Does foraging mode affect metabolic responses to feeding? A study of pygopodid lizards

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Abstract Foraging mode (ambush vs. active) profoundly affects many aspects of organismal biology, including metabolic rates and their relationship with food intake. Previous studies on snakes suggest that ambushers tend to have lower standard metabolic rates (SMR) and higher energetic costs of digestion and assimilation of prey (specific dynamic action, or SDA) than do active foragers. However, phylogenetic considerations may be at least partly responsible for such patterns, as foraging mode is strongly conserved evolutionarily and most SDA studies have focused on species from only two lineages of ambush foragers (pythonid and viperid snakes) and one lineage of active foragers (colubrid snakes). We sought to deconfound the effects of phylogeny and foraging mode, investigating SMR and SDA in two closely related pygopodid lizards, the common scaly-foot Pygopus lepidopodus (active forager) and Burton’s legless lizard Lialis burtonis (ambush forager). Consistent with the pattern seen in snakes, L. burtonis exhibits a significantly lower SMR and a higher SDA than does P. lepidopodus. The magnitude of SDA in L. burtonis is comparable to that of some pythons and vipers, providing yet more evidence for the remarkable convergence between this species and ambush-foraging snakes [Current Zoology 59 (5): 618–625, 2013].

Keywords Ecology, Metabolic rates, Reptile, Specific dynamic action

Predatory animals can be classified into one of two categories, depending upon how they capture their food: active foragers chase prey down, whereas ambushers wait for prey to come to them (Pianka, 1966; Schoener, 1971; Huey and Pianka, 1981). Although this dichotomy undoubtedly is an oversimplification (e.g., Perry, 1999), many predator species can unambiguously be assigned to one or the other of these foraging modes. Further, many other organismal traits are closely associated with this dichotomy. For example, foraging mode in squamate reptiles (lizards and snakes) influences many aspects of morphology, behavior, ecology, life history, and evolution. Ambush-foraging lizards and snakes tend to be more heavy-bodied than active foragers (Vitt and Congdon, 1978; Secor, 1995), rely more on crypsis than flight to avoid predators (Secor, 1995; Pianka and Vitt, 2003), experience lower predation rates (Huey and Pianka, 1981; Bonnet et al., 1999; Webb et al., 2003), feed less frequently (Anderson and Karasov, 1981; Hailey and Davies, 1986; Secor, 1995), and take a lower diversity of prey types (Naulleau and Bonnet, 1995; Pianka and Vitt, 2003).

Foraging mode also has profound physiological consequences for squamates. Ambushers generally have lower resting metabolic rates than do active foragers (Anderson and Karasov, 1981; Secor and Nagy, 1994), and, at least in snakes, exhibit a higher energetic cost of digesting and assimilating prey (specific dynamic action, or SDA: Secor and Diamond, 2000; Secor, 2001). These patterns likely result from the difference in feeding frequency between the two foraging modes: ambush-foraging snakes down-regulate their gut in the long intervals between meals, saving considerable energy. However, they must rapidly up-regulate gut morphology and function upon feeding, and this energetically costly process results in a large SDA (Secor and Diamond, 1997a; Secor, 2001; but see Overgaard et al., 2002).

Despite these broad patterns, causation of these myriad differences remains unclear because foraging mode is conservative phylogenetically in lizards and snakes (Greene, 1997; Pianka and Vitt, 2003; Butler, 2005). Many lineages exhibit only one foraging mode or the other; reversals are rare. In lizards, for instance, iguanids, agamids, chamaeleonids and gekkotans primarily ambush prey, while teiids, scincids, and most varanids forage actively (Pianka and Vitt, 2003). Similarly, boas, pythons, and vipers hunt mainly by ambush, whereas elapids and colubrids tend to be more active (Greene,
1997). To understand the impact of foraging mode on squamate ecology, we must deconfound phylogeny by investigating closely related species that differ in foraging mode.

The lizard family Pygopodidae provides such an opportunity. Pygopodids are elongate, functionally limbless lizards endemic to Australia and New Guinea (Cogger, 2000); their closest relatives are carphodactyline geckos (Kluge, 1976; Donnellan et al., 1999). Pygopodids are ecologically diverse; the 38 species (Jennings et al., 2003) range from actively foraging burrowers that specialize on ant larvae (Aprasia sp.; Webb and Shine, 1994) to taxa that take scincid lizards from ambush (Lialis burtonis and L. jicari: Patchell and Shine, 1986b; Murray et al., 1991).

We investigated the effect of foraging mode on lizard physiology by studying two pygopodid species: the common scaly-foot Pygopus lepidopodus, which forages actively, and the ambushing Burton’s legless lizard Lialis burtonis. Ambush foraging in Lialis burtonis has been confirmed by detailed radiotelemetric monitoring (Wall and Shine, 2013). There are no equivalent field studies of Pygopus, but stomach-contents analysis has shown that many of the spiders (with egg sacs) consumed by these lizards are sedentary, rarely leaving their home burrows (Patchell and Shine, 1986b). Such sedentary prey can be captured only by an active forager. Predicted differences in feeding frequency also are borne out in these two species: P. lepidopodus stomachs contain prey about 74% of the time (Patchell and Shine, 1986b), while L. burtonis have food in their guts only 17–33% of the time (Huey et al., 2001; Wall, 2006).

These two species are very similar to each other in general body shape (Cogger, 2000) and body size (snout-vent lengths [SVLs] of adult males = 140 to 217 mm in Lialis burtonis vs 122 to 209 mm in Pygopus lepidopodus; for adult females, 160 to 291 mm vs 137 to 224 mm respectively: Patchell and Shine, 1986b). Both taxa are distributed across a wide range of habitat types, often in sympatry (Cogger, 2000). We tested the often-reported prediction that ambushers will have lower standard metabolic rates (SMR) and higher SDAs than do active foragers (Secor, 2001).

1 Materials and Methods

1.1 Study animals and maintenance

Ten non-gravid adult female Lialis burtonis and four non-gravid adult female Pygopus lepidopodus were collected from the Sydney area between March 2003 and March 2004. Lizards were brought to the University of Sydney, where they were maintained individually in plastic cages (22 × 22 × 7.5 cm) on a 12:12 light:dark cycle. Room temperature was kept at 20°C, but heated strips running under one end of each cage allowed lizards to thermoregulate behaviorally during the diurnal part of their daily cycle. They also had access to shelter and water ad libitum. Lialis burtonis were fed skinks biweekly, while P. lepidopodus, which eats spiders and other arthropods in the wild (Patchell and Shine, 1986b), received crickets 2–3 times a week.

1.2 Respirometry

We quantified the rate of oxygen consumption (\(\dot{V}O_2\), a measure of metabolic rate) using flow-through respirometry. Respirometry chambers consisted of Perspex tubes measuring 136 mm wide × 157 mm long (volume 228 cm\(^3\)). Chambers were placed in an incubator at 30°C, within the range of normal activity temperatures for many squamate species (Avery, 1982), including L. burtonis (Bradshaw et al., 1980; Wall, 2006) and P. lepidopodus (Greer, 1989). This temperature has also been used for most other studies of SDA in lizards and snakes (e.g., Secor, 2001; McCue and Lillywhite, 2002; Toledo et al., 2003; Zaidan and Beaupre, 2003). Lights within the incubator were on for the duration of each trial to eliminate or minimize any diurnal rhythms (which occur in some other squamate species; Iglesias et al., 2003; Roe et al., 2004), and to allow for visual monitoring of lizard activity via a fisheye lens installed in the incubator door. Half of each tube was covered with white paper, providing lizards with cover. All lizards were habituated to the chambers in the incubator for at least five 4-hour periods beginning several weeks before experiments commenced. Such conditioning trials increase the likelihood that lizards are truly at rest when standard metabolic rates are measured (Hare et al., 2004).

Air was drawn through the chambers by a flow controller at 23.6 mL min\(^{-1}\) and passed through Drierite\(^\text{®}\) to absorb water, Carbasorb\(^\text{®}\) to absorb carbon dioxide, and then through Drierite\(^\text{®}\) once again. Oxygen concentration of the air was measured using a 2-channel Ametek N-37M oxygen sensor and Ametek S/3A-11 oxygen analyzer.

1.3 Experimental procedures

Six adult female L. burtonis (mean snout-vent length [SVL] 19.5 ± 0.43 cm; mass 15.23 ±1.47 g) were habituated to the apparatus and fasted for 2 weeks to ensure a post-absorptive state. Four lizards (one to a chamber) were placed in the incubator at 1300 h and allowed to equilibrate for one day. The first \(\dot{V}O_2\)
measurement was taken 24 h after lizards were introduced to the incubator; another was taken 19 h later. Measurements were made in one-hour stretches during which lizards were not visibly active; a representative sample of this period was used to calculate oxygen consumption. Forty-eight hours after introduction, two of the *L. burtonis* were fed one locally caught skink representing 10% of their body mass (mean relative prey mass [RPM] = 0.102 ± 0.001). All *L. burtonis* were fed in their respirometry chambers. VO$_2$ was then measured at specified times over the next five days: at 24 and 5 h before feeding, and 6, 12, 18, 24, 36, 54, 72, 90, and 114 h post-feeding. The other two *L. burtonis* in the incubator served as unfed controls; their VO$_2$ was measured at the same times.

This process was repeated two more times, until all six *L. burtonis* had been measured in both the fasting and fed states. Half of the lizards were measured first when fasted, and half when fed. Lizards were always given at least two weeks between successive trials to ensure they were post-absorptive. Handling was kept to a minimum; lizards remained in the incubator for the duration of each trial. They were disturbed only when necessary (when clearing feces from respirometry chambers, for example, and when providing water every second day).

The same protocol was followed with four adult female *P. lepidopodus* (SVL 18.2 ± 0.64 cm; mass 29.52 ± 2.74 g). They were given a meal of house crickets (*Acheta domesticus*) with an RPM of 0.099 ± 0.0007, not significantly different from the relative size of the meals eaten by *L. burtonis* ($t_8 = 1.77, P = 0.12$).

In addition, we measured VO$_2$ in this manner for four different adult female *L. burtonis* (20.6 ± 0.82 cm SVL; 17.3 ± 2.61 g mass) at a larger prey size (RPM = 0.253 ± 0.005). Again, each *L. burtonis* was fed a single skink in its respirometry chamber. We measured VO$_2$ at the same intervals as described above but continued for two additional days (138 and 162 h post-feeding). We performed this experiment for two reasons: to investigate the effects of prey size on SDA in *L. burtonis*, as has been done in numerous snake species (e.g., Andrade et al., 1997; Secor and Faulkner, 2002; Toledo et al., 2003; Zaidan and Beaupre, 2003); and to compare the SDA of *L. burtonis* with that of ambush-foraging snakes (with which it is strongly convergent: Patchell and Shine, 1986a,b,c; Murray et al., 1991) more directly, by using a similar RPM as in previous studies of snakes (typically, 0.25: Secor, 2001). All experiments were performed from November 2004 to February 2005.

### 1.4 Determining SMR and the magnitude of SDA

We found no evidence of circadian rhythms in either species; VO$_2$ of unfed lizards was similar during the day and at night (paired t-tests, day vs. night: *L. burtonis*: $t_9 = 0.48, P = 0.64$; *P. lepidopodus*: $t_1 = 1.76, P = 0.18$). We therefore calculated SMR for each individual *L. burtonis* ($n = 10$) and *P. lepidopodus* ($n = 4$) by averaging all of its fasting measurements.

There are several ways to quantify the SDA response (Jobling, 1981; Secor and Diamond, 1997a; Wang et al., 2001). We chose four of the most common: (1) time, in hours, to peak VO$_2$; (2) time, in hours, to return to SMR; (3) metabolic peak (peak VO$_2$/SMR); and (4) the SDA coefficient (the percentage of the meal’s energy lost to SDA). To arrive at this last value, which is probably the most relevant measure of the bioenergetic meaning of SDA (Kleiber, 1961; Beaupre, 2005), we first calculated the total oxygen consumed above baseline during digestion, using Simpson’s approximation (Stein and Barcellos, 1992), to compute the area under VO$_2$ curves of fed and unfed lizards. We converted this value to energy, assuming that 19.8 joules were expended per mL of O$_2$ consumed (Gessaman and Nagy, 1988). We then compared this number to the total energy represented by each meal, assuming conversion factors of 6.4 kJ g$^{-1}$ for skinks [lizards contain 80% of the meal energy of rodents (Crissey and Toddes, 1998), which is 8.0 kJ g$^{-1}$ (Secor and Faulkner, 2002)] and 8.0 kJ g$^{-1}$ for crickets (Secor and Faulkner, 2002).

### 1.5 Statistical analyses

We log-transformed all VO$_2$ data to achieve normality and homogeneity of variances. The nature of the SDA response within each species and prey size was investigated using repeated-measures ANOVA; the post-hoc Fisher’s PLSD test was employed to determine when oxygen consumption of fed lizards departed significantly from that of unfed animals. However, as the relationship between SDA and body mass is allometric (Beaupre, 2005), we utilized ANCOVA, with log mass as the covariate, to compare SDA among groups. We also compared SMR between *L. burtonis* and *P. lepidopodus* in this manner, because SMR often scales allometrically with body mass as well (Packard and Boardman, 1999; Beaupre, 2005).

### 2 Results

#### 2.1 Standard metabolic rate

*Liolis burtonis* had a significantly lower SMR than
did *P. lepidopodus* (ANCOVA; $F_{1,11} = 43.46, P < 0.0001$); the covariate, mass, also had a significant effect, with larger animals having higher metabolic rates ($F_{1,11} = 8.99, P = 0.012$; Fig. 1). The mass-specific SMR values, reported here only for comparison with other studies, are: *L. burtonis*, 0.038 ± 0.002 mL O$_2$ h$^{-1}$ g$^{-1}$; *P. lepidopodus*, 0.060 ± 0.005 mL O$_2$ h$^{-1}$ g$^{-1}$.

### 2.2 SDA

In all three experiments, feeding caused a significant increase in VO$_2$ (*L. burtonis* at 0.10 RPM: $F_{1,5} = 146.81$, Fig. 1A; *P. lepidopodus* at 0.10 RPM: $F_{1,3} = 24.84, P = 0.016$; *L. burtonis* at 0.25 RPM: $F_{1,3} = 108.46, P = 0.002$; Fig. 1B). VO$_2$ of *L. burtonis* at 0.25 RPM, however, did not return to baseline until the 138 h post-feeding measurement (Fisher’s PLSD, $P = 0.17$; Fig. 1C, Table 1).

Metabolic peak of *L. burtonis* at 0.10 RPM was 4.22, significantly higher than that of *P. lepidopodus* at the same meal size (2.83; Table 1). Metabolic peak of *L. burtonis* at 0.25 RPM (6.46) was significantly greater than both of these values (Table 1). At 0.10 and 0.25 RPM, *L. burtonis* burned about the same proportion of its meal energy during the SDA response (17.0% and 18.8%, respectively); both of these numbers were higher than the relevant value for *P. lepidopodus* (12.8%; Table 1). The covariate, log mass, had a significant effect; in both species, larger animals had higher SDA coefficients ($P = 0.043$).

### 3 Discussion

Circadian rhythms in metabolic rate are common in lizards and snakes (e.g., Niewiarowski and Waldshmidt, 1992; Iglesias et al., 2003; Zaidan, 2003; Roe et al., 2004). The lack of any day-night differences in metabolic rates of *L. burtonis* and *P. lepidopodus* (see Materials and Methods) may be a result of their broad activity patterns. Both species may be active at any time of day or night (Greer, 1989).

In accord with foraging mode theory (Anderson and Karasov, 1981; Secor and Nagy, 1994), the ambush-foraging *L. burtonis* exhibits a significantly lower SMR than does the actively-foraging *P. lepidopodus*. Further, both species have substantially lower SMRs than predicted by interspecific allometric curves for lizards at 30°C (Andrews and Pough, 1985). Specifically, the observed rate of oxygen consumption in *P. lepidopodus* is 65% of the expected value for a lizard of similar mass, whereas that of *L. burtonis* is only 36% of that expected. In their analysis of squamate metabolic rates, Andrews and Pough (1985) found no differences between VO$_2$ of gekkos (pygopodids’ closest relatives) and that of other lizard families, but phylogeny may still be a factor. Ours
Time to reach peak oxygen consumption and time to return to resting VO₂ at a meal size of 0.10 RPM are similar in the two pygopodid species (Table 1). However, consistent with predictions from foraging mode theory (Secor and Diamond, 2000; Secor, 2001), L. burtonis experiences a higher SDA than does P. lepidopodus, with a higher metabolic peak (4.22 vs. 2.83) and SDA coefficient (17.0 vs. 12.8%; Table 1). However, the link between foraging mode and these physiological variables may be indirect. A correlated trait, feeding frequency, likely exerts the most direct influence. Ambushers tend to feed less frequently than do active foragers (Anderson and Karasov, 1981; Secor, 2001), and as a result may down-regulate their gut in the relatively long intervals between meals to save energy (Secor and Diamond, 1997a). When they do feed, ambushers must up-regulate their gut function, and doing so contributes substantially to SDA (Secor, 2001; but see Overgaard et al., 2002 for a dissenting view). In keeping with this interpretation, P. lepidopodus feeds more frequently than does L. burtonis (Patchell and Shine, 1986b; Huey et al., 2001).

Of course, the SDA response is affected by factors other than foraging mode and feeding frequency. Meal size, body size, body temperature, and different respirometry methodology and equipment all have a significant impact (Andrade et al., 1997; Secor and Faulkner, 2002; Wang et al., 2002; Toledo et al., 2003; Zaidan and Beaupre, 2003). We were able to control for these variables in our study. However, prey type and composition also strongly affect the magnitude and duration of SDA in reptiles and amphibians (Hailey, 1998; Secor and Faulkner, 2002; McCue et al., 2005), and we could not hold this variable constant; P. lepidopodus and L. burtonis eat different prey in the wild (arthropods and scincid lizards, respectively; Patchell and Shine, 1986b). Nonetheless, these dietary divergences cannot explain the SDA difference between the two taxa. The protein content of a meal influences the magnitude of SDA; meals composed of more protein and less carbohydrate and fat produce a stronger response (Lusk, 1931; McCue et al., 2005), likely because of the large contribution of protein synthesis to SDA (Jobling, 1981; Houlihan, 1991; McCue et al., 2005). Our two prey types, crickets and lizards, contain similar amounts of protein (63% and 66%, respectively; Crissey and Todderud, 2003). We were able to control for these variables in our study. However, prey type and composition also strongly affect the magnitude and duration of SDA (Secor, 2001; but see Overgaard et al., 2002 for a dissenting view). In keeping with this interpretation, P. lepidopodus feeds more frequently than does L. burtonis (Patchell and Shine, 1986b; Huey et al., 2001).

Table 1  SDA variables for Lialis burtonis at two prey sizes (relative prey mass [RPM] = 0.10 and 0.25) and Pygopus lepidopodus at RPM = 0.10

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Lialis burtonis RPM = 0.10</th>
<th>Pygopus lepidopodus RPM = 0.10</th>
<th>Lialis burtonis RPM = 0.25</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to maximum VO₂ (hours)</td>
<td>16.0 (2.00)</td>
<td>18.0 (0.00)</td>
<td>21.0 (1.73)</td>
<td>F&lt;sub&gt;2,10&lt;/sub&gt; = 3.29, P = 0.08</td>
</tr>
<tr>
<td>Time to return to resting VO₂ (hours)</td>
<td>90</td>
<td>90</td>
<td>138</td>
<td>N/A</td>
</tr>
<tr>
<td>Metabolic peak</td>
<td>4.22 (0.18)</td>
<td>2.83 (0.25)</td>
<td>6.46 (0.45)</td>
<td>F&lt;sub&gt;2,10&lt;/sub&gt; = 21.83, P = 0.0002; P &lt; 0.01 in all posthoc comparisons</td>
</tr>
<tr>
<td>SDA coefficient</td>
<td>17.0% (0.89)</td>
<td>12.8% (1.77)</td>
<td>18.8% (1.48)</td>
<td>F&lt;sub&gt;2,10&lt;/sub&gt; = 8.84, P = 0.0061; L. burtonis at 0.10 and 0.25 RPM &gt; P. lepidopodus (P &lt; 0.05 in both cases); L. burtonis at 0.10 vs. 0.25 RPM, P = 0.28.</td>
</tr>
</tbody>
</table>

Numbers given are means; standard errors are in parentheses. Metabolic peak was calculated by dividing peak rate of oxygen consumption (VO₂) of fed lizards by their resting (unfed) VO₂. The SDA coefficient represents the portion of the meal’s total energy lost to the SDA response. Statistical analyses consisted of ANCOVAs with log mass as the covariate; all variables were log-transformed. Significant differences were further investigated with Fisher’s PLSD post-hoc tests. See text for further details.
the chitinous exoskeletons of arthropods (Secor and Faulkner, 2002), it is possible that SDA differences between _L. burtonis_ and _P. lepidopodus_ would be even greater if they ate similar prey. Most importantly, our results are relevant to the field: free-ranging _L. burtonis_ and _P. lepidopodus_ likely exhibit SDA responses similar in magnitude (but perhaps more variable) than those we measured in the laboratory.

At a larger meal size (RPM = 0.25), metabolic peak of _L. burtonis_ increases (from 4.22 to 6.46); further, the lizards take longer to reach peak VO$_2$, and to return to fasting rates of oxygen consumption than at an RPM of 0.10 (Table 1). Similar effects of meal size occur in other squamate taxa (e.g., Andrade et al., 1997; McCue and Lillywhite, 2002; Toledo et al., 2003; Roe et al., 2004). _Lialis burtonis_ loses about the same percentage of its meal energy to SDA at both prey sizes (18.8% at 0.25 RPM, compared to 17.0% at 0.10; Table 1). Some snake species show this pattern, in which increasing oxygen consumption due to SDA is largely offset by the greater energy content of larger prey items (Toledo et al., 2003; Roe et al., 2004). In other reptile and amphibian taxa, however, the SDA coefficient increases with increasing prey size (Andrade et al., 1997; Secor and Diamond, 1997b; Secor and Faulkner, 2002). Interestingly, no studies have yet demonstrated that smaller prey items can be energetically more costly to process, digest, and assimilate than larger ones, relative to their energy content; the well-documented tendency of large snakes to drop small prey items from their diets (Arnold, 1993) thus cannot be explained by such physiological considerations.

Metabolic peak and the SDA coefficient of _L. burtonis_ are similar to those of ambush-foraging snakes at the same temperature and relative prey mass (Table 2). While we acknowledge that comparing such values among taxa and among studies can be problematic, owing to the effects of methodology and mass allometry on SDA (Zaidan and Beaupre, 2003), such similarities provide yet more evidence for the remarkable convergence of _L. burtonis_ and ambush-foraging snakes. In addition to being functionally limbless, _L. burtonis_ feeds relatively infrequently and exhibits a suite of adaptations (such as pointed, recurved, and hinged teeth, highly mobile mesokinetic and hypokinetic joints, and an extremely elongate skull) that enable it to subdue and swallow large scincid prey (Patchell and Shine, 1986a). In the laboratory, for example, _L. burtonis_ is capable of killing and eating lizards with an RPM of at least 0.41 (Wall and Shine, 2007).

This convergence with ambush-foraging snakes highlights the fact that _L. burtonis_ is an unusual lizard, and it underlines the possibility that the magnitude of its SDA may not apply to ambush-foraging lizards (or snakes) in general. For example, ambushing lizards may not feed less frequently than active foragers overall (Huey et al., 2001), calling into question whether the SDA patterns identified in snakes are relevant to the

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**Table 2** SDA variables for ambush-foraging snakes (and _Lialis burtonis_) at 30°C

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>RPM</th>
<th>Metabolic Peak</th>
<th>SDA Coefficient</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Boa constrictor</em></td>
<td>Boidae</td>
<td>0.25</td>
<td>18.5</td>
<td>33</td>
<td>Secor and Diamond, 2000</td>
</tr>
<tr>
<td><em>B. constrictor</em></td>
<td>Boidae</td>
<td>0.20</td>
<td>4.0</td>
<td>14</td>
<td>Toledo et al., 2003</td>
</tr>
<tr>
<td><em>Lichanura trivirgata</em></td>
<td>Boidae</td>
<td>0.25</td>
<td>15.9</td>
<td>18</td>
<td>Secor and Diamond, 2000</td>
</tr>
<tr>
<td><em>Python molurus</em></td>
<td>Pythonidae</td>
<td>0.25</td>
<td>3.2</td>
<td>18</td>
<td>Overgaard et al., 1999</td>
</tr>
<tr>
<td><em>P. molurus</em></td>
<td>Pythonidae</td>
<td>0.20</td>
<td>9.5</td>
<td>27</td>
<td>Overgaard et al., 2002</td>
</tr>
<tr>
<td><em>P. molurus</em></td>
<td>Pythonidae</td>
<td>0.25</td>
<td>17.7</td>
<td>30</td>
<td>Secor and Diamond, 2000</td>
</tr>
<tr>
<td><em>P. molurus</em></td>
<td>Pythonidae</td>
<td>0.20</td>
<td>6.3</td>
<td>31</td>
<td>Wang et al., 2002</td>
</tr>
<tr>
<td><em>P. regius</em></td>
<td>Pythonidae</td>
<td>0.25</td>
<td>3.0</td>
<td>12</td>
<td>Starck et al., 2004</td>
</tr>
<tr>
<td><em>Agkistrodon piscivorus</em></td>
<td>Viperidae</td>
<td>0.25</td>
<td>5.5</td>
<td>21</td>
<td>McCue and Lillywhite, 2002</td>
</tr>
<tr>
<td><em>Crotalus cerastes</em></td>
<td>Viperidae</td>
<td>0.25</td>
<td>9.9</td>
<td>12</td>
<td>Secor and Diamond, 2000</td>
</tr>
<tr>
<td><em>C. cerastes</em></td>
<td>Viperidae</td>
<td>0.25</td>
<td>6.1</td>
<td>12</td>
<td>Zaidan and Beaupre, 2003</td>
</tr>
<tr>
<td><em>C. durissus</em></td>
<td>Viperidae</td>
<td>0.30</td>
<td>5.2</td>
<td>12</td>
<td>Andrade et al., 1997</td>
</tr>
<tr>
<td><em>C. horridus</em></td>
<td>Viperidae</td>
<td>0.25</td>
<td>6.9</td>
<td>19</td>
<td>Zaidan and Beaupre, 2003</td>
</tr>
<tr>
<td><em>Lialis burtonis</em></td>
<td>Pygopodidae</td>
<td>0.25</td>
<td>6.5</td>
<td>12</td>
<td>Present study</td>
</tr>
</tbody>
</table>

Metabolic peak is peak rate of oxygen consumption divided by standard metabolic rate (SMR); the SDA coefficient represents the proportion of the meal’s total energy lost to the SDA response.
majority of lizard species. Most SDA studies focus on infrequently feeding snakes such as pythons and vipers because it is in these taxa that the most dramatic SDA responses are to be expected. With a few exceptions (e.g., Robert and Thompson, 2000; Iglesias et al., 2003; Pan et al., 2005), SDA has not been measured in “typical” lizards. More studies of such species are needed to clarify whether large SDA responses are restricted to ambush-foraging snakes (and analogues such as Lialis burtonis), or whether the physiological effects of foraging mode extend to squamates in general.

Acknowledgements We thank F. Seebacher and S. Iglesias for their valuable advice, S. Ruggeri for building the respirometer chambers, and J. Herbert and A. Ching for putting up with substantial inconvenience. Funding was provided by a National Science Foundation (USA) Graduate Research Fellowship (to MW) and the Australian Research Council (to MBT and to RS). All animals were collected with the permission of the New South Wales Parks and Wildlife Service, and all activities were undertaken with the consent of the University of Sydney Animal Ethics Committee (Approval number L04/5-2002/3/3563).

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