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

Michael WALL1,2, Michael B. THOMPSON1, Richard SHINE1*

1 School of Biological Sciences A08, University of Sydney, NSW 2006, Australia
2 Current address: 4940 Anza St. #4, San Francisco, CA 94121, USA

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 lepidopus (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. lepidopus. 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 predator 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,
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® to absorb water, Carbasorb® to absorb carbon dioxide, and then through Drierite® 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. VO₂ 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 VO₂ 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* (\(t_6 = 1.77, P = 0.12\)).

In addition, we measured VO₂ 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 VO₂ 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; VO₂ 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*: \(t_5 = 1.76, P = 0.18\)). 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 VO₂; (2) time, in hours, to return to SMR; (3) metabolic peak (peak VO₂/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 VO₂ curves of fed and unfed lizards. We converted this value to energy, assuming that 19.8 joules were expended per mL of O₂ 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⁻² for crickets (Secor and Faulkner, 2002).

### 1.5 Statistical analyses

We log-transformed all VO₂ 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

*Lialis 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*, $0.038 \pm 0.002 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-1}$; *P. lepidopodus*, $0.060 \pm 0.005 \text{ mL O}_2 \text{ h}^{-1} \text{ g}^{-1}$.

### 2.2 SDA

In all three experiments, feeding caused a significant increase in VO$_2$ (*L. burtonis* at 0.10 RPM: $F_{1,5} = 146.81$, $P < 0.001$; *P. lepidopodus*: $F_{1,3} = 24.84, P = 0.016$; *L. burtonis* at 0.25 RPM: $F_{1,3} = 108.46, P = 0.002$; Fig. 1). In each case, VO$_2$ was significantly elevated by 6 h after feeding (Fisher’s PLSD, $P < 0.01$ in all cases; Fig. 1) and peaked at around 18 h (Fig. 1, Table 1). For *L. burtonis* and *P. lepidopodus* at 0.10 RPM, VO$_2$ returned to baseline rates by the 90 h measurement (Fisher’s PLSD for fed vs unfed *L. burtonis* at 90 h, $P = 0.21$; for *P. lepidopodus*, $P = 0.24$; Figs 1A,B, Table 1). 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 Waldsmith, 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
is the first study to report VO₂ in any pygopodid, so it is possible that the entire family has lower-than-expected rates of oxygen consumption; more species need to be studied to determine if this is the case. Ecology, however, is usually a better predictor of metabolic rate in squamates than is phylogeny (Andrews and Pough, 1985). For example, “reclusive lizards” have lower VO₂s than “day-active predators” (Andrews and Pough, 1985); both *L. burtonis* and *P. lepidopodus* would be assigned to the former group. Measurement of metabolic rates in other pygopodids would be interesting in this regard; the great ecological diversity within the Pygopodidae (from burrowers convergent on blind-snakes to spider specialists to ambush-foraging snake analogues; Patchell and Shine, 1986b) makes it an ideal group for investigating ecological impacts on SMR.

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 Beaupré, 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; Pan 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 Todds, 1998). Further, both marine toads (*Rhinella marina*) and Speke’s hingeback tortoise (*Kinixys spekii*) exhibit a stronger SDA in response to arthropod prey than to other food types (Hailey, 1998; Secor and Faulkner, 2002). If this reflects the general difficulty of digesting

| Measurement                  | *Lialis burtonis* RPM = 0.10 | *Pygopus lepidopodus* RPM = 0.10 | *Lialis burtonis* RPM = 0.25 | Statistics       |
|------------------------------|------------------------------|---------------------------------|-------------------------------|------------------|
| Time to maximum VO₂ (hours)  | 16.0 (2.00)                  | 18.0 (0.00)                     | 21.0 (1.73)                   | *F*<sub>2,10</sub> = 3.29, *P* = 0.08 |
| Time to return to resting    | 90                           | 90                              | 138                           | N/A              |
| VO₂ (hours)                  |                              |                                 |                               |                  |
| Metabolic peak               | 4.22 (0.18)                  | 2.83 (0.25)                     | 6.46 (0.45)                   | *F*<sub>2,10</sub> = 21.83, *P* = 0.0002; |
|                             |                              |                                 |                               | *P* < 0.01 in all posthoc comparisons |
| SDA coefficient              | 17.0% (0.89)                 | 12.8% (1.77)                    | 18.8% (1.48)                  | *F*<sub>2,10</sub> = 8.4, *P* = 0.0061; |
|                             |                              |                                 |                               | *L. burtonis* at 0.10 and 0.25 RPM > *P. lepidopodus* (*P* < 0.05 in both cases); *L. burtonis* at 0.10 vs. 0.25 RPM, *P* = 0.28. |

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 VO₂, 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, ambush 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

---

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

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

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 respirometry 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).

References

Anderson RA, Kansov WH, 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia 49: 67–72.

Andrade DV, Cruz-Neto AP, Abe AS, 1997. Meal size and specific dynamic action in the rattlesnake Crotalus durissus (Serpentes: Viperidae). Herpetologica 53: 485–493.

Andrews RM, Pough FH, 1985. Metabolism of squamate reptiles: Allometric and ecological relationships. Physiol. Zool. 58: 214–231.

Arnold SJ, 1993. Foraging theory and prey-size - predator-size relations in snakes. In: Seigel RA, Collins JT ed. Snakes: Ecology and Behavior. New York: McGraw-Hill, 87–115.

Avery R, 1982. Field studies of body temperatures and thermoregulation. In: Gans C ed. Biology of the Reptilia, Vol. 12. New York: Academic Press, 93–166.

Beaupre SJ, 2005. Ratio representations of specific dynamic action (mass-specific SDA and SDA coefficient) do not standardize for body mass and meal size. Physiol. Biochem. Zool. 78: 126–131.

Bonnet X, Naulleau G, Shine R, 1999. The dangers of leaving home: Dispersal and mortality in snakes. Biol. Conserv. 89: 91–99.

Bradshaw SD, Gans C, Saint-Girons H, 1980. Behavioral thermoregulation in a pygopodid lizard Lialis burtonis. Copeia 1980: 738–743.

Butler MA, 2005. Foraging mode of the chameleon Bradypodion pumilum: A challenge to the sit-and-wait versus active forager paradigm? Biol. J. Linn. Soc. 84: 797–808.

Cogger HG, 2000. Reptiles and Amphibians of Australia. Sydney: Reed New Holland.

Crissey S, Toddes B, 1998. Diets for Micronesian kingfisher Halcyon c. cinnamomina. In: Bahner B, Balza A, Diebold E ed. Micronesian Kingfisher Species Survival Plan Husbandry Manual. Silver Spring, MD: American Association of Zoos and Aquariums, 41–51.

Donnellan SC, Hutchinson MN, Saint KM, 1999. Molecular evidence for the phylogeny of Australian gekkonid lizards. Biol. J. Linn. Soc. 67: 97–118.

Gessaman JA, Nagy KA, 1988. Energy metabolism: Errors in gas-exchange conversion factors. Physiol. Zool. 61: 507–513.

Greene HW, 1997. Snakes: The Evolution of Mystery in Nature. Berkeley, CA: University of California Press.

Greer A, 1989. The Biology and Evolution of Australian Lizards. Chipping Norton, NSW: Surrey Beauty and Sons.

Hailey A, 1998. The specific dynamic action of the omnivorous tortoise Kinixys speki in relation to diet, feeding pattern, and gut passage. Physiol. Zool. 71: 57–66.

Hailey A, Davies PMC, 1986. Lifestyle, latitude and activity metabolism of natricine snakes. J. Zool. 209: 461–476.

Hare K, Pledger S, Thompson MB, Miller J, Daugherity C, 2004. Conditionining reduces metabolic rate and time to steady-state in the lizard Naultinus manukanus (Reptilia: Gekkonidae). Comp. Biochem. Physiol. A 139: 245–250.

Houlahan DE, 1991. Protein turnover in ectotherms and its relationships to energetics. Adv. Comp. Physiol. Biochem. 7: 1–43.

Huey RB, Pianka ER, 1981. Ecological consequences of foraging mode. Ecology 62: 991–999.

Huey RB, Pianka ER, Vitt LJ, 2001. How often do lizards "run on empty"? Ecology 82: 1–7.

Iglesias S, Thompson MB, Seebacher F, 2003. Energetic cost of a meal in a frequent feeding lizard. Comp. Biochem. Physiol. A 135: 377–382.

Jennings WB, Pianka ER, Donnellan S, 2003. Systematics of the lizard family Pygopodidae with implications for the diversity of Australian temperate biotas. Syst. Biol. 52: 757–780.

Johling M, 1981. The influences of feeding on the metabolic rates of fishes: A short review. J. Fish. Biol. 18: 385–400.

Kleiber M, 1961. The Fire of Life: An Introduction to Animal Energetics. New York: Wiley.

Kluge AG, 1976. Phylogenetic relationships in the lizard family Pygopodidae: An evaluation of theory, methods, and data. Misc. Publ. Mus. Zool. Univ. Michigan 152: 1–72.

Lusk G, 1931. The specific dynamic action. J. Nutr. 3: 519–530.

Mccue MD, Bennett AF, Hicks JW, 2005. The effect of meal composition on specific dynamic action in Burmese pythons Python maurus. Physiol. Biochem. Zool. 78: 182–192.

McCue MD, Lillywhite HB, 2002. Oxygen consumption and the energetics of island-dwelling Florida cottonmouth snakes. Physiol. Biochem. Zool. 75: 165–178.

Murray BA, Bradshaw SD, Edward DH, 1991. Feeding behavior and the occurrence of caudal luring in Burton's pygopodid Li-
alis burtonis (Sauria: Pygopodidae). Copeia 1991: 509–516.

Naulleau G, Bonnet X, 1995. Reproductive ecology, body fat reserves and foraging mode in females of two contrasted snake species: Vipera aspis (terrestrial, viviparous) and Ealphe long-
issima (semi-arboreal, oviparous). Amphibia-Reptilia 16: 37–46.

Niewiarski PH, Waldsmith SR, 1992. Variation in metabolic rates of a lizard: Use of SMR in ecological contexts. Funct.
Ecol. 6: 15–22.
Overgaard J, Busk M, Hicks JW, Jensen FB, Wang T, 1999. Respiratory consequences of feeding in the snake Python molurus. Comp Biochem Physiol 124A: 359–365.
Overgaard J, Andersen JB, Wang T, 2002. The effects of fasting duration on the metabolic response to feeding in Python molurus: An evaluation of the energetic costs associated with gastrointestinal growth and upregulation. Physiol. Biochem. Zool. 75: 360–368.
Packard GC, Boardman TJ, 1999. The use of percentages and size-specific indices to normalize physiological data for variation in body size: Wasted time, wasted effort? Comp. Biochem. Physiol. A 122: 37–44.
Pan ZC, Ji X, Lu HL, Ma XM, 2005. Influence of food type on specific dynamic action of the Chinese skink Eumeces chinen-sis. Comp. Biochem. Physiol. A 140: 151–155.
Patchell FC, Shine R, 1986a. Feeding mechanisms in pygopodid lizards: How can Lialis swallow such large prey? J. Herpetol. 20: 59–64.
Patchell FC, Shine R, 1986b. Food habits and reproductive biology of the Australian legless lizards (Pygopodidae). Copeia 1986: 30–39.
Patchell FC, Shine R, 1986c. Hinged teeth for hard-bodied prey: A case of convergent evolution between snakes and legless lizards. J. Zool. 208: 269–276.
Perry G, 1999. The evolution of search modes: Ecological versus phylogenetic perspectives. Am. Nat. 153: 98–109.
Pianka ER, 1966. Convexity, desert lizards, and spatial heterogeneity. Ecology 47: 1055–1059.
Pianka ER, Vitt LJ, 2003. Lizards: Windows to the Evolution of Diversity. Los Angeles: University of California Press.
Robert KA, Thompson MB, 2000. Influence of feeding on the metabolic rate of the lizard Eulamprus tympanum. Copeia 2000: 851–855.
Roe JH, Hopkins WA, Snodgrass JW, Congdon JD, 2004. The influence of circadian rhythms on pre- and post-prandial metabolism in the snake Lampropithis fuliginosus. Comp. Biochem. Physiol. A 139: 159–168.
Schoener T, 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2: 369–404.
Secor SM, 1995. Ecological aspects of foraging mode for the snakes Crotalus cerastes and Masticophis flagellum. Herpetol. Monogr. 9: 169–186.
Secor SM, 2001. Regulation of digestive performance: A proposed adaptive response. Comp. Biochem. Physiol. A 128: 565–577.
Secor SM, Diamond J, 1997a. Determinants of the postfeeding metabolic response of Burmese pythons Python molurus. Physiol. Zool. 70: 202–212.
Secor SM, Diamond J, 1997b. Effects of meal size on postprandial responses in juvenile Burmese pythons Python molurus. Am. J. Physiol. 272: R902–R912.