

AN ABSTRACT FOR THE THESIS OF

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Title: Digestive parameters of the Eastern Collared Lizard, *Crotaphytus collaris*.

Abstract approved: *Sydney Sievert*

Digestive physiology is important because animals can only obtain calories needed for growth, maintenance, and reproduction by feeding. The purpose of my study was to examine the digestive efficiency (DE) and food passage time for the Eastern Collared Lizard, *Crotaphytus collaris*, when fed different meals: neonatal mouse (*Mus musculus*), two masses of cricket (*Acheta domestica*), and two masses of mealworm larva (*Tenebrio molitor*). The mass of food ingested and defecated by 13 *C. collaris* during five four-day feeding trials was recorded. Different colored beads were fed to the lizards each day of the feeding trials to estimate food passage times. Fifteen neonatal mice, 19 crickets, and 10 mealworms were chosen as food samples. Linear regression equations were made by regressing food sample wet mass with dry mass and dry mass with calories. The mass of meals ingested was converted to calories using these equations. Fecal calories were determined by bomb calorimetry. Percent DE was calculated using the equation:  $(\text{Calories Consumed} - \text{Fecal Calories}) / \text{Calories Consumed} \times 100$ . An Analysis of Covariance (ANCOVA) was performed, followed by a multiple comparison test. It was determined that meal size did not affect the DE of *C. collaris*, but meal type did. The DEs of the 3.5% body mass-sized mealworm and cricket meals were significantly different ( $P = 0.0023$ ), as was the DEs of the 1.0% body mass-sized mealworm and cricket meals ( $P = 0.0020$ ). There were no significant differences ( $P > 0.05$ ) among the

DIGESTIVE PARAMETERS OF THE EASTERN COLLARED LIZARD,

*CROTAPHYTUS COLLARIS*

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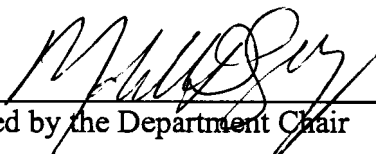
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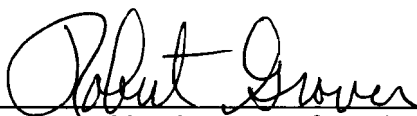
food passage times of *C. collaris* when fed the four insect meals. The neonatal mouse meal took significantly longer ( $P < 0.05$ ) to pass than the insect meals. In summary, meal size did not affect the DE or food passage time of *C. collaris*, but meal type did affect its DE and food passage time.

  
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## PREFACE

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## INTRODUCTION

Reptiles, as with other animals, obtain chemical energy needed for growth, body maintenance, and reproduction by feeding. Thus, digestive studies are important in understanding an organism's fitness and life history, as well as calculating ecological or nutritional energy budgets. Digestive studies also allow us to elucidate the impact of prey type, temperature, genetics, ontogeny, and other variables on energy uptake. Previous studies of reptilian digestion have focused heavily on the effect of temperature (Harwood, 1979; Johnson and Lillywhite, 1979; Naulleau, 1983), but some have considered diet composition (Waldschmidt *et al.*, 1987) and genetics (Beaupre *et al.*, 1993; Beaupre and Dunham, 1995; Angilletta, 2001) on energy consumption.

In ectotherms, digestion is greatly influenced by temperature (Harwood, 1979; Johnson and Lillywhite, 1979). Food consumption (appetite) of different species of lizards is dependent upon ambient temperature. As temperature increases within reasonable limits, the number of prey items consumed increases (Waldschmidt *et al.*, 1986; Van Damme *et al.*, 1991; Alexander *et al.*, 2001). Common Flat Lizards, *Platysaurus intermedius*, have a decreased appetite at low temperatures, and most do not feed at temperatures below 18 C (Alexander *et al.*, 2001). At 10 C, a temperature much lower than preferred temperatures, meals consumed by the European Asp, *Vipera aspis*, (Naulleau, 1983) and the Viperine Water Snake, *Natrix maura*, (Hailey and Davies, 1987) were regurgitated. Temperatures much higher than preferred body temperatures also resulted in regurgitation (Harwood, 1979; Naulleau, 1983).

Many reptiles exhibit thermophilic behavior after feeding (Naulleau, 1983; Sievert, 1989). An increase in body temperature results in faster digestion, allowing animals to perform other activities, rather than waiting for meals to be processed, as would be the

case at cooler temperatures. Angilletta (2001) stated that if lizards maintained preferred body temperatures for longer times, they should be able to assimilate greater amounts of energy from their meals.

Two digestive parameters, digestive efficiency and food passage time, play roles in determining the amount of energy that an animal can obtain from its meal. Digestive efficiency (DE) is the percent of ingested calories an animal absorbs across its gut from a meal, and the number of calories ingested and defecated by a meal can be estimated by using bomb calorimetry (Johnson and Lillywhite, 1979). One objective of this study was to formulate linear regression equations that future researchers could use to convert wet mass of fecal samples to calories without having to bomb fecal samples.

Various factors such as temperature, type of food, and consumption rate affect DE (Harwood, 1979; Johnson and Lillywhite, 1979; Beaupre *et al.*, 1993). In the Desert Iguana, *Dipsosaurus dorsalis*, and the Western Fence Lizard, *Sceloporus occidentalis*, DE is dependent upon temperature, within normal body temperatures, and an increase in body temperature leads to an increase in DE up to a critical level, at which point DE levels off (Harlow *et al.*, 1976; Harwood, 1979). However, some lizards possess a temperature independent DE such as *P. intermedius*, the Grass Lizard, *Takydromus septentrionalis*, and the Namib Sand-dune Lizard, *Angolosaurus skoogi*, which are able to absorb nutrients and calories at lower body temperatures just as well as they can at higher body temperatures (Clarke and Nicolson, 1994; Xiang *et al.*, 1996; Alexander *et al.*, 2001). At lower temperatures, food travels through an animal's gut slower and is exposed to digestive enzymes for longer periods, even though enzyme activity is decreased (Van Marken Lichtenbelt, 1992; Xiang *et al.*, 1996; Alexander *et al.*, 2001). In the Rusty Lizard, *Sceloporus olivaceus*, the Side-blotched Lizard, *Uta stansburiana*, and

the Common Lizard, *Lacerta vivipara*, temperature only had a slight effect on DE (Dutton *et al.*, 1975; Waldschmidt *et al.*, 1986; Van Damme *et al.*, 1991).

Age of an organism is another factor that may influence DE. Hatchling and juvenile Green Iguanas, *Iguana iguana*, that are gaining body mass have higher energy demands compared to adults and process meals at a quicker rate, and thus, assimilate more energy than adults per a given time (Troyer, 1984). Adult *I. iguana* have temperature independent DE, but the DE of a juvenile *I. iguana* is temperature dependent (Troyer, 1987).

The type of food greatly affects the DE of lizards. When *P. intermedius* was fed a high-quality diet of canned dog food and cake flour, its DE was 88% versus 52% when fed a low-quality diet of canned dog food and less digestible wheat husks (McKinon and Alexander, 1999). Herbivorous lizards eating their normal diet generally have lower DEs compared to insectivorous lizards because of cellulose and other indigestible plant matter (Waldschmidt *et al.*, 1986). Herbivorous species have a DE of 50%, which is much less than the 70-90% DE of carnivorous or insectivorous species (Harwood, 1979).

Insectivorous lizards may obtain more than twice as many calories per gram of food compared to herbivorous lizards (Pough, 1973). When the herbivorous Chuckwalla, *Sauromalus obesus*, was fed a carnivorous diet it had DE rates as high as *C. collaris*, a carnivorous lizard (Ruppert, 1980). This demonstrates that herbivorous lizards can assimilate as much energy as carnivorous lizards and that DE depends on the quality of food ingested. Conversely, when *C. collaris* was fed dandelion flowers it was unable to maintain weight (Ruppert, 1980). Its stomach was not large enough to store the mass of flowers needed to assimilate the number of calories it required. Herbivorous lizards generally have a larger body size compared to insectivorous lizards because they need a

larger stomach to hold the large amounts of plant material that are needed to obtain sufficient calories for body maintenance, growth, and reproduction.

The nutritive state of a lizard, which is defined as if the animal is fasted or fed, does not influence DE. Ballinger and Holscher (1983) found no significant difference between the DE of a well-fed Striped Plateau Lizard, *Sceloporus virgatus*, versus a starved individual. Meal size did not have a significant effect on DE in *U. stansburiana* when the feeding regime was changed from one cricket every 3 days to an *ad libitum* diet (Waldschmidt *et al.*, 1986). Similarly, increasing meal size had no significant effect on the DE of Green Anoles, *Anolis carolinensis* (Kitchell and Windell, 1972). However, Bjorndal (1987) stated that in Gopher Tortoises, *Gopherus polyphemus*, larger meals resulted in lower DE because of shorter passage times.

DE appears to be independent of an animal's mass. Bjorndal (1987) found that in *G. polyphemus*, body mass had no significant effect on DE. Similarly, Greenwald and Kanter (1979) found that a 500 g Corn Snake, *Elaphe guttata guttata*, had the same DE as a 150 g individual.

Food passage time is the length of time between ingestion of a meal and defecation of the waste. Food passage time of reptiles is extremely temperature sensitive (Clarke and Nicolson, 1994; Alexander *et al.*, 2001; Angilletta *et al.*, 2001). As body temperature increases, food passage time significantly decreases (Greenwald and Kanter, 1979; Naulleau, 1983; Xiang *et al.*, 1996). In *U. stansburiana* an *Acheta domestica* (domestic cricket) meal was passed 4.6 days after ingestion at 22 C compared to 1.2 days at 32 C (Waldschmidt *et al.*, 1986). Similarly, *L. vivipara* passed an *A. domestica* meal after 18.8 hours at 20 C versus 10.0 hours at 32.5 C (Van Damme *et al.*, 1991). In *E. guttata*

*guttata* and the Painted Turtle, *Chrysemys picta*, (Parmenter, 1981), an increase in body temperature significantly increased food passage time, but only had a slight effect on DE.

At the present there is no clear pattern of the influence of meal size on food passage time. In the Grass Snake, *Natrix natrix*, food passage time was affected by temperature, as well as meal size (Skoczylas, 1970). When *N. natrix* ate one frog, the meal left the stomach after 24 hours versus four days after a meal of two frogs (Skoczylas, 1970). Naulleau (1983) found that *V. aspis* had a significantly longer food passage time after ingestion of a large meal compared to a small meal. Similarly, when *A. carolinensis* (Windell and Sarokon, 1976) and the Prairie Ring-necked Snake, *Diadophis punctatus arnyi* (Henderson, 1970), were fed large and small meals, it took longer to digest the large meal. Van Marken Lichtenbelt (1992) stated that an increased food consumption lead to an increased gut transit time. However, in *P. intermedius* and *S. undulatus* meal size did not affect food passage time (Alexander *et al.*, 2001; Angilletta, 2001).

Type of food ingested can influence the rate of food passage. *Iguana iguana* passed a meal of berries in half the time required for a meal of leaves (Van Marken Lichtenbelt, 1992). The berries contained more indigestible matter relative to the leaves. However, when *A. carolinensis* was fed different insect meals, mealworm, *Tenebrio molitor*, larvae, *T. molitor* adults, and crickets (*Gryllus* sp.), there was little or no difference among gastric evacuation rates (Windell and Sarokon, 1976).

Meal frequency and meal size may affect food passage time in reptiles. Waldschmidt *et al.* (1986) found that the passage time of *U. stansburiana* fed *ad libitum* meals was 1.8 days faster than when fed one cricket daily or one cricket every third day. The nutritive state of an individual may also have a significant effect on food passage time. Windell and Sarokon (1976) observed that a starved *A. carolinensis* had a meal pass through the

stomach 50% slower than a well-fed individual. Large meals, 5.1 times the size of a small meal, took *A. carolinensis* longer to process (Windell and Sarokon, 1976).

Body mass did not affect the digestive rate of *E. guttata guttata* (Greenwald and Kanter, 1979), the Red-eared Slider, *Pseudemys scripta*, (Parmenter, 1981), or *G. polyphemus* (Bjorndal, 1987). However, age of an individual may have a significant effect on digestive rate. There were significant differences among the digestive rates of all age classes of *I. iguana* (hatchlings, juveniles, and adults) when fed the same type of food (Troyer, 1984).

The Eastern Collared Lizard, *Crotaphytus collaris*, is an ambush predator that opportunistically feeds upon insects, primarily grasshoppers and beetles, soft-bodied arthropods, and smaller lizards (Fitch, 1956; Best and Pfaffenberger, 1987). McAllister and Trauth (1982) found a *C. collaris* that had ingested a small Cotton Rat, *Sigmodon hispidus*. McAllister (1985) stated that *C. collaris* eats food items based on availability rather than food preference. Other than food habits, feeding behavior, (Fitch, 1956; McAllister, 1985) and diet composition (Husak and McCoy, 2000), little is known about the digestive physiology of *C. collaris*. It is important to study the digestive physiology of *C. collaris* to determine the effect on the feeding behavior and consequently the effect on its ecosystem. I examined the digestive efficiency and food passage time of *C. collaris* fed different meal types and meal sizes. These parameters are important in understanding the digestive physiology of *C. collaris* because they can determine how much energy *C. collaris* will obtain from its meal.

## MATERIALS AND METHODS

Thirteen male *C. collaris* were collected from Chase Co., Kansas in May to June 2001. Lizard masses ranged from 25.05 to 42.99 g. Lizards were housed individually in plastic containers (59 cm x 43 cm x 30.5 cm) with hardware cloth lids in the Animal Care Facility at Emporia State University on a LD 14:10 photoperiod (centered at 1500 h) at 25 C. I placed basking lamps with 60-watt light bulbs on a LD 12:12 photoperiod (centered at 1400 h) over a brick in the containers, and water was provided *ad libitum*. Lizards could regulate their body temperatures by basking or retreating into a 16 cm long x 9 cm diameter PVC tube cut in half lengthwise.

### Digestive Efficiency

Five feeding trials were conducted during the experiment to determine the effects of meal size and meal type on digestive efficiency. Lizards were given: neonatal mouse (*Mus musculus*), two meal sizes of cricket (*Acheta domestica*), and two meal sizes of mealworm larva (*Tenebrio molitor*). The two meal sizes selected for the insect treatments were meals equal to 1.0% and 3.5% of an individual lizard's body mass. These meal sizes were chosen because they represented a large meal and a small meal. *Crotaphytus* fed a cricket meal approximately 5% of its body mass frequently regurgitate. Lizards were fed each of the five meal types for four consecutive days and the mass of food ingested by each lizard was recorded. Lizards were weighed each day prior to feeding. The neonatal mouse meal represented a novel diet, even though there are instances of *Crotaphytus* ingesting rodents in the wild (Montanucci, 1971; McAllister and Trauth, 1982). The neonatal mouse meals were approximately 4.0% to 6.5% of an individual lizard's body mass. The crickets represented a natural food source and mealworm larvae represented a typical insect larvae containing higher fat and less chitin



than crickets (Kitchell and Windell, 1972; Harwood, 1979; Witz and Lawrence, 1993).

I checked for fecal samples at half-hour or shorter intervals during the light phase of the day on days 3 and 4, and I recorded the wet mass of fresh fecal samples. Uric acid was not collected because it is a protein catabolism end product and does not contain calories from food that has just been ingested (Harwood, 1979). Fecal samples were placed in a drying oven at 70C and dried to a constant mass.

Because I could not use the ingested food items to assess caloric content, I selected representative food samples of neonatal mice (n=15), crickets (n=19), and mealworms (n=10). The samples were of similar mass to those fed to the lizards. I recorded wet masses, euthanized the prey, placed the food samples in a drying oven at 70 C, and dried the samples to a constant mass.

Once all of the food and fecal samples were dried, I used an oxygen bomb calorimeter (Parr Instrument Co., Moline, IL) to determine the caloric content of the samples (Harwood, 1979; Johnson and Lillywhite, 1979). The caloric values of the fecal samples represented the number of calories defecated by each lizard during each feeding trial. Calories from all feces for each lizard in each feeding trial were summed. To determine the number of calories ingested in all meals during the five feeding trials, I added the wet masses of food ingested during each feeding trial by each lizard and used linear regression equations to convert the ingested wet masses to dry masses and dry masses to calories. Once I determined the number of calories consumed and defecated during each feeding trial, I used the following equation to calculate digestive efficiency:  $DE = C - F / C \times 100$  where C = Calories Consumed and F = Fecal Calories (Johnson and Lillywhite, 1979).

A two-way analysis of variance was performed using SAS software (SAS Institute,

Carey, NC) to determine if an interaction was present between the number of calories consumed versus defecated among the five treatments, and if the slopes of the five treatments were homogeneous. SAS software was also used to perform an analysis of covariance (ANCOVA) to determine if there were any significant differences among the DE of *C. collaris* during the five treatments. Consumption (in calories), body mass, and treatments were entered as covariates. A multiple comparison test was then used to determine what treatments statistically differed. Linear regressions were performed using Sigma Stat software (Jandel Scientific, San Rafael, CA) to compare calories ingested and defecated per day by *C. collaris* during the five treatments.

### **Food Passage Time**

The same five feeding trials of the digestive efficiency experiment were used to determine the effect that meal size and meal type had on food passage time. I fed two plastic colored beads (2 mm diameter) with each meal during the feeding trials. The beads were used as markers to estimate the length of time it took for a meal to pass through the gut of *C. collaris*. I hand fed all individuals to eliminate stress differences and to ensure all beads were ingested. Different colored beads were used each day of the experiment to indicate what day the beads were ingested.

I checked for fecal samples every 15 to 20 minutes during photophase and checked for the appearance of beads in the feces. Times of ingestion and defecation of the colored beads by the lizards were recorded. To further support that the beads were a good estimate of passage time I used two other marking techniques and repeated the 3.5% cricket meal trial. I used fluorescent powder and rubber pieces (3 mm x 2 mm) as meal markers. I used an ultraviolet light to examine the fluorescent powder in the feces, and a fecal sample that contained the most powder was recorded as the defecation time.

Statistical analyses of food passage time data were performed using SigmaStat software (Jandel Scientific, San Rafael, CA). A one-way analysis of variance (ANOVA) was done to determine if there were any significant differences in the food passage times among the five feeding trials. Then I performed a Student-Newman-Keul's test to determine which treatments statistically differed from each other. A one-way ANOVA was performed to determine if there were any significant differences among the three different marking techniques.

## RESULTS

### Digestive Efficiency

The regression of dry mass on the wet mass was significant (Table 1). The percent variation in calories as explained by dry mass ( $r^2$ ) was lower in mealworms and neonatal mice (Table 2). The percent variation in dry mass for fecal samples as explained by wet mass was higher in both cricket and the 1.0% body mass-sized mealworm treatments. The percent of the variation in fecal sample dry mass as explained by wet mass was not as great in the neonatal mouse and 3.5% body mass-sized mealworm treatments (Table 3). There was no significant relationship between dry mass and calories of fecal samples from the neonatal mouse treatment ( $P = 0.336$ ). There was a significant relationship between dry mass and calories of fecal samples in all other treatments; however, the percent of explained variation in calories per fecal sample was lowest in the 1.0% body mass-sized cricket treatment (Table 4).

*Crotaphytus collaris* had the highest DE when fed either mealworms or neonatal mice (Table 5). The number of calories ingested did not significantly influence the number of calories defecated (Table 6). There was a significant difference ( $P = 0.0001$ ) among the five meal types in the number of calories defecated (Table 7). The multiple comparison test showed a significant difference between the DE of 3.5% body mass-sized cricket and 3.5% body mass-sized mealworm meals ( $P = 0.0023$ ) and a significant difference between the DE of 1.0% body mass-sized cricket and 1.0% body mass-sized mealworm meals ( $P = 0.0020$ ). The DE of the neonatal mouse meals was not significantly different ( $P > 0.05$ ) from the other four treatments. Meal size did not have a significant effect on the DE of *C. collaris*, but meal type did (Table 7). The multiple comparison test indicated that the two mealworm meal size treatments and the neonatal mouse treatment

were more similar to each other in terms of digestibility, and these meals yielded higher DE values compared to the cricket treatments. A two-way ANOVA indicated that there was homogeneity among the slopes of the five treatments ( $P < 0.0001$ ).

### **Food Passage Time**

Results of the one-way ANOVA indicated significant differences among the five treatments ( $F = 3.01$ ;  $df = 4$ ,  $P = 0.025$ ). The multiple comparison test showed that there were no significant differences ( $P > 0.05$ ) in passage times among the four insect treatments (Table 8). The size of an insect meal (3.5% vs. 1.0% of lizard's body mass) did not have a significant effect on the food passage time in *C. collaris*. The Student-Newman-Keul's test indicated that the neonatal mouse meal took significantly longer ( $P < 0.05$ ) to pass than the other four treatments (Table 8). There were no significant differences ( $F = 1.72$ ;  $df = 2$ ,  $P = 0.193$ ) among the food passage values obtained using three different marking techniques during a 3.5% body mass-sized meal (Table 9).

Table 1. Linear regression equations comparing dry mass ( $y$ ) of food sample on to wet mass ( $x$ ).

Treatment	Wet mass to Dry mass	$r^2$	DF	$F$	$P$
Neonatal mice	$y = 0.151 x + 0.015$	0.821	14	59.572	<0.001
Crickets	$y = 0.357 x - 0.025$	0.789	18	63.725	<0.001
Mealworms	$y = 0.384 x - 0.001$	0.808	9	33.772	<0.001

Table 2. Linear regression equations comparing calories (y) of food sample on to dry mass (x).

Treatment	Dry mass to Calories	$r^2$	DF	$F$	$P$
Neonatal mice	$y = 5.073 x + 0.066$	0.650	14	24.110	<0.001
Crickets	$y = 8.223 x - 0.366$	0.760	18	53.757	<0.001
Mealworms	$y = 5.924 x + 0.037$	0.562	9	10.281	0.012

Table 3. Linear regression equations comparing wet mass (x) and dry mass (y) of fecal samples by *Crotaphytus collaris*.

Treatment	Wet Mass to Dry Mass	$r^2$	DF	$F$	$P$
Neonatal mouse	$y = 0.228 x + 0.001$	0.588	12	15.684	0.002
3.5% bm-sized cricket	$y = 0.185 x - 0.005$	0.930	22	277.455	< 0.001
1.0% bm-sized cricket	$y = 0.147 x + 0.008$	0.837	19	92.399	< 0.001
3.5% bm-sized mealworm	$y = 0.140 x + 0.011$	0.663	19	35.396	< 0.001
1.0% bm-sized mealworm	$y = 0.123 x + 0.005$	0.911	17	162.889	< 0.001



Table 4. Linear regression equations comparing dry mass (x) and calories (y) of fecal samples by *Crotaphytus collaris*.

Treatment	Dry Mass to Calories	$r^2$	DF	$F$	$P$
Neonatal mouse	$y = 0.840 x + 0.108$	0.084	12	1.014	0.336
3.5% bm-sized cricket	$y = 4.602 x + 0.090$	0.854	22	123.187	< 0.001
1.0% bm-sized cricket	$y = 4.869 x + 0.050$	0.323	19	8.598	0.009
3.5% bm-sized mealworm	$y = 4.687 x + 0.017$	0.634	19	31.238	< 0.001
1.0% bm-sized mealworm	$y = 4.150 x + 0.043$	0.521	17	17.400	< 0.001

Table 5. Digestive efficiency (DE) values for *Crotaphytus collaris* during five meal treatments. DE was calculated using the equation:  $C - F / C \times 100$ , where C =Calories Consumed and F = Fecal Calories.

Treatment	DE (%)
Neonatal mouse meal	90.03
3.5% body mass-sized cricket	89.15
1.0% body mass-sized cricket	70.17
3.5% body mass-sized mealworm	92.71
1.0% body mass-sized mealworm	90.94

Table 6. Linear regressions comparing calories ingested and defecated by *Crotaphytus collaris* per day during the five meal treatments.

Source	Regression	$r^2$	DF	$F$	$P$
Neonatal mouse	$y = 0.042 x + 0.077$	0.002	1, 7	0.014	0.909
3.5% bm-sized cricket	$y = 0.080 x + 0.100$	0.299	1, 11	4.693	0.053
1.0% bm-sized cricket	$y = -0.208 x + 0.364$	0.145	1, 9	1.520	0.249
3.5% bm-sized mealworm	$y = -0.087 x + 0.440$	0.171	1, 11	2.261	0.161
1.0% bm-sized mealworm	$y = 0.047 x + 0.037$	0.026	1, 10	0.264	0.618

Table 7. ANCOVA for calories lost in feces collected from *Crotaphytus collaris* during the five feeding treatments. The slopes for consumption and lizard mass were homogeneous among meal treatment groups.

Source	DF	Type III SS	<i>F</i>	<i>P</i>
Treatment	4	0.24277639	7.01	0.0001
Lizard mass (g)	1	0.00076340	0.09	0.7677
Consumption (Cal)	1	0.00749679	0.87	0.3565

Table 8. Food passage times for *Crotaphytus collaris* fed the five meal treatments.

<sup>a</sup> Indicates means not significantly different from each other.

Treatment	Time (h)	S. D.
Neonatal mouse	69.94	17.32
3.5% body mass-sized cricket	54.55 <sup>a</sup>	12.75
1.0% body mass-sized cricket	58.69 <sup>a</sup>	10.17
3.5% body mass-sized mealworm	55.62 <sup>a</sup>	13.33
1.0% body mass-sized mealworm	54.38 <sup>a</sup>	13.55

Table 9. Food passage times measured by three different marking techniques for *Crotaphytus collaris* fed 3.5% body mass-sized cricket meals ( $P > 0.05$ ).

Marking Technique	Time (h)	S. D.
Colored beads	54.93	12.73
Rubber bands	56.15	17.65
Fluorescent powder	46.54	12.13

## DISCUSSION

### Digestive Efficiency

The DE values of *C. collaris* obtained during the five feeding trials were comparable to values reported for other insectivorous lizards (Johnson and Lillywhite, 1979). The DE of the lizards fed mealworm meals was higher than the DE for the cricket meals, possibly because mealworms contain less chitin and are easier to digest (Witz and Lawrence, 1993) and have more calories due to a higher fat content than crickets (Ruppert, 1980). *Klauberina riversiana* had a DE of 93%, similar to *C. collaris*, when fed mealworm larvae (Johnson and Lillywhite, 1979). Kitchell and Windell (1972) advised against using mealworm larvae in digestive studies because they may cause an unnatural physiological reaction in the digestive tract due to their high fat content, but I observed no adverse effects in the lizards after ingestion of mealworms.

*Crotaphytus collaris* assimilated 90.03% of the total energy in its neonatal mouse meals. The mice lacked chitin and other indigestible parts found in insects, but they contained unknown amounts of milk in the gut. Lizards do not have lactases; therefore, calories in the milk sugar represent energy unattainable by the lizards. Even though neonatal mice are novel food items for *C. collaris*, the high DE value obtained demonstrates the efficiency of a lizard that is a feeding generalist. The ability of *C. collaris* to digest mammalian prey in the field has been documented (McAllister and Trauth, 1982).

The cricket meals closely represent the natural diet of *C. collaris*. Despite the large amount of chitin in crickets, *C. collaris* had a DE of 89.15% when fed meals 3.5% of its body mass. Crickets are similar to grasshoppers, a natural prey item of *C. collaris* (Fitch, 1956); thus, I expected them to digest the crickets efficiently. The value reported in this

study for *C. collaris* fed cricket meals 1.0% of its body mass (70.17%) was much lower than expected. There are two possible reasons for the low value obtained. First, the feeding trial was not long enough to collect adequate samples, even though the food passage time is 58.7 h for cricket meals 1.0% of a lizard's mass. I monitored the consumption and fecal output over a four-day period. Second, once a meal enters the digestive tract, it may become divided and appear in more than one fecal pellet. One lizard included in the 1.0% body mass-sized cricket treatment had a DE value of only 20.50%, because the number of calories defecated was almost equal to the number of calories ingested during the experiment. Future studies should last at least one week to ensure more meals can be consumed and more fecal samples can be collected.

Ruppert (1980) reported that *C. collaris* had a DE of 65% on a cricket diet (*Gryllus* sp.). The mass of the meals was not reported. His lizards were force-fed and did not bite into the crickets and pierce their exoskeletons; thus, digestive enzymes were not as likely to flow into the crickets to begin digestion. Also, the lizards did not have access to basking lights, perhaps influencing their efficiencies. These factors may have resulted in decreased levels of digestion and the low DE value that was observed.

The body mass of *C. collaris* did not affect its DE during the five feeding trials, even though some of the lizards were almost two times the mass of the smallest individual. Similarly, Greenwald and Kanter (1979) observed that the DE of *E. guttata guttata* was not influenced by body mass. Body mass had a significant effect on the consumption rate of *S. undulatus*, and that significantly affected its DE (Angilletta, 2001).

The fairly low correlation found between neonatal mouse dry mass and calories per gram mouse ( $r^2 = 0.65$ ) is perhaps due to individual variation of the mice used as food samples. For example, there may have been different quantities of milk in the guts of



individual mice. A mouse with more milk may have a different effect on digestion than a mouse with less milk. Feces produced from mouse meals contained noticeable amounts of mucus.

The low correlation found between mealworm dry mass and calories per mass of mealworm ( $r^2 = 0.56$ ) may be due to the fact that it is impossible to know at which stage of the molting cycle individuals were, even though they were approximately the same size. A mealworm getting ready to molt would have a greater amount of indigestible cuticle than a mealworm that had just molted. The correlation found between cricket dry mass and calories per cricket ( $r^2 = 0.76$ ) was slightly higher than for the other food samples, perhaps because the crickets used were the same age and size and therefore had the same amount of cuticle.

Linear regression equations of fecal sample dry masses versus calories for the five feeding trials were made in the hope that future researchers could determine the number of calories in a fecal sample without using bomb calorimetry. However, the  $r^2$  values obtained indicate that the correlations among wet to dry masses and dry mass to calories are not sufficiently high to rely on the equations to provide a good estimate of caloric content.

Fecal samples collected from the 3.5% body mass sized meals had a high correlation between fecal wet mass and dry mass ( $r^2 = 0.93$ ) and fecal dry mass and calories ( $r^2 = 0.85$ ). Conversely, there was a lower correlation between fecal wet mass and dry mass ( $r^2 = 0.84$ ) and fecal dry mass and calories ( $r^2 = 0.32$ ) of fecal samples from the 1.0% body mass-sized cricket meals. I am not sure why a difference between the fecal samples of the two cricket treatments was found.

The fecal samples deposited from the 3.5% body mass-sized cricket meals were

overall fairly consistent among and within individuals, containing similar amounts of indigested cricket parts. There was a greater amount of individual variation in the fecal samples deposited by the lizards during the other four feeding trials. The consistency of wet samples differed among individuals because there was variation in the amount of water and / or mucus. Differences in the consistency of fecal samples deposited by the same individual during a single trial were also observed.

The lowest correlation of fecal sample dry mass and calories ( $r^2 = 0.08$ ) resulted from comparing samples collected during the neonatal mouse trial. Perhaps because the mice were a novel food, the lizards' digestive tracts may have reacted differently to the non-insect meals that contained indigestible milk sugar. The fecal samples collected during the neonatal mouse trial had an abnormal consistency (contained more water and mucus) compared to fecal samples collected during the other four trials. This difference in consistency may be indicating that the lizards were processing the mouse meals differently than the insect meals. The low correlation between fecal dry mass and fecal calorie content indicates that some individuals were better at procuring energy from a mouse meal, or that some individuals produced greater quantities of mucus.

For decades, DE values were calculated using the following equation:  $\text{Calories Consumed-Fecal Calories} / \text{Calories Consumed} \times 100$ . Raubenheimer and Simpson (1992) identified potential problems involving the use of ratios when analyzing a nutritional data set using that traditional formula. The equation used by researchers for many years introduces error because it shows a correlation between ingestion and defecation calories even when no correlation is present (Raubenheimer and Simpson, 1992). Analyzing digestive efficiency data with an ANCOVA removes the use of ratios when comparing the number of calories ingested versus defecated during a trial.

Although I did not do statistical analyses on DE values calculated this way, I have included the values I obtained so that my data can be compared with the older literature values.

### **Food Passage Time**

The insect meals may have passed faster than the neonatal mouse meals because they more closely resemble a natural diet of *C. collaris*, and contain a considerable amount of indigestible chitin. Among all four insect treatments, no significant differences were found in the food passage times through *C. collaris*. This is similar to the results observed for *A. carolinensis* where no difference was found among the food passage times of lizards fed mealworm larvae, mealworm adults, and crickets (Windell and Sarokon, 1976).

The neonatal mouse meals may have taken longer to process due to the fact that the individual mice fed to *C. collaris* were larger than individual crickets or mealworms. Naulleau (1983) reported that a slight increase in individual prey item size increased digestion time in *V. aspis*, even though the meals compared were all 10% of the snake's total body mass. In this experiment the neonatal mice ranged from 4% to 6.5% of the lizards' body masses; thus, longer processing times may have been required for the mouse meals because they were larger than the insect meals.

The size of an insect meal (3.5% vs. 1.0% of lizard body mass) did not significantly affect the food passage time of *C. collaris*. Similarly, meal size did not have a significant effect on the digestive rates of the Wandering Garter Snake, *Thamnophis elegans*, (Stevenson *et al.*, 1985) and *P. intermedius* (Alexander *et al.*, 2001). However, in the snakes, *N. natrix* (Skoczylas, 1970) and *V. aspis* (Naulleau, 1983), ingestion of large meals required longer processing times compared to small meals. In the field it is

optimal for an animal to pass a meal as quickly as possible without decreasing DE, regardless of meal size. This provides the animal with more time for other activities, such as courtship and territorial defense. Also, it allows more meals and therefore, greater consumption per activity season, and that translates into more energy available for growth and reproduction.

Body mass did not affect the food passage time for *C. collaris*. Similarly, body mass did not have a significant effect on the digestive rate of the snake, *E. guttata guttata*, (Greenwald and Kanter, 1979) or the turtles, *G. polyphemus* (Bjorndal, 1987) and *P. scripta* (Parmenter, 1981). However, in the Giant Tortoise, *G. gigantea*, body mass had a significant effect on the food passage time (Hamilton and Coe, 1982). As the size of an individual increased, the food passage time significantly increased, although the significance is hard to interpret because the authors did not specify the mass of the animals in each size class or the meal size fed to *G. polyphemus*. Large animals generally have higher consumption rates and in *G. gigantea*, the larger meals required longer processing times (Hamilton and Coe, 1982). Troyer (1984) found that adult *I. iguana* process meals for a significantly longer time compared to hatchling and juvenile *I. iguana* fed the same diet.

Hatch and Afik (1999) found no significant differences in retention times of the Six-lined Racerunner, *Cnemidophorus sexlineatus*, when cricket meals were marked with three different markers (fluorescent pigment, lipid marker, and aqueous markers). Thus, it was not surprising that I found no significant differences among the food passage times of *C. collaris* fed 3.5% body mass-sized cricket meals when measured with three different markers. The benefits of using the plastic colored beads as a marking technique include the convenience of getting the lizards to ingest the beads and the great visibility

of the beads once they appear in the feces. However, there are a couple of problems associated with using the beads as a marking technique. I fed each lizard two beads per day and observed that the beads could become separated inside the gut, as the meal is divided during processing. Also, there were a few beads that were retained inside the digestive tract of the lizards for several days. This did not appear to influence the subsequent feeding or defecation behavior of the lizard.

In summary, meal size did not affect the DE of *C. collaris*, but the type of food ingested had a significant effect on DE. Lizards had the highest DE when fed mealworms and neonatal mice. *Crotaphytus collaris* was able to pass the four insect meals much quicker than the neonatal mouse meals. Insect meal size did not have a significant effect on the passage time of *C. collaris*. The faster *C. collaris* is able to pass its meals, the more time and energy it will have available for other activities, such as foraging, courtship, and territoriality. This study was important because *C. collaris* is a typical lizard whose digestive physiology is similar to many lizard species. Thus, one may infer that how *C. collaris* processes its meals may be similar to other generalist feeding species.

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