the body from maintaining cell membrane potential and osmotic equilibrium to aiding control of blood pressure and flow. Because plants have such high concentrations of K, herbivores tend to minimize potassium intake (Mickelson and Christian 1991).

Digestibility Calculations

The assimilation efficiencies of different age/sex classes of C. pectinata for nutrient components of the six food types tested were calculated with the equation:

([consumption of X - output of X in feces]/ [consumption of X]) x 100

where consumption and output of the dietary component X (nutrient, plant fiber) are measured in grams. Consumption and output were calculated as the mean daily intake and fecal product from the duration of the feeding trial. Plant fiber intake and digestion

samples were ash-corrected and thus organic material and not dry matter values were used in these assimilation calculations.

The metabolizable energy coefficient for each food type was calculated with the equation:

([consumption of Y - output of Y in feces - output of Y in uric acid]/ [consumption of Y]) x 100

where consumption and output (Y) represent the energetic value (kJ/g) of food, feces, and urates. Ash-corrected values were also used in these calculations to limit metabolizable energy to organic matter contents.

Due to low sample size, analysis of variance between the different age/sex classes was carried out with a Kruskal-Wallis non-parametric test. These and other statistical tests were made with Statview 4.5 for Macintosh (Abacus 1996). Significance for all analyses was at $\alpha = 0.05$.

Results

Diet Composition

The six natural dietary food items examined in these feeding trials varied substantially in their energetic and nutritional content (Table 1). All foods had a high percent of organic matter, although leaves contained more minerals and inorganic salts than other foods. Insect larvae had higher percentages of water, energy, crude protein, and phosphorus than did plant matter. Flowers of Senna wislizenii had the largest proportion

of protein of all plant parts tested. Both flowers and seed pods had calcium levels comparable to those in eruciform larvae. Leaves did not contain large percentages of calcium, but had the highest levels of magnesium of any food tested. Fiber content varied among plant parts, with seed pods containing the most fiber. Flowers had the least fiber content with the lowest ADF values indicating the smallest amount of lignified cellulose.

Nutritional Acquisition

The mean passage rate for all foods by C. pectinata was 4.4 ± 0.17 days. Juvenile lizards passed food faster than other age classes (Table 2). The transit time of insects was the longest of all food types tested ($\bar{x}$ = 5.6 ± 0.4 days). Passage rates in herbivorous reptiles are sensitive to changes in body temperature (Zimmerman and Tracy 1989). The mean maximum and minimum cage temperatures ($\bar{T}_{max}$ = 37.2 ± 0.7 °C and $\bar{T}_{min}$ 18.4 ± 0.2 °C, respectively) during this field study fell within the natural range of temperatures experienced by free-ranging lizards ($\bar{T}_b$ = 34.8 ± 0.6 °C, R. D. Durtsche, unpublished data).

Lizards maintained a relatively constant body mass on all food types tested but differed in the acquisition of various nutrients and energies from these foods (Table 2). Mean daily body mass of lizards fluctuated < 1.5% of the initial feeding trial body mass. The largest daily proportional changes in body mass were in subadults (range 0.5 - 1.4%). The juvenile age class was restricted to the wet season and thus was not tested on Haematoxylon campechianum flowers or Coursetia glaudulifera fruits found only in the dry season. Four of the 5 juveniles fed Croton suberosus leaves were found dead within 8

hours of the feeding. Because of this plant's xenobiotic effects, no further feeding attempts were made with juveniles. Ctenosaura pectinata had the highest percentages of organic matter assimilation for fruit (C. glaudulifera 79.8 ± 2.2 %) and flowers (Senna wislizenii 78.0 ± 2.2 % and Haematoxylon campechianum 73.5 ± 1.7%). The metabolizable energy gained from these natural foods was highly correlated with the proportion of organic material assimilated ($R^2 = 0.85$, $F_{1,91} = 550.4$, $P < 0.0001$; Fig. 1).

Age classes did not differ in assimilation of organic material on any diet, with the single exception that juveniles assimilated significantly more organic matter from an insect diet (eruciform larvae, Table 2) than did other age classes. Moreover, juveniles were more efficient at metabolizing the energetic component of insects than were older ctenosaurs. In fact, the ability to metabolize energy from insect larvae has a decreasing trend with an increase in body size with large male lizard having the lowest mean energy extraction on this food.

Crude protein was assimilated to the greatest extent with diets of insect larvae ($\bar{x}$ = 73.1 ± 2.6%) and S. wislizenii flowers ($\bar{x}$ = 66.8 ± 2.8%) that contained the highest crude protein values of any food tested. Ctenosaurs increased their assimilation of crude protein with increased proportions of protein in the diet (Fig. 2). Most lizards digested 35-75 % of the crude protein available. Juveniles had significantly higher digestion of higher protein foods than did other age classes and assimilated a significantly higher proportion of protein from insect larvae than other age classes (Table 2). Although adults were relatively uniform in ability to digest protein from various foods, adult females

digested significantly more protein than adult males when fed S. wislizenii flowers (Table 2).

Cell wall digestion of plant foods was evident from all age classes to varying degrees. Juvenile breakdown of cell walls (NDF) was significantly less than immature or adult lizards fed the same food (S. wislizenii, Table 2). This difference among age groups may exist for other plant foods but a lack of juvenile fecal samples from feeding trials did not permit this examination. Similar limitations in fecal samples resulted in limited tests for immature lizards. Immature ctenosaurs digested plant materials nearly as well as adults. Ctenosaurs were much more efficient at digesting the cell wall contents and cellulose of C. glaudulifera fruit pods in the dry season than they were with the leaves in the wet season. The coefficient of variation for fiber digestion (CV = 0.35) reflected the variability among the different plant types, suggesting individual variation both within and among age groups.

Macromineral Assimilation

The apparent assimilation of mineral elements by C. pectinata varied depending on the mineral concentrations and ratios of these elements within the diets, and the age/sex class of the lizard (Table 3). Subadults assimilated a significantly higher proportion of Ca than did adults and lost relatively less P on foods with high mineral values (e.g., S. wislizenii flowers, eruciform larvae; Table 1). Phosphorus assimilation increased in most lizards with an increase in the Ca–P ratio for the foods tested ($R^2 = 0.18$, $F_{1,81} = 17.98$, $P < 0.0001$; Fig. 3). Only juveniles retained a constant assimilation efficiency for P among

all diets. Other age classes actually experienced a net loss of P when the Ca–P ratio dropped below 6:1. Calcium assimilation for all lizards but adult females remained relatively constant near 70% for diets with varied Ca–P ratios. Adult females increased their assimilation of Ca with an increase in the Ca–P ratio ($R^2 = 0.38$, $F_{1,28} = 17.38$, $P = 0.0003$).

Juveniles fed insects assimilated a higher proportion of Mg than other age classes (Table 3). Immatures and adults both lost Mg (net) on an insect diet. Adults varied significantly in Mg digestibility when eating S. wislizenii flowers with females assimilating more than either adult males or immatures. Potassium assimilation only varied among age classes on the insect diet where assimilation efficiency decreased with age or size of the lizard.

Discussion

Ontogenetic diet shifts from insects to plants in Ctenosaura pectinata were accompanied by changes in the digestive physiology between small juveniles and large adults. Juveniles had reduced digestibilities of some plant organic matter when compared to other age classes. However, on an experimental diet of insect larvae, which most closely approximated their natural diet, juveniles assimilated significantly more energy (on a percentage basis) than other age classes. Juveniles were over 25% better at assimilating energy from insects than the largest adults (males). The largest ctenosaurs (adult males)

had reduced energy extraction on this food. Organic material assimilated and energy metabolized were highly correlated (Fig 1).

Protein is a major nutritional component as a source of amino acids required for growth in juveniles (Stevens and Hume 1995). Eruciform larvae had the highest energy content (22.5 kJ/g) and percentage of protein (51%). Juveniles were significantly better at assimilating protein from these insects than from any other food source, and their assimilation efficiency was greater than that of any other age class on the same diet (e.g., 20% better than adults). Juveniles also had high protein assimilation efficiencies from Senna wislizenii flowers, which were the primary plant foods consumed by this age class (R. D. Durtsche unpublished data). Senna wislizenii is a legume, which in general contain more nitrogen than other plants as a result of nitrogen-fixing bacteria associated with root nodules (Bidwell 1979). Although all plants tested except C. suberosus were also legumes, S. wislizenii flowers had the highest protein (Table 1). Adult females were significantly better than adult males at assimilating protein from these flowers. Not surprisingly, these flowers made up close to 50% of the natural diet of adult female C. pectinata while constituting a much smaller portion (≈ 18%) of the adult male diet (R. D. Durtsche unpublished data).

The amount of plant fiber in the diet can affect the digestibility of a food source (Bjorndal 1997). Throckmorton (1973) reported an energetic digestibility coefficient of 86.3% for adult C. pectinata fed a low fiber (2.5%) food of sweet potatoes. Natural diet plant foods used in this study contained high cell wall content (NDF = 39 - 61%, Table 1). Still, C. pectinata had high metabolizable energy coefficients on these foods (ca. 75%

for adults fed flowers and fruits, Table 2). These high values were the result of cell wall digestion (up to 75% on flowers and fruit) by these adult lizards. Low digestibilities of lignocellulose (ADF) in Coursetia glaudulifera leaves suggest that the fiber in these leaves was highly lignified. Immature C. pectinata digest cell wall components as efficiently as adults, verifying that any ontogenetic shift in capacity to digest plant fiber is completed by this immature stage. Juveniles were able to digest plant fiber in S. wislizenii flowers, but were significantly less efficient than other age classes. Juveniles may rely more on the digestion of cell contents (soluble proteins, carbohydrates, lipids) than cell wall fermentation for energy assimilation from plants. Because the food particles fed to juveniles were smaller than those fed to adults, the digestive efficiency of juveniles may have been increased artificially by the larger digestible surface area of the particles in the juveniles' diet. However, this may reflect reality, because in nature juveniles would be more likely than adults to tear plant particles into smaller pieces (Bjorndal 1997).

Because these lizards were tested under field conditions in which daily temperature fluctuations were similar to those experienced by free-ranging lizards, the digestive rates and transit time of test foods were probably similar to their natural passage rates. Juveniles had faster passage rates than adults when fed C. glaudulifera leaves and S. wislizenii flowers, although the latter trend was not significant. Processing plant foods at a faster rate allows small herbivorous lizards to compensate for a lack of fiber digestion through the extraction of additional soluble nutrients from cell contents. Juveniles of most iguanids maintain growth rates through increased passage rates of low fiber, high protein plant foods (Troyer 1984; Mautz and Nagy 1987; Wikelski et al. 1993; Bjorndal 1997).

These increased passage rates to compensate for lower quality (e.g., low energy or high plant fiber) foods was verified through dietary dilution experiments on emydid turtles (McCauley and Bjorndal 1999). These turtles (Trachemys scripta) have an ontogenetic shift from carnivory to herbivory similar to C. pectinata. The slower passage rate of insect larvae compared to plant foods may reflect the inability to effectively digest this food by adult C. pectinata and may reflect the increased retention needed for added nutrient extraction by juveniles. Chitin or high lipid contents associated with insect larvae and the potential lack of enzymes (chitinase/chitobiase and lipase, respectively) and bile salts to digest these components may have influenced these passage rates. Slower rate of passing insect food also occurred in feeding experiments with another iguanid (Dipsosaurus dorsalis) where transit time was similar to the time required to digest lower quality, high fiber plant foods (Mautz and Nagy 1987).

Macrominerals

The role of macrominerals may be important in the selection of foods by animals. At least 22 inorganic elements are required nutrients for some animal species (Pond et al. 1995). I evaluated the assimilation of four of the most essential elements or macrominerals (Ca, P, Mg, and K). Calcium and phosphorus, and to a lesser extent magnesium, are important to maintain skeletal structure in the body. Moreover, calcium is used in neural activity and muscle contraction, while phosphorus is used in construction of tissue membranes and in energy metabolism. The relationship of Ca to P, often stated as a ratio, reflects the balance required for the body to maintain skeletal continuity (Frye 1997). For

example, excess P in the body can lead to nutritional secondary hyperparathyroidism resulting in resorption of bone to balance Ca levels (Pond et al. 1995). Based on the Ca–P ratios in the test foods, adult C. pectinata did not assimilate P (on average) until these ratios were greater than 6:1 (Fig. 3). The elemental proportions in food near the point where P begins to be assimilated was 1.4% Ca – 0.06% P (H. campechianum flowers). The low percentage of Ca in leaves (Table 1) accounts for much of the loss of phosphorus by C. pectinata . The endogenous loss of P in the feces when intake exceeds P demands also occurs in white-tail deer (Grasman and Hellgren 1993) and in sheep (Braithwaite 1984). Braithwaite (1984) suggests that excess P found in the feces is secreted mainly in the saliva, and is thought to act as a buffer against volatile fatty acids produced in plant fiber fermentation. Despite the lowest Ca–P ratio, juveniles and immatures assimilated significantly more P from insect larvae than did adults (Table 3). Immatures also assimilated more P than adults from H. campechianum flowers in the dry season. Increased P assimilation by subadults may reflect growth requirements. Adults assimilated their highest proportions of P from flowers and fruit which maintained the highest Ca-P ratios. Calcium assimilation was variable among ctenosaurs in relation to Ca–P ratios, but on average was at approximately 70% (Fig. 3). Adult females increased their Ca assimilation with a decrease in the P in the diet. Both flower diets were high in Ca and low in P, and all age classes were efficient at assimilating this mineral from these plants. Adults had significantly higher assimilation efficiencies from S. wislizenii flowers than subadults, but subadults were significantly better than adults in Ca acquisition from insect foods (Table 3). The reduced ability of adult females to extract Ca from leaves or insect

larvae may reflect the higher proportion of P in these foods and potentially from the lack of these foods in their natural diet. Females had high Ca assimilation on dry season foods (flowers and fruit) which corresponds to their mineral need for egg production at that time of the year (R.D. Durtsche personal observation).

Magnesium is a required mineral in skeletal development, metabolic processes, and enzyme activation (Pond et al. 1995). Magnesium is the third most abundant mineral in the body (after Ca and P). Again, juvenile C. pectinata were significantly more efficient at assimilating Mg from insects than were other age classes (that actually lost Mg on the insect diet). The high levels of Mg in leaves (Table 1) suggests that they are a staple source for this mineral. High Mg assimilation from Croton suberosus leaf, containing the highest food concentration of Mg measured, supports this assumption. Despite lower Mg assimilation efficiencies on C. glaudulifera leaves, the total Mg gained were greater than higher efficiency assimilation on fruit of the same species.

The use of C. suberosus as a food source apparently comes at a price for these lizards. Croton suberosus is in the Euphorbiaceae, a group of plants with phenols and alkaloids as secondary compound toxins (Harborne et al. 1996). I assume that it was these toxins that killed juveniles within 8 hrs. Immatures and adults survived and processed these plant foods. It is not known whether larger body size had a dilution effect on these toxins or if the switch to herbivory acts to detoxify these compounds, but other iguanids use Croton as a major food source (e.g., Mitchell 1999).

Potassium is an important electrolyte with many body functions (e.g., cellular osmotic control), however, high plant concentrations can often be osmotically stressful to

reptilian herbivores (Nagy and Medica 1986, Smits et al. 1986, Peterson 1996). While K concentrations in insect larvae were similar to those found in the plant foods, assimilation by C. pectinata generally decreased with an increase in body size, where juveniles and adult males differed significantly. Potassium control in these lizards is through nasal salt glands and loss in urates (Nagy 1975). Higher potassium than sodium concentrations were found in nasal fluids of C. pectinata (Templeton 1967) confirming salt glands as one avenue of excess electrolyte removal.

Ramifications of ontogenetic diet shifts

Earlier reasoning suggested that large lizards were herbivorous because of the energetic limitations to harvesting prey (Pough 1973). This may be the case since all adult iguanid lizards are large and herbivorous. But, in most iguanids herbivory is the feeding strategy of all age classes, including small juveniles. Ctenosaura pectinata differs from other iguanids by eating insects as small lizards, and the capacity to digest insects in this species decreases with growth in body size. Although other studies (Ruppert 1980; Mautz and Nagy 1987) indicated high assimilation efficiencies of adult iguanids fed a diet of crickets and Tenebrio larvae, my study is the first to test dietary assimilation of an iguanid on the types of insects naturally ingested by juveniles of the species. The digestive physiology of adult C. pectinata established on an herbivorous diet had decreased efficiencies when fed an experimental diet of insects shortly after capture. This difference in efficiencies from adults fed an herbivorous diet signifies the degree to which my experimental diets represented an abrupt change from the animals' previous diet. The

digestive system may not have had enough time to change enzymes in response to an insect diet. The digestive system in juveniles was already physiologically adjusted to a diet of insects and, perhaps as a result, they did best on these foods. Lag times in digestive efficiency for birds that switch their diet seasonally (Levey and Karasov 1989) support the differences in digestive physiology associated with ontogenetic diet shifts found in C. pectinata.

Ctenosaura is one of the more derived groups within the clade of herbivorous iguanid lizards (Fig. 4; Sites et al. 1996). Within this family, only members of the genus Ctenosaura exhibit ontogenetic diet shifting. All other genera are herbivorous throughout life. They compensate for a lack of plant fiber digestion in smaller (juvenile) individuals by cell content extraction through feeding on small, low fiber, high protein plant foods, and by passing these foods at a faster rate than adults (Troyer 1984; Mautz and Nagy 1987; Wikelski et al. 1993). An ontogenetic feeding strategy that differs from other members of the clade suggests an evolutionary change in ancestors of modern Ctenosaura. This change is not merely a plastic shift in behavioral patterns or habitat use (R.D. Durtsche unpublished data) but also a difference in the physiology of digestion between different size classes. These differences allow each particular size class to optimize the foods that they eat naturally for maximal gains in growth rates, maintenance, reproduction and ultimately individual fitness. My study provides evidence that the Ctenosaura are the only members of the extant Iguanidae to show an evolutionary change back to insectivory in the juvenile life history stage from an ancesteral herbivorous juvenile stage.

Acknowledgments

I thank E. Anzures-Vázquez, R. Castro-Franco, A. Holloway, H. Mejia-Mojica, and A. Ramirez-Bautista for field assistance throughout portions of this study. L. Lina and E. Aranda-Escobar graciously cultivated and provided the Lepidoptera larvae for the feeding trials. I am greatly indebted to my colleagues in the Centro de Investigacion at the Universidad Autonoma del Estado de Morelos for their logistic support and friendship throughout my stay in Morelos. C. Peterson was kind enough to loan me his semi-micro oxygen bombs and I am indebted to the University of Oklahoma Chemistry Department for use of their calorimetry equipment. I thank P. Gier, and S. Sartorius for comments on earlier versions of this manuscript. I thank my committee members V. Hutchison, W. Matthews, M. McInerney, C. Peterson, and L. Vitt for support and constructive editorial suggestions. Animal care was in full compliance with the University of Oklahoma Animal Care and Use Committee. This research was conducted under the research permits granted to the Centro de Investigacion at the Universidad Autonoma del Estado de Morelos and I.N.E. DOO750.6824 to A. Ramirez-Bautista and R. D. D.. Partial funding for this research was provided by research grants from the Univ. of Oklahoma Dept. of Zoology, Graduate Student Senate, and Graduate College; Sigma Xi Grants-in-Aid of Research; The Hach Company, and the American Museum of Natural History Theodore Roosevelt Fund. This research was submitted in partial fulfillment of a Ph.D. in Zoology at the University of Oklahoma.

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Table 1. Nutritional components of six different natural foods of Ctenosaura pectinata used in the feeding trials. Dry matter data are the percentage of wet mass. Neutral detergent fiber (NDF) represents total plant fiber and acid detergent fiber (ADF) represents the lignocellulose content of plant fiber. Both plant fiber values are expressed in percentages of organic matter. Gross energy content is in kJ / g dry mass. All other values represent percentages of dry matter.

food type	Dry Matter	Organic Matter	Crude Protein	NDF	ADF	Energy kJ/g	Ca	P	Mg	K
Flowers										
Senna wislizenii	21.80	94.90	32.12	41.32	24.41	19.52	2.40	0.44	0.21	1.47
Haematoxylon campechianum	20.09	95.05	15.05	39.03	20.27	17.19	1.77	0.29	0.04	1.95
Leaves										
Croton suberosus	27.85	85.19	17.31	45.68	30.38	15.52	0.60	0.18	0.84	1.72
Coursetia glaudulifera	25.32	90.41	25.65	52.71	39.41	18.38	0.65	0.23	0.68	1.45
Fruit										
Coursetia	41.46	93.16	12.85	61.44	43.76	16.19	2.03	0.22	0.27	0.96

glaudulifera									
Insects									
Eruciform larvae	12.02	91.07	50.80		22.54	1.63	0.95	0.28	1.81

Table 2. Mean transit times (TT) and digestibilities of organic matter (OM), crude protein (CP), cell walls (NDF), lignocellulose (ADF), and metabolizable energy (ME) for six pure diets fed to different age classes of C. pectinata. Measures of metabolizable energy is in kJ/g, and transit time of food is in days. Mean body masses (M_b) are given in g for age classes and adult sexes tested on these diets. Means are given ± SE within parentheses. Values beneath the age/sex classes represent the n of lizards tested. Different letters (a, b) within a column indicate significant differences among means ($P < 0.05$). († indicates subject death within 8 hrs of feeding)

Assimilation Efficiencies	M_b (g)	TT (days)	OM (%)	CP (%)	NDF (%)	ADF (%)	ME (%)
Flowers							
Senna wislizenii							
Juvenile	8.0	2.7	69.7	62.7 [ab]	49.0 [a]		54.6
6	(1.0)	(0.3)	(4.8)	(5.9)	(8.1)		(6.9)
Immature	110	3.8	75.1	71.2 [ab]	71.2 [b]	64.1	63.4
4	(14)	(0.5)	(4.3)	(5.0)	(5.0)	(6.2)	(5.7)
Adult Female	586	5.0	78.0	78.9 [a]	74.9 [b]	68.4	73.0
4	(185)	(0)	(2.2)	(2.3)	(1.7)	(3.5)	(3.6)
Adult Male	791	3.4	62.3	58.7 [b]	60.5 [b]	49.2	54.9
5	(150)	(0.2)	(2.6)	(2.5)	(2.9)	(6.3)	(0.6)

Haematoxylon campechianum							
Immature	129	5.5	72.5	55.9	65.8	60.6	64.6
5	(45)	(0.5)	(9.9)	(14.9)	(12.2)	(14.1)	(12.2)
Adult Female	805	4.5	73.5	54.0	52.2	38.9	68.1
5	(83)	(0.5)	(1.7)	(2.9)	(4.2)	(7.9)	(3.3)
Adult Male	1111	5.0	68.3	56.5	54.7	40.9	76.4
4	(76)	(0)	(6.7)	(8.0)	(5.9)	(9.2)	(6.6)
Leaves							
Croton suberosus							
Juvenile	7.4	†	†	†	†	†	†
5	(0.6)						
Immature	160	3.0	56.3	29.8	46.7	40.3	47.6
5	(24)	(0.6)	(11.2)	(17.9)	(13.6)	(15.2)	(9.4)
Adult Female	781	4.0	63.7	42.0	61.6	48.8	46.0
5	(56)	(0)	(7.7)	(14.7)	(9.5)	(16.7)	(12.7)
Adult Male	931	5.5	61.4	35.9	59.7	49.6	43.1
5	(201)	(1.5)	(11.5)	(18.8)	(11.3)	(15.0)	(15.7)
Coursetia glaudulifera							

Juvenile	8.1	2.3 [a]	57.5	12.6			36.5
3	(0.5)	(0.7)	(3.2)	(6.6)			(3.1)
Immature	106	2.7 [a]	43.4	42.0	51.7	18.3	31.3
3	(24)	(0.3)	(8.9)	(12.9)	(8.0)	(0.0)	(14.4)
Adult Female	580	5.4 [b]	43.4	45.6	47.5	11.8	26.6
5	(74)	(0.7)	(5.9)	(6.6)	(5.9)	(1.7)	(6.5)
Adult Male	736	5.2 [b]	52.3	39.0	56.4	27.0	39.0
5	(130)	(0.4)	(7.7)	(12.8)	(10.3)	(6.0)	(10.8)
Fruit							
Coursetia							
glaudulifera							
Immature	54	4.0	84.5	73.8			81.3
3	(14)	(0)	(9.0)	(8.6)			(8.8)
Adult Female	797	4.3	79.8	63.5	75.9	77.6	75.9
6	(87)	(0.3)	(5.5)	(7.7)	(8.4)	(7.2)	(5.7)
Adult Male	817	3.8	66.8	55.7	59.3	65.6	55.4
5	(148)	(0.2)	(6.3)	(8.2)	(8.4)	(7.6)	(8.0)
Insects							
Eruciform							
larvae							
Juvenile	5.2	4.8	82.9 [a]	82.8 [a]			75.4 [a]

5	(0.5)	(0.2)	(3.2)	(3.2)	(3.7)
Immature	128	5.4	65.5 [b]	66.3 [b]	47.0 [b]
5	(25)	(0.5)	(5.1)	5.6	(6.5)
Adult Female	586	6.6	61.1 [b]	62.7 [b]	41.5 [b]
5	(185)	(1.1)	(6.6)	4.8	(3.4)
Adult Male	791	6.0	62.0 [b]	62.7 [b]	27.3 [b]
4	(150)	(0.4)	(11.7)	(7.2)	(13.9)

Table 3. Mean assimilation efficiencies of macromineral elements of test foods by C. pectinata. Means are given ± SE within parentheses. Values beneath the age/sex classes represent the n of lizards tested. Different letters (a,b) within a column indicate significant differences among means ($P < 0.05$).

Assimilation Efficiencies	Calcium (%)	Phosphorus (%)	Magnesium (%)	Potassium (%)
Flowers				
Senna wislizenii				
Juvenile	63.6 [a]	30.6 [ab]	51.5 [ab]	62.7
6	(5.8)	(11.1)	(7.7)	(5.9)
Immature	78.0 [a]	42.3 [a]	32.2 [b]	68.2
4	(3.8)	(10.0)	(11.7)	(5.5)
Adult Female	93.8 [b]	52.7 [a]	84.4 [a]	76.5
4	(1.1)	(7.4)	(4.9)	(3.2)
Adult Male	89.6 [b]	–4.0 [b]	37.8 [b]	59.5
5	(2.1)	(7.0)	(8.4)	(3.0)
Haematoxylon campechianum				
Immature	74.2	56.4 [a]	61.7	78.9
5	(9.6)	(17.8)	(17.0)	(6.3)

Adult Female	78.7	7.4 [b]	72.4	71.5
5	(4.7)	(5.6)	(17.4)	(3.3)
Adult Male	68.6	– 13.8 [b]	76.8	55.3
4	(9.1)	(16.0)	(14.1)	(9.5)
Leaves				
Croton				
suberosus				
Juvenile	†	†	†	†
5				
Immature	56.3	–134.4	91.9	51.2
5	(11.1)	(59.9)	(2.1)	(12.4)
Adult Female	63.1	–92.2	80.3	64.8
5	(6.8)	(42.5)	(7.5)	(8.8)
Adult Male	69.9	–163.8	74.8	57.6
5	(8.9)	(71.9)	(8.1)	(15.8)
Coursetia				
glaudulifera				
Juvenile	50.2	–66.5	49.0	72.0
3	(3.7)	(12.5)	(3.8)	(5.1)
Immature	51.7	–98.1	61.5	34.1
3	(10.7)	(44.1)	(8.6)	(10.4)

Adult Female	56.1	–89.1	53.2	44.7
5	(5.8)	(26.0)	(8.8)	(6.1)
Adult Male	69.3	–86.1	79.8	61.1
5	(5.6)	(43.2)	(8.1)	(10.0)
Fruit				
Coursetia				
glaudulifera				
Immature	77.9	38.7	84.7	69.0
3	(14.0)	(33.4)	(9.7)	(16.5)
Adult Female	79.7	26.9	77.1	46.2
6	(4.9)	(17.1)	(3.3)	(14.0)
Adult Male	43.1	18.4	73.6	57.4
5	(14.8)	(8.9)	(6.3)	(5.1)
Insects				
Eruciform				
larvae				
Juvenile	87.9 [a]	54.0 [a]	48.3	83.8
5	(3.6)	(8.5)	(15.3)	(3.8)
Immature	86.6 [a]	28.2 [a]	–42.0	71.2
5	(3.6)	(10.6)	(43.3)	(6.4)
Adult Female	52.4 [b]	–43.3 [b]	–46.2	57.7

5	(5.8)	(13.8)	(23.7)	(4.3)
Adult Male	48.1 [b]	–52.2 [b]	–113.2	55.9
4	(11.3)	(45.0)	(88.5)	(10.5)

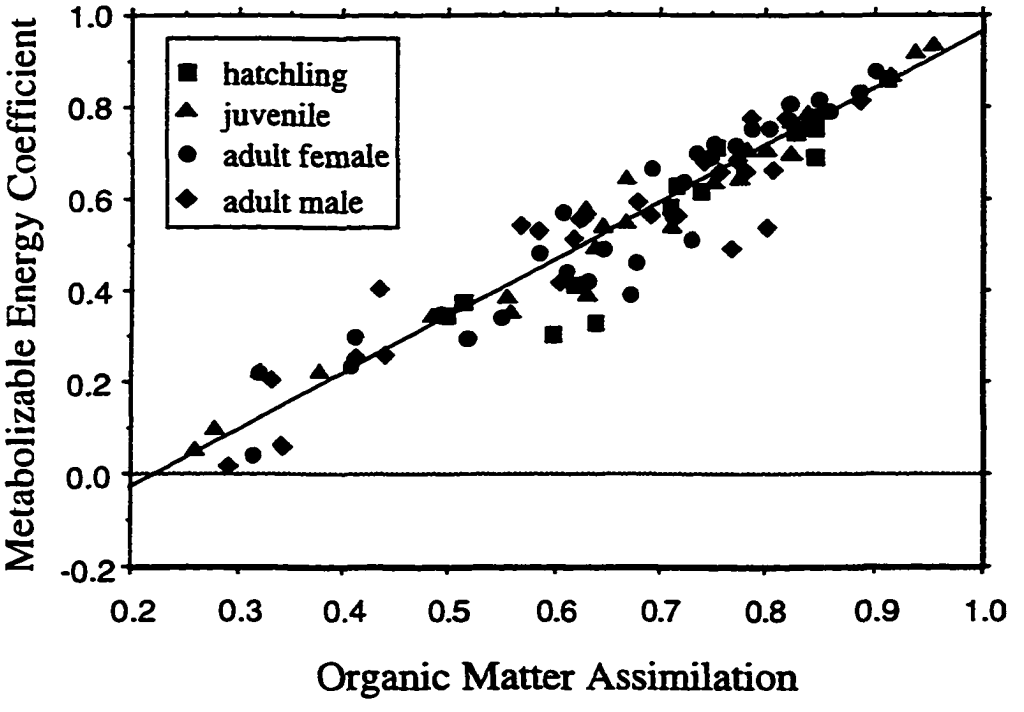
Figure Legends

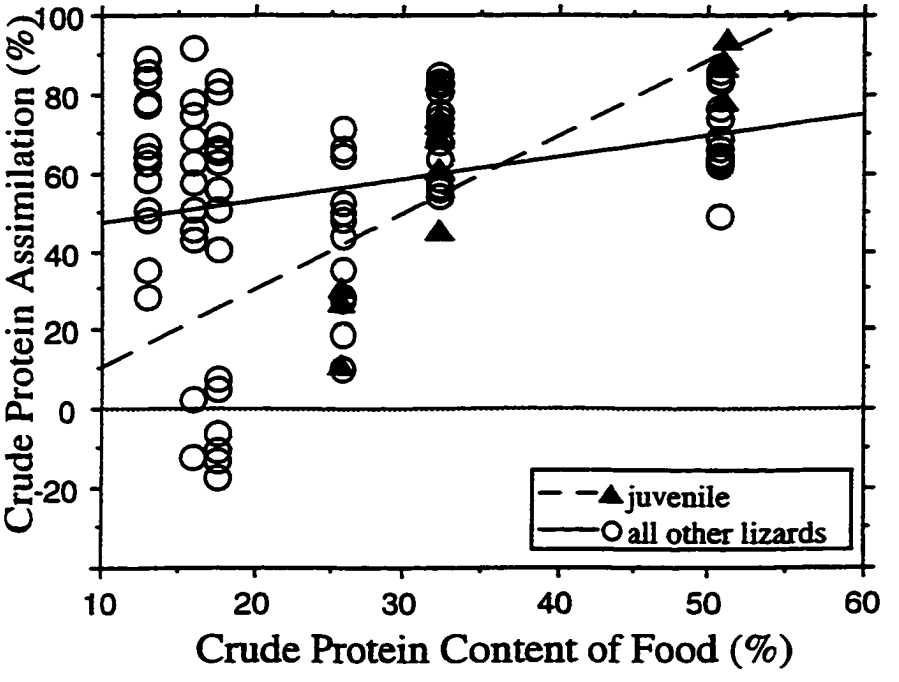
Fig. 1. Correlation between organic material assimilated and the metabolizable energy coefficient. The regression (Metabolizable Energy = 1.24 • Organic Matter Assimilation – 0.28) was significant ($R^2 = 0.85$, $F_{1,91} = 550.5$, $P < 0.0001$).

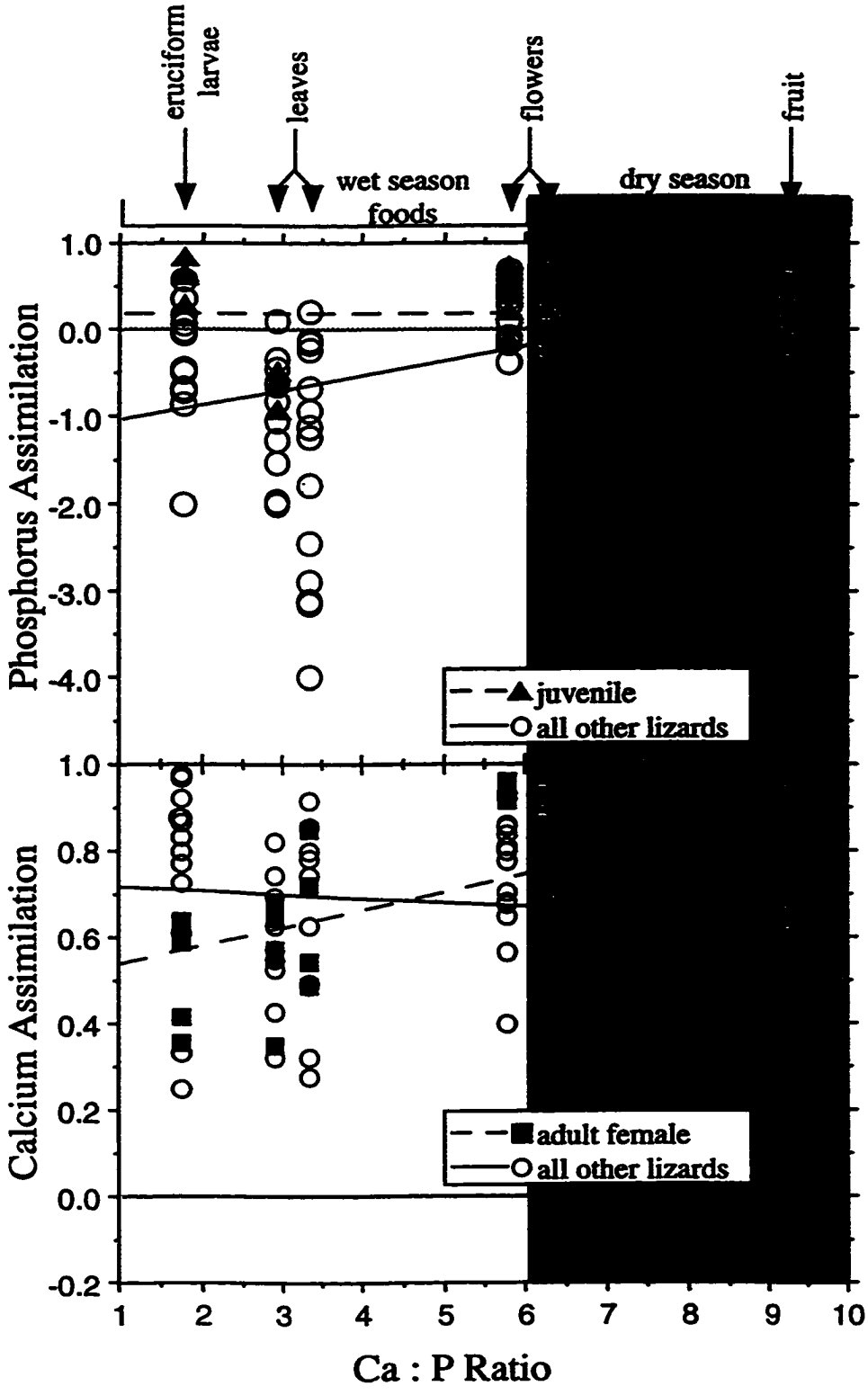
Fig. 2. Relationship between apparent crude protein assimilation against crude protein in the diet was highly significant for juvenile lizards (Protein Assimilation = 0.022 • Food Protein - 0.225, $R^2 = 0.63$, $F_{1,12} = 20.48$, $P = 0.0007$) but weaker for older lizards (Protein Assimilation = 0.005 • Food Protein + 0.41, $R^2 = 0.08$, $F_{1,82} = 6.87$, $P = 0.011$).

Fig. 3. Relationship between apparent phosphorus (P) assimilation and calcium (Ca) assimilation against the Ca–P ratio in six pure test diets from the wet and dry season. Juvenile lizards had no relationship between P assimilation and varying Ca–P ratios ($Y = -4.326\ E{-5} \cdot X + 0.181$, $F_{1,12} = 3.02\ E{-7}$, $P = 0.9996$). All other lizards had a significant positive relationship between P assimilation and Ca–P ratios ($Y = 0.156 \cdot X - 1.56$, $R^2 = 0.18$, $F_{1,81} = 20.93$, $P < 0.0001$). Most lizards had a weak relationship between Ca assimilation and Ca–P ratios ($Y = -0.009 \cdot X + 0.73$, $R^2 = 0.10$ $F_{1,65} = 0.64$, $P = 0.428$) but adult females had a strong relationship ($Y = 0.049 \cdot X + 0.44$, $R^2 = 0.38$, $F_{1,28} = 17.38$, $P = 0.0003$).

Fig. 4. Basic phylogeny of Iguanidae (modified from Sites et al. 1996) showing transitional switch to a different ontogenetic feeding strategy.


Metabolizable Energy Coefficient
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
hatchling
juvenile
adult female
adult male
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Organic Matter Assimilation


Crude Protein Assimilation (%)
100
80
60
40
20
0
-20
10
20
30
40
50
60
Crude Protein Content of Food (%)
juvenile
all other lizards


eruciform larvae
leaves
flowers
fruit
wet season foods
dry season
Phosphorus Assimilation
1.0
0.0
-1.0
-2.0
-3.0
-4.0
juvenile
all other lizards
Calcium Assimilation
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
adult female
all other lizards
1
2
3
4
5
6
7
8
9
10
Ca : P Ratio

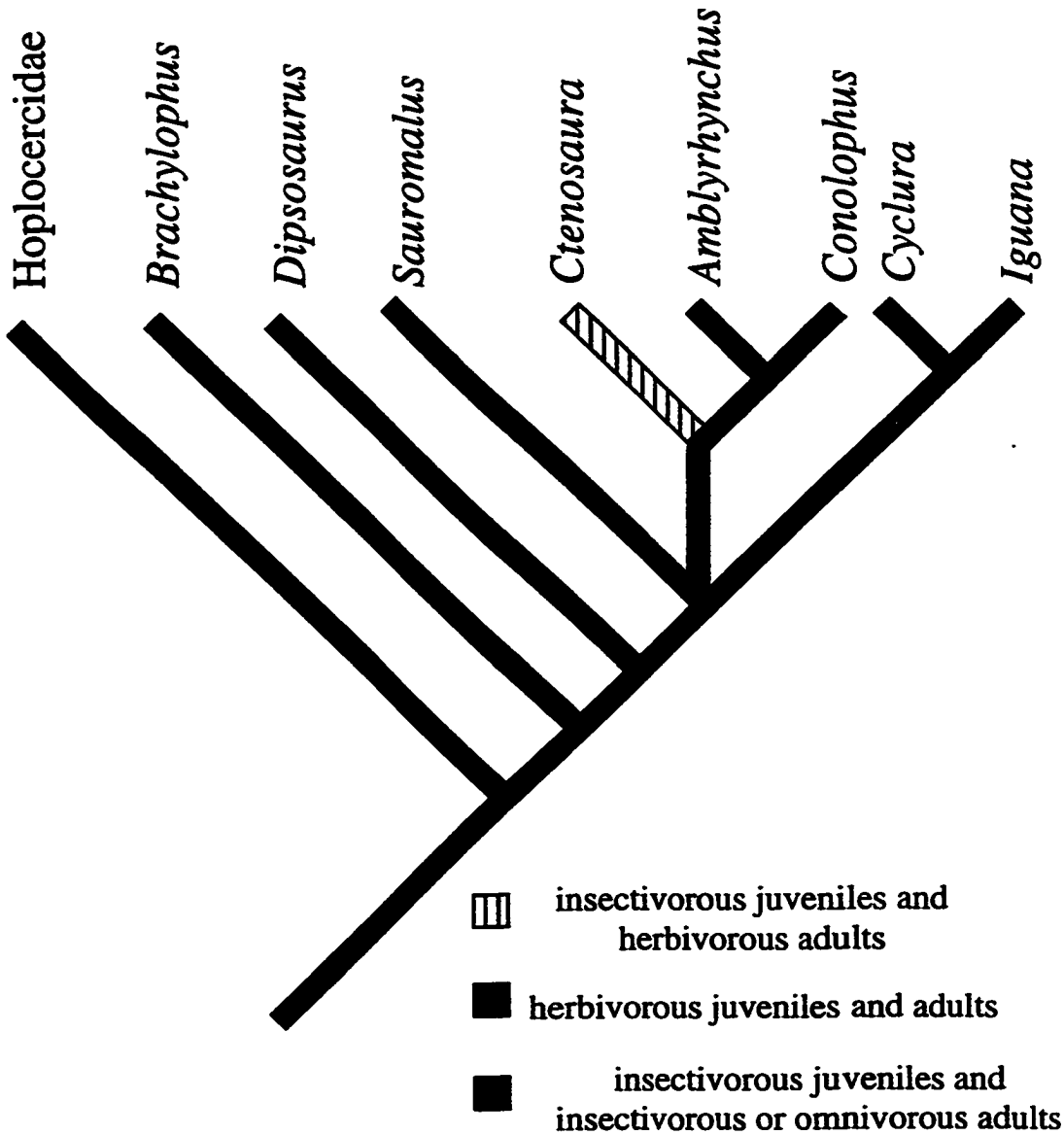
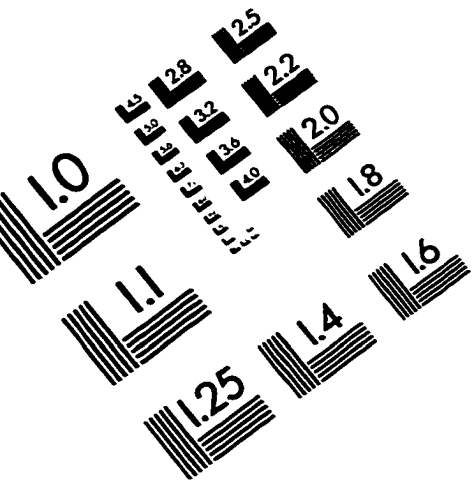
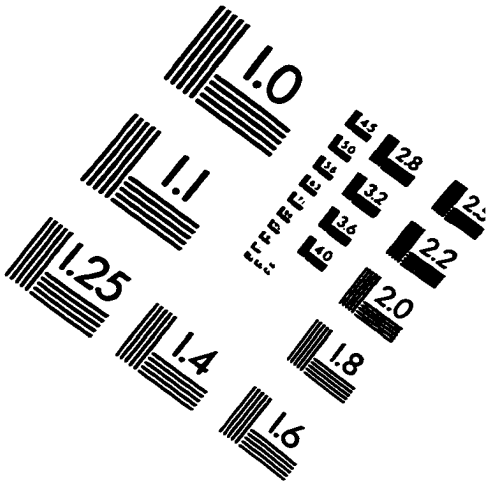
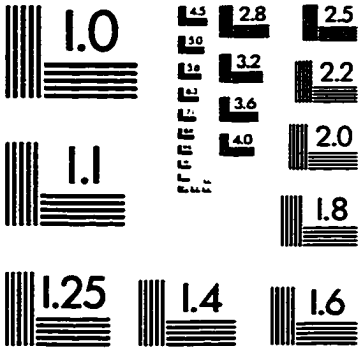
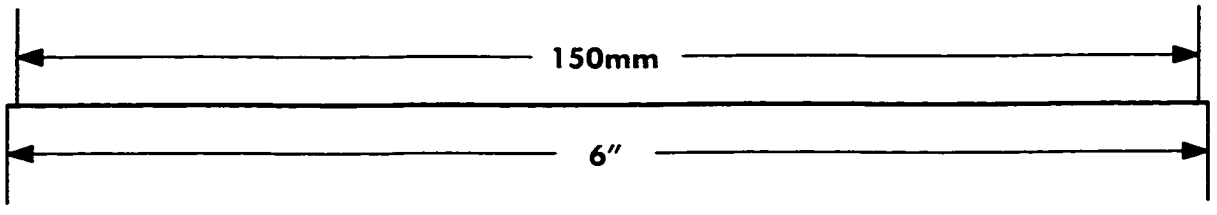

Hoplocercidae
Brachylophus
Dipsosaurus
Sauromalus
Ctenosaura
Amblyrhynchus
Conolophus
Cyclura
Iguana
insectivorous juveniles and herbivorous adults
herbivorous juveniles and adults
insectivorous juveniles and insectivorous or omnivorous adults

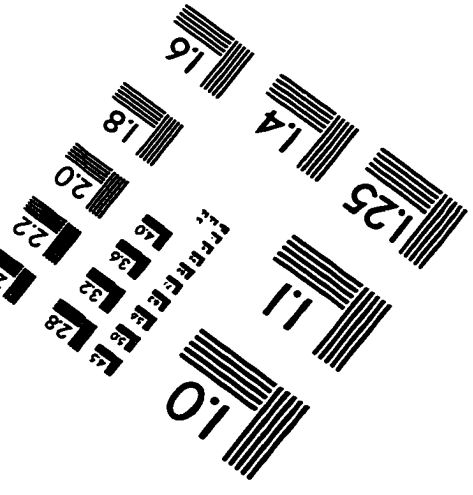
IMAGE EVALUATION TEST TARGET (QA-3)

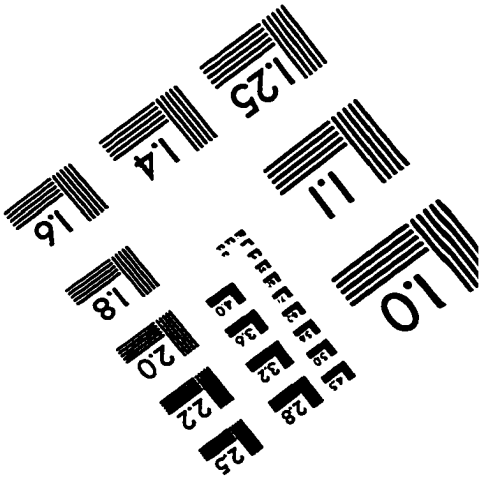












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