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Author(s): Graham J. Alexander, Charl van Der Heever and Shirleen L. Lazenby

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Thermal Dependence of Appetite and Digestive Rate in the Flat Lizard, Platysaurus intermedius wilhelmi

GRAHAM J. ALEXANDER,1 CHARL VAN DER HEEVER, AND SHIRLEEN L. LAZENBY

Ecophysiological Studies Research Programme, Department of Animal, Plant, and Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa

ABSTRACT.—We investigated the thermal dependence of appetite and digestive rate in the flat lizard, Platysaurus intermedius wilhelmi, over a wide thermal range (12°–34°C). Because Platysaurus seldom venture off rock outcrops, their body temperatures are determined to a large extent by the thermal characteristics of this microhabitat. Our results demonstrate that appetite, measured as the number of food items eaten in a given time, is clearly temperature-dependent, increasing to a maximum that coincides with the thermal preference of 32°C for the species. Our measures for digestive rate, measured as the time to the first passing of feces after a meal, are temperature-dependent below 22°C but are temperature-independent between 22° and 34°C. Furthermore, our data indicate a critical body temperature of 12°C, below which all feeding ceases. We predict that lizards of this species with Tb below 20°C are effectively excluded from nutritive energy gain under natural conditions.

To remain in positive nutritive energy balance, organisms must ensure that energy gain through feeding exceeds energy expenditure through growth, work, and reproduction (Campbell and Norman, 1998). Energy gain may be constrained by food availability, digestive efficiency, digestive rate (Andrews, 1982), and food acceptance. Any of these constraints, operating singly or in combination, could prevent organisms from surviving in certain areas. We investigated the effect of temperature on food acceptance and digestive rate, in the lizard Platysaurus intermedius wilhelmi.

Temperature affects food ingestion rates in reptiles at two levels. First, at an ecological level, environmental conditions may limit food availability so that at extreme temperatures vegetable food may either not grow or prey may not be active and thus not accessible. Hence, at these extremes, reptiles may require food but be unable to procure it. Second, at an organismal level, temperature affects various physiological processes associated with energy gain. Both Naulleau (1983) and Stevenson et al. (1985) have shown that, in snakes, as Tb increases, digestive rate increases, and if Tb drops soon after consumption, food may even be regurgitated. Waldschmidt et al. (1986), Van Damme et al. (1991), and Beaufre et al. (1993) have reported similar relationships in lizards. Within the thermoregulatory set point range, enzymatic function is usually optimal, resulting in increased rates of digestion (Peterson et al., 1993).

Digestive efficiency, the proportion of the energy ingested that is actually absorbed through the gut, is usually also affected by Tb in lizards (Harlow et al., 1976; Ruppert, 1980; Troyer, 1987), although there are exceptions (Karasov and Diamond, 1985; Zimmerman and Tracy, 1989; McKinon and Alexander, 1999). Where digestive efficiency is independent of Tb, this is probably the result of the longer processing times allowed by slower gut passage times at lower Tb. The slower gut passage times may allow gastric enzymes more time to digest food at reduced temperatures and compensate for the reduced efficiency of the gastric enzymes. Temperature effects may therefore result in negligible differences in the absolute amount of energy extracted from any particular food item in these species. This type of temperature-independent digestion could represent a physiological adaptation either to situations where food availability is a primary limiting factor or in situations where thermoregulatory options are significantly constrained by the environment.

In species that have temperature-dependent digestive efficiency, daily and seasonal temperature fluctuations may have an important influence on their energy budgets. Grant and Dunham (1990), for example, demonstrated that Scoloporus merriami has lower growth rates in habitats that constrain thermoregulatory options even if food abundance is high, probably as a result of lower processing rates. If thermoregulatory adjustments are insufficient to maintain Tb in the preferred range, reptiles may thus be unable to remain in positive energy balance.

We investigated the effect of Tb on two physiological aspects of food intake in the common flat lizard, P. i. wilhelmi: food acceptance rate (hereafter referred to as appetite), under con-

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1 Corresponding Author. E-mail: graham@gecko.biol.wits.ac.za.
ditions where food availability was not limiting; and digestive rate, measured indirectly as gut passage time. Previous work by McKinon and Alexander (1999) has shown *P. i. wilhelmi* to have temperature-independent digestive efficiency, at least over the temperature range tested (26°–31°C), and temperature-dependent digestive rate, measured as time taken for all feces from a meal to be passed, over the same temperature range. Our definition of gut passage time differed from McKinon and Alexander's in the respect that our measure was defined as the time taken for the first feces from a meal to be passed. Our intention was to quantify constraints to food acquisition in this species in an attempt to further understand which factors may be important constraints to the occurrence of the species.

*Platysaurus* is a speciose genus of saxicolous, omnivorous lizards (Whiting and Greeff, 1997) endemic to southern Africa (Mouton and van Wyk, 1997). The genus is extraordinary because all species are highly dorso-ventrally flattened, allowing them access to narrow crevices. All *Platysaurus* occur exclusively on granite, gneiss or sandstone outcrops (Branch, 1988), from which they seldom venture. The fact that *Platysaurus* does not occur on some apparently suitable outcrops in southern Africa (Broadley, 1978; C. L. Marshall, unpubl.data) could be explained by either of two hypotheses. First, because the genus is highly specialized for life on rock outcrops, the lizards have poor dispersal abilities (Broadley, 1978), and they may simply not have reached uninhabited outcrops. Alternatively, uninhabited outcrops might be unsuitable for sustaining populations of the lizards resulting from, for example, inappropriate thermal conditions or other limiting factors. Certainly, the thermal characteristics of the outcrops are likely to define the thermal opportunities available to the lizards and may thus impose real thermal constraints on their digestive physiology. Egan (1997) reported preferred *T*ₚ's of between 32°C and 34°C of *P. i. wilhelmi* in a thermal gradient, but reports that the average *T*ₚ's achieved by free-ranging individuals average less than 25°C in the field. It is from this perspective that we attempted to gain an understanding about how the thermal environment affects the biology of *Platysaurus*.

The subspecies that we worked on, *P. i. wilhelmi*, is limited to Zimbabwe and the eastern parts of Mpumalanga Province in South Africa (Branch, 1988) and occurs exclusively on granite outcrops. Individuals reach a maximum snout-vent length of 80 mm and rarely exceed 10 g in mass. Their small size and flattened body shape ensures that individuals that are denied basking opportunities, such as in the laboratory conditions of our study, are unable to maintain significant temperature differentials between body and environment over time.

**Methods and Materials**

**Capture and Acclimatization.**—Twenty-eight *P. i. wilhelmi* (5.8 g ± 1.8; mean ± SD) were captured in Mpumalanga Province, South Africa (24°35’S; 31°11’E; altitude 700 m) using sticky-traps. Lizards (eight males; 20 females) were housed individually in glass terraria (300 mm × 225 mm × 225 mm). Each terrarium contained several rocks as retreat sites and lizards were acclimatized for one month before feeding trials commenced. During acclimatization and during measurements, photoperiod remained constant with a L:D of 12:12. During the acclimatization period, ambient temperature remained constant at 28°C and lizards were fed ad libitum on a diet including various insects (*Tenebrio* beetle larvae and adults, termites, and cockroaches) and canned dog food supplemented with Beefy Powder. Water was provided at all times in small petri dishes.

**Inferring *T*ₚ by Measuring Ambient Temperature.**—Because the only feasible method available to us for measuring *T*ₚ directly in such small lizards involved restraining the lizards, we measured the relationship between lizard *T*ₚ and air temperature (*T*ₐ) under our experimental conditions. Terraria containing lizards were placed in a walk-in environmental chamber (temperature range of less than 1°C), and lizard *T*ₐ was measured after one hour by inserting a T-type thermocouple into their cloacas. Measures were made at both the lower and upper extremes of the temperature range over which we made our digestion measures (12°C and 34°C). At both of these temperatures, the *T*ₚ of the lizards (*N* = 28) was within 1°C of *T*ₚ of the chamber, and thus, we assumed that *T*ₚ approximated lizard *T*ₚ under the conditions of our experimental protocol.

**Measurement of Appetite and Gut Passage Time.**—Ambient temperatures during feeding trials did not vary by more than 1°C and were monitored on a PC-based Powerlab/800 (AD-Instruments) linked to a thermistor (MCS; South Africa). Measures of appetite and gut passage times were made at 2°C intervals, from a low of 12°C to a high of 34°C. This range spans much of the environmental temperature range that these lizards are likely to encounter in the field. The sequence of the trials was randomized to avoid any seasonal effects or other time-based influences on our measures of appetite and digestion rate.

Because recent feeding history dictates the degree of satiation in an individual, it has an important influence on appetite (Woods et al.,
1998). We minimized this effect by separating each feeding trial with a rest period of nine
days, during which time the lizards were main-
tained at 33°C (midpoint of selected thermal
range). They were fed an unrestricted diet of
canned dog food for the first four days of this
rest period, followed by a five-day starvation pe-
riod. Thus lizards entered each trial with a sim-
ilar recent feeding history and, thus, similar de-
gree of satiation.

The first 24-h period of each feeding trial was
used to stabilize the temperature of the chamber
at the new trial temperature and to allow the Tb
of the lizards to equal the ambient temperature.
On the second day of each trial, lizards were fed
mealworms (Tenebrio beetle larvae; mass per
mealworm 0.179 g ± 0.037; mean ± SD; we
used only mealworms of premetamorphosis
stage to minimize variation in mealworm size)
ad libitum; initially 10 mealworms were offered
to each lizard, and they were then checked reg-
ularly to assess the need for more. None of the
lizards ever consumed more than five meal-
worms during a feeding trial; five mealworms
equaled approximately 15% of the average liz-
ard’s body mass. The excess amount of food of-
tered to each lizard prevented any effect of food
availability on our measures of appetite. Appeti-
te was measured as the number of mealworms
consumed by each lizard in 24 h. We measured
appetite as the number of mealworms eaten,
rather than as the mass of food eaten for the
following reasons. First, measuring the number
of food items consumed by a lizard is a more
direct measure on the number of “choices mo-
tivated by appetite” that the lizard has made.
*Platysaurus intermedius wilhelmii* are unable to
break mealworms into pieces and usually swal-
low the beetle larvae whole. Second, because
mealworm mass is variable, it would have been
difficult to monitor the identity of mealworms
consumed by each lizard, especially since meal-
worms dehydrate at different rates under each
trial temperature.

We assessed digestion rate using the indirect
measure of gut passage time, which was record-
ed as the number of days to first defecation after
feeding. We used time to first defecation rather
than the more usual measure of time to last de-
fecation to minimize the time that the lizards
had to spend at each trial temperature. We did
not use artificial markers to distinguish whether
feces were derived from food ingested during a
trial or rest periods (see Zimmerman and Tracy,
1989), since lizards were only fed canned dog
food during rest periods and feces derived from
mealworm meals were easily distinguished by
their exoskeleton fragments. Trials were termi-
nated once all the lizards that fed had passed
feces or after 21 days.

Statistical Analysis.—Appetite and gut pas-
sage time data were normally distributed (Kol-
mogorov-Smirnov test for normality; *P* > 0.05
for each temperature trial). We used one-way
ANOVA (gender as factor) with repeated mea-
sures (temperature) and a Tukey pairwise com-
parison posthoc test to test for gender and tem-
perature effects on appetite. We also related the
number of lizards that accepted any food dur-
ing each trial to temperature to predict the tem-
perature at which all feeding would cease.

Lizards that did not eat during a particular
feeding trial did not produce feces, giving no
measure of gut passage time for that trial. This
resulted in an incomplete dataset on gut pas-
sage time and precluded use of a one-way AN-
OVA with repeated measures. Instead, we test-
ed for temperature effects on gut passage time
using a repeated-measures ANOVA and tested
for gender-based differences in passage time us-
ing ANCOVA (gender as factor; temperature as
covariate) to test whether linearized (log-trans-
formed) measures of gut passage time and tem-
perature were different for males and females.
Because there is not true independence among
temperatures (the same lizards were used in
each trial), we reduced the lower degree of free-
dom of the ANCOVA by dividing by the num-
ber of lizards used (28).

We also tested whether the amount of food
consumed by a lizard had any effect on gut pas-
sage time. We used regression analysis and test-
ed for a relationship for each temperature trial
from 34°C to 18°C. Lower temperature trials
were excluded from this analysis since very few
lizards consumed any food at trials below 18°C.

RESULTS

Temperature had a significant effect on ap-
petite (*F*11,286 = 50.3; *P* < 0.001). At low tem-
peratures, lizards had reduced appetite, and few
lizards fed at all during feeding trials at tem-
peratures below 18°C (Fig. 1). Tukey pairwise
comparisons revealed significant differences in
45 of 66 comparisons. Generally, significant dif-
f erences were between low and high tempera-
ture trials. Appetite was uniformly high be-
tween 24°C to 34°C; only the trial at 28°C
showed any significant differences from the oth-
er temperatures in this range. Trials at 12°C,
14°C, and 16°C were not significantly different
from one another, probably because appetite
was uniformly suppressed at these tempera-
tures. The relationship between *Tb* and the per-
centage of lizards that fed indicated that these
lizards effectively stop feeding at approximately
12°C (Fig. 1). The maximum *Tb* for feeding in *P.
wilhelmii* was above our highest trial tempera-
ture (34°C) and so we were unable to measure
the upper temperature limit for feeding. We de-
detected no significant differences in appetite because of gender ($F_{1,29} = 0.64; P = 0.43$), and there was no significant interaction between temperature and gender ($F_{1,286} = 0.54; P = 0.87$).

Temperature had a significant effect on our measures of gut passage time ($F_{3,32} = 42.3; P < 0.001$; Fig 2). However, because few lizards fed at low temperatures, and those that did feed failed to produce feces within 21 days, both the 12°C and 14°C feeding trials were excluded from our analysis. Logistical reasons prevented a measure at 20°C and we were unable to repeat this trial because of time constraints. Tukey pairwise comparisons revealed significant differences in 15 of 36 comparisons. Gut passage time to first feces was not significantly different for trials between 22°C and 34°C but increased significantly for trials at 16°C and 18°C, indicating reduced digestive rates at these temperatures. We detected no significant differences in gut passage time resulting from gender using ANCOVA ($F_{1,21} = 0.35; P = 0.57$) and found no relationship between meal size and time to first feces at any of the trial temperature tested ($P > 0.35$ in all cases).

**Discussion**

We clearly demonstrated that the digestive physiology of *P. i. wilhelmi* is profoundly affected by $T_s$ when $T_s$ is below preferred levels but is relatively insensitive to changes in $T_s$ above the preferred temperature range. Our measures show that appetite is suppressed at $T_s$s below 22°C, whereas our measures of gut passage time increased sharply for the 16°C and 18°C trials. Gut passage times for trials at 12°C and 14°C were so slow that the trials had to be terminated before the lizards passed feces. These relationships between digestive physiology and temperature were expected because the higher temperatures of the selected thermal range are conducive to high rates of digestion. Together, our measures suggest that *P. i. wilhelmi* require $T_s$s of at least 20°C to be capable of gaining energy through food consumption, and this limitation may well have important implications for the persistence of populations of this species in areas where temperatures remain below 20°C for extended periods.

Other researchers have reported temperature-dependent appetite in various species of lizards (Waldschmidt et al., 1986; Van Damme et al., 1991; Beaupré et al., 1993). However, these researchers did not explicitly control for the confounding influence of recent feeding history when measuring appetite in response to an extrinsic variable such as temperature. We removed the influence of recent feeding history on our measures of appetite by standardizing a rest period that all lizards went through between each trial. The rest period also served to quickly reestablish energy balance in the lizards after the colder trials, during which most lizards fasted. Although we did not standardize their level of satiation in response to other factors, such as body condition, we assumed that these effects would be have been similar for each temperature trial. We also removed the effect of food availability on our measures of appetite by supplying food in excess during trials, allowing us to separate the effects of food availability from the physiological characteristics of the lizards.

Ji et al. (1993) argued that higher rates of food intake in another species of lizard, *Takydromus septentrionalis*, were a result of warmer lizards having higher energy demands for somatic maintenance. Their explanation would be defined as a "depletion-repletion" model by
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Woods et al. (1998) because meals are initiated by decreasing levels of available energy. *Platy-
saurus intermedius wilhelmi* ceased feeding completely at approximately 12°C, indicating that other factors may have an influence on appetite in these lizards. Lizards still require energy, albeit at reduced rates, for somatic maintenance at 12°C. Other lizard species, under various experimental protocols, have been shown to stop eating at temperatures well above the 12°C threshold that we measured for *P. i. wilhelmi*. For example, Harwood (1979) reported that Scel-
oporus occidentalis stopped eating at 20.2°C, whereas Beaupre et al. (1993) reported that the vast majority of *S. merriami* tested would not eat at 28°C. Clearly, these lizards would also have metabolic requirements at these temperatures.

Our low estimate for cessation of feeding in *P. i. wilhelmi* may not be a result of real differences between species but rather a result of differences in experimental protocol. In studies by Harwood (1979), Waldschmidt et al. (1986), and Beaupre et al. (1993), lizards were not starved before food consumption measures were made. Because our lizards experienced a five-day starvation period at 33°C before each trial, their motivation to eat may well have been increased. Waldschmidt et al., (1986) reported an increased appetite in *Uta stansburiana* that had restricted access to food. However, Waldschmidt et al. (1986) also contend that a restricted food ration most likely approximates the response of lizards under natural conditions.

Woods et al. (1998) defined a second category of models explaining the regulation of food intake, which they name “lipostatic models.” In these models, regulation of food intake is mediated through an integration of signals proportional to the size of fat reserves with other regulators of food intake, such as learned associations, opportunity, social factors, or time of day. We believe the regulation of food intake with our lizards is not well explained by this type of model since most of these factors remained constant throughout all feeding trials in our study. A more likely explanation is that temperature-mediated limits on the physiology of the lizards limited the rate at which our lizards could process food and that it was this limitation that resulted in the suppression of appetite at lower temperatures. Congdon (1989) has implicated limitations in process rate in aquatic turtles that occupy cold, productive habitats. In situations such as these, food intake is mediated, not by the energetic requirements of the individual but rather is limited by the physiological capabilities of the organism.

Our finding that gut passage time is temperature-independent above 22°C appears to be at odds with the findings of McKinon and Alexander (1999) who found differences in passage time between 26°C and 31°C for *P. i. wilhelmi*. However, McKinon and Alexander (1999) measured gut passage time as “time to the last feces being passed after a meal,” whereas we used “time to the first feces” as our measure. Viewed in combination, the results from these two studies indicate that *P. i. wilhelmi* increase the time available for digestion by increasing the lag between the first and last feces when temperature decreases. Thus, at Tₛ above 30°C, all the feces derived from a particular meal are passed during the third day after the meal, whereas at temperatures below this, feces are passed over a more extended period, even though the first feces are passed on day three. We suggest that this relationship persists down to Tₛ of 22°C, when time to first feces begins to increase in response to lower Tₛ, resulting from impaired functioning of the lizard’s digestive physiology. Beaupre et al. (1993) found a similar relationship between gut passage time and temperature in *S. merriami*; only their measure of time from ingestion to the final appearance of the marker in the feces was significantly affected by temperature.

Peterson et al. (1993) contended that gut passage time is not an accurate measure of digestive rate, at least not for snakes. They argue that snakes are able to retain feces in their large intestines for considerable periods of time. Thus, gut passage time is determined both by the digestive rate plus the length of time between digestion and defecation. Although it is unlikely that gut passage time measures on lizards suffer from this effect to the same extent (lizards tend to be frequent, small meal feeders with a more continuous throughput), a comparison of the results of our study with that of McKinon and Alexander (1999) does highlight the importance of how the gut passage measures are made. Although our measures show temperature-indepen-
dence of gut passage time, they really only indicate that the initiation of defecation is temperature-independent over this temperature range. A better measure of digestion rate would be to measure both the time to first feces and the duration of time over which feces were passed for a meal. However, these data could be especially problematic to collect at low temper-
atures, considering that in some instances *P. i. wilhelmi* had not produced their first feces 21 days after the meal.

Our goal was to explore the relationship between temperature and digestive physiology in *P. i. wilhelmi*, to understand better the factors that may be limiting the distribution of this species to particular areas. Although we are now able to predict that *P. i. wilhelmi* with Tₛ of 20°C or lower are effectively excluded from nutritive
energy gain under natural conditions, it would be enlightening to measure how important the effect of recent feeding history is on appetite. We standardized the recent feeding history of our lizards between feeding trials so that all lizards were equally hungry during trials. However, this factor might well have a large effect on whether lizards are willing to eat under any particular conditions.

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