Ecology, 82(1), 2001, pp. 1–7

HOW OFTEN DO LIZARDS "RUN ON EMPTY"?

RAYMOND B. HUEY,[1,4] ERIC R. PIANKA,[2] AND LAURIE J. VITT[3]

[1]*Department of Zoology, Box 351800, University of Washington, Seattle, Washington 98195-1800 USA*
[2]*Section of Integrative Biology (C0930), School of Life Sciences, University of Texas, Patterson Laboratories, 24th at Speedway, Austin, Texas 78712-1064 USA*
[3]*Sam Noble Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, Oklahoma 73072-7029 USA*

Abstract. Energy balance is relevant to diverse issues in ecology, physiology, and evolution. To determine whether lizards are generally in positive energy balance, we synthesized a massive data set on the proportion of individual lizards ($N = 18\,223$) with empty stomachs (127 species), representing nine families distributed on four continents, primarily in temperate zone deserts but also in the neotropics. The average percentage of individuals with empty stomachs is low (13.2%) across all species, even among desert lizards, suggesting that most lizards are in positive energy balance. Nevertheless, species vary substantially in this regard (among all species, 0% to 66% of individuals have empty stomachs). Several patterns are detectable among species with unusually high frequencies of empty stomachs. In particular, nocturnal lizards "run on empty" more often on average than do diurnal species (24.1% vs. 10.5%); and this pattern holds even for nocturnal vs. diurnal geckos (21.2% vs. 7.2%, respectively). Several (but not all) top predators have a higher frequency of empty stomachs than do species that feed at lower trophic levels. Diet breadth and body size appear unrelated to frequency of empty stomachs. Widely foraging species sometimes have a high frequency of empty stomachs relative to sit-and-wait species, but patterns vary among continents and appear to be confounded by phylogeny and trophic level. Ant-eating specialists have uniformly low frequencies of empty stomachs. Diurnal termite specialists also have low frequencies of empty stomachs, but nocturnal ones have high frequencies. Lizards from certain families (Gekkonidae [including Pygopodidae], Gymnophthlamidae, and Varanidae) are more likely to have empty stomachs than are those of other families (Agamidae, Iguanidae, Lacertidae, Scincidae, and Teiidae).

Key words: body size, impact on feeding success; dietary specialization, impact on feeding success; energetics; energy balance of individual lizards; feeding success, diurnal vs. nocturnal lizards; feeding success of lizards, desert and Neotropical; lizards, diet and energetics; nocturnality; trophic level, impact on feeding success.

INTRODUCTION

The amount and predictability of energy input is crucial to organisms. On an ecological time scale, energy levels influence maintenance, growth, survival, and reproduction (Townsend and Calow 1981, Dunham et al. 1989, Nagy et al. 1999) as well as foraging behavior (Nagy et al. 1984, Perry and Pianka 1997). On an evolutionary time scale, energy may influence the general potential for adaptation and diversification (Vermeij 1995, Parsons 1998). Variability of energy supply is also important. For example, species that routinely deal with feast vs. famine may have specialized digestive adaptations (e.g., digestive organs atrophy during fasts, Secor et al. 1994) as well as enhanced fat storage (Bustard 1967, Pond 1981).

Here we address variability of energy supply of many species of lizards from very diverse habitats (see Plate 1). Specifically, we ask whether most individual lizards are in positive energy balance, or whether most alternate between feast and famine. We use the percentage of individuals with empty stomachs as a simple index of instantaneous energy balance. If individuals have food in their stomachs, they will be gaining energy and be in positive energy balance. Conversely, if individuals routinely alternate between feast and famine, then many individuals will have empty stomachs and thus will be relying (at least at that instant) on fat or other tissue stores for maintenance energy needs. Pythons are archetypal examples of "intermittent" feeders and are thought to go for months between meals (Secor et al. 1994).

Manuscript received 20 September 1999; revised 1 May 2000; accepted 2 May 2000; final version received 13 June 2000.

[4] E-mail: hueyrb@u.washington.edu

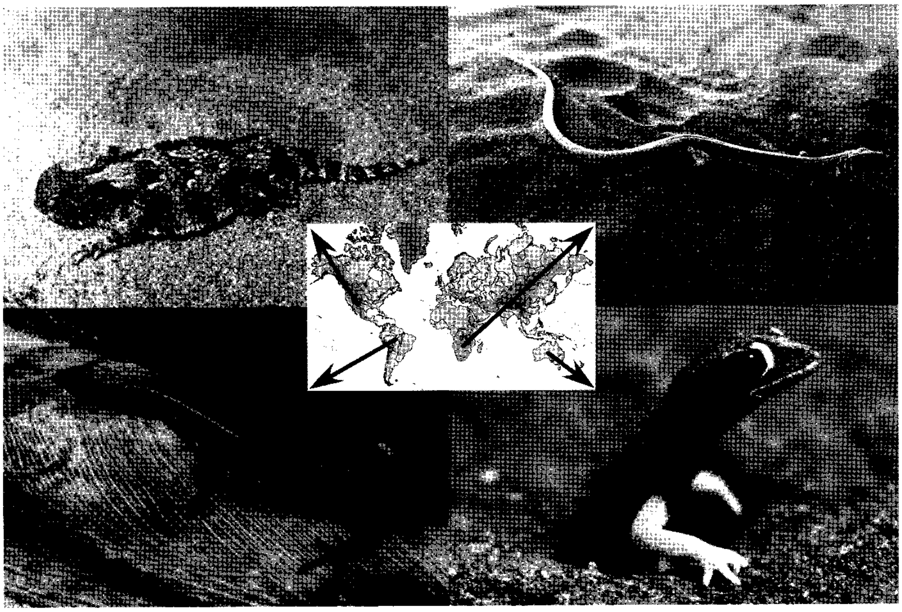

PLATE. 1. Four lizards (from different continents and from different families) chosen to typify diverse patterns of foraging success. Clockwise from upper left: *Phrynosoma platyrhinos*, an iguanid from the North American deserts, has a low frequency of empty stomachs (0.0%), as do other diurnal ant specialists; *Nucras tesselata*, a scorpion-eating lacerid from the Kalahari desert of south Africa, has a moderate frequency of empty stomachs (16.1%), as is the case with most top predators; *Rhynchoedura ornata*, a diplodactylid gecko and nocturnal termite specialist from the Australian deserts, has a high frequency of empty stomachs (43.4 %), as do most nocturnal geckos (especially termite specialists); and *Cercosaura ocellata*, in common with other gymnophthalmids from the Amazonian basin in South America, forages in leaf litter and has a high frequency of empty stomachs (44.0%).

We analyze dietary data for 81 lizard species from temperate-zone deserts on three continents (Africa, Australia, North America—collected by Pianka and colleagues) and also for 46 species from two Neotropical regions (Central and South America—collected by Vitt and colleagues). A special attraction of our data set is that single teams did all collecting and stomach analyses for each region, and so resulting data should be largely free of an investigator effect, which potentially haunts most comparative studies. Moreover, our analyses are based on many species of geographically and phylogenetically diverse taxa and thus should be general for lizards. We find that the vast majority of these lizards do have food in their guts, suggesting that lizards are routinely in positive energy balance. However, as we note below, a few taxa are exceptional.

METHODS

Lizards used in this study were collected over many years by Pianka (1986) and colleagues in the deserts of western North America ($N = 11$ species, 3940 individuals), the Kalahari desert of southern Africa (18 species, 5683 individuals), and the deserts of western Australia (52 species, 5091 individuals) and by Vitt and colleagues (Vitt and Zani 1996, 1998*a*, *b*) in the neotropics (5 species, 243 individuals from lowland Caribbean rain forest in Nicaragua; and 41 species, 3266 individuals from lowland Amazon rain forest in Ecuador and Brazil, and Amazon savanna in northern Brazil [Roraima]). We included only species that were represented by at least 10 individuals for the desert species and at least 14 individuals for the tropical ones (see Plate 1). Lizards collected in all seasons are included; the data set is available in the Appendix.

Lizards were measured (snout–vent length) and preserved soon after being collected, and stomach contents were later removed and identified (Pianka 1986, Vitt and Zani 1996). We calculated the percentage of individuals of each species that had empty stomachs and calculated standardized dietary niche breadth (Pianka 1986). Prior to analyzing patterns of interspecific variation (e.g., nocturnal vs. diurnal, familial, habitat, foraging mode), we chose not to do formal phylogenetic analyses (Harvey and Pagel 1991, Martins and Hansen 1997, Garland et al. 1999). Although we normally advocate phylogenetic approaches, we do not use one here for two main reasons.

First, the taxa studied here are phylogenetically and geographically diverse, and their relationships are not yet known well enough to undertake explicit phylogenetic analyses (but see Martins 1996). Second, in our data set phylogeny is inextricably confounded with geography. Thus most families are found on only some continents, confounding observed lineage effects with geographic effects, and vice versa. A formal comparative analysis would thus be unreliable, even if a robust phylogeny were available for these taxa. Consequently, we bypass formal phylogenetic testing and instead treat

TABLE 1. Percentage of lizards with empty stomachs, averaged by family within area.

Family	Empty stomachs (%) Mean ± 1 SE	Empty stomachs (%) Range	N†
Neotropics			
Gekkonidae	10.7 ± 2.79	0.0–22.4	8
Gymnophthalmidae	20.7 ± 3.26	6.3–44.2	11
Iguanidae	7.8 ± 1.78	0.0–24.0	18
Scincidae	9.0	···	1
Teiidae	12.4 ± 1.96	4.4–22.2	8
North America			
Gekkonidae	24.1	···	1
Iguanidae	1.5 ± 0.71	0–5.7	8
Teiidae	1.1	···	1
Xantusiidae	14.8	···	1
Australia			
Agamidae	3.0 ± 0.79	0–9.1	12
Gekkonidae‡	30.6 ± 5.11	0–65.6	15
Scincidae	14.0 ± 1.84	4.7–31.2	20
Varanidae	26.5 ± 2.41	22.2–35.9	5
Africa (Kalahari)			
Agamidae	0.8	···	1
Gekkonidae	15.5 ± 2.81	3.6–26.4	7
Lacertidae	4.9 ± 2.29	0.9–16.1	6
Scincidae	6.9 ± 3.13	2.6–16.2	4

† N = number of species in the group.
‡ Includes Pypogopodidae.

observed patterns as exploratory. In any case, we make our data set fully accessible to anyone who wishes to attempt phylogenetic analyses (see Appendix). Certainly, inspection of the data at the family level (Table 1) demonstrates an exceedingly strong phylogenetic signal, which is reinforced by a Kruskal-Wallis test ($P < 0.0001$).

Several biases are possible in our data. First, individuals captured early during their activity period may be less likely to have food in their stomachs than would individuals captured later; this bias would inflate the percentage of empty stomachs in our samples. However, because few lizards proved to have empty stomachs (see *Results and Discussion,* below), this bias appears more potential than real. Second, because lizards examined here were almost always captured while active, all observed dietary patterns can strictly apply only to active lizards. However, if individuals were to retreat to cover immediately after a large meal, we would likely not sample such individuals; and thus the bias here would be to inflate the percentage of empty stomachs. This potential bias is unlikely to be important for most lizards, which typically eat many small prey; but it could well be important for snakes, which typically eat larger and fewer prey (Greene 1997).

RESULTS AND DISCUSSION

Remarkably few lizards had empty stomachs (average of 13.9 ± 14.3% for 81 species of desert lizards, 12.2 ± 9.4% for 46 tropical species [means ± 1 SE]; Tables 1 and 2). This pattern is general and holds for lizards from very different continents, habitats, taxa, and life styles (Table 2, Fig. 1, Appendix). Moreover, the frequency distribution of species with varying degrees of percentage of empty stomachs is strongly left skewed (Fig. 1), and only a few species exhibit relatively high values. Thus, the vast majority of lizards should be in positive energy balance.

Desert lizards

The low incidence of empty stomachs in desert lizards (North America, Australia, Kalahari; Table 2) is somewhat surprising, not only because deserts are famous for having fluctuating productivity (Pianka 1986), but also because desert lizards have lower growth rates than do congeners living in more productive habitats (Andrews 1982). Low growth rates of desert lizards could in principle result from relatively low energy intake, or from relatively high metabolic rates associated with life in hot desert environments, or from both. Although our categorical data (presence vs. absence of food) cannot directly address a quantitative issue, they do suggest that most desert lizards are normally in positive energy balance. Interestingly, desert iguanids do not have elevated field metabolic rates relative to non-desert iguanids (Nagy 1988). Thus, why desert lizards have relatively low growth rates currently remains an enigma: a more detailed approach (see *Concluding remarks*, below) will be necessary to address this question.

Neotropical lizards

Most Neotropical lizards had food in their stomachs, and only gymnophthalmids had a high frequency of empty stomachs (Table 1, Fig. 1). The relatively low feeding success of gymnophthalmids may reflect their unusual foraging behavior: these small lizards typically forage actively in leaf litter, but are extremely secretive and appear to spend relatively little time active, perhaps because of risk of predation from other leaf-litter species (e.g., other reptiles, frogs, birds, and spiders).

Nocturnal vs. diurnal lizards

Nocturnal lizards were conspicuously more likely to have empty stomachs than were diurnal lizards (Table 2: 24.1 ± 17.2% vs. 10.5 ± 9.6%, respectively). This pattern appears universal: it holds in all three deserts as well as in the tropics (Table 2). However, because most nocturnal lizards in our samples are geckos (but two *Egernia* skinks in Australia are nocturnal), this pattern could be a phylogenetic artifact more indicative of the reduced foraging success of geckos vs. other lizard taxa. Fortunately, a few geckos are diurnal; so we can use within-family and within-desert comparisons to determine whether phylogeny or time of activity actually influences feeding success (Table 2). Interestingly, the one diurnal gecko (*Lygodactylus*) in the Kalahari has a much lower average percentage of empty stomachs (3.6%) than do any of six species of nocturnal geckos (range: 11.3–26.4%). Similarly, the six diurnal

TABLE 2. Percentage of lizards with empty stomachs, averaged by group.

Group	Empty stomachs (%)		
	Mean ± 1 SE	Range	*N*†
Neotropics			
Diurnal species	11.8 ± 9.4	0–44.2	44
Diurnal geckos	7.2 ± 5.3	0–15.3	6
Nocturnal geckos	21.2	20.0–22.4	2
North America			
Diurnal species	1.4 ± 1.9	0–5.7	9
Nocturnal species	21.2	···	2
Nocturnal geckos	24.1	···	1
Top predator (*Gambelia*)	2.6	···	1
Australia			
Diurnal species	13.0 ± 10.3	0–35.9	36
Nocturnal species	27.6 ± 21.0	0–65.6	16
Diurnal gecko (pygopodid)	27.8	···	1
Nocturnal geckos	30.8 ± 20.6	0–65.6	14
Termite specialists (geckos)	55.1 ± 10.1	43.4–61.8	3
Top predators (*Varanus*, *Lialis*, *Pygopus*)	33.1 ± 15.2	22.2–65.6	7
Africa (Kalahari)			
Diurnal species	5.1 ± 5.3	0.8–16.2	12
Nocturnal species	17.5 ± 5.7	11.3–26.3	6
Diurnal gecko	3.6	···	1
Nocturnal geckos	17.5 ± 5.7	11.3–26.4	6
Top predator (*Nucras*)	16.1	···	1
All diurnal lizards	10.5 ± 9.6	0–44.2	101
All nocturnal lizards	24.1 ± 17.2	0–65.6	26
All top predators	27.8 ± 5.1	2.6–65.6	10
All termite specialists	29.8 ± 9.4	4.8–61.8	7
All ant specialists	0.9 ± 0.7	0–3.4	5
All wide-foraging lizards	15.1 ± 1.3	0.9–44.2	53
All sit-and-wait lizards	11.7 ± 1.7	0–65.6	72

Note: Lower-ranking groups (e.g., nocturnal geckos) are included in higher-ranking groups (e.g., nocturnal species) within each geographic class.

† *N* = number of species.

geckos in the neotropics all have a lower frequency of empty stomachs (0–15.3%) than do either of the two nocturnal neotropical geckos (20.0–22.4%). In contrast, the two nocturnal (and also crepuscular) skinks (*Egernia*) do not have a higher frequency of empty stomachs than do diurnal skinks (Appendix). No diurnal gecko occurs in the Australian or North American desert samples, so comparable comparisons cannot be made for these faunas. The single nocturnal gecko in North America, *Coleonyx,* has the highest percentage of empty stomachs of any North American desert lizard species. Another (presumably) nocturnal North American species (*Xantusia vigilis*, Xantusiidae) also has a relatively high percentage of empty stomachs (14.8%).

Because patterns for nocturnal vs. diurnal geckos parallel those of nocturnal vs. diurnal lizards (*Egernia*

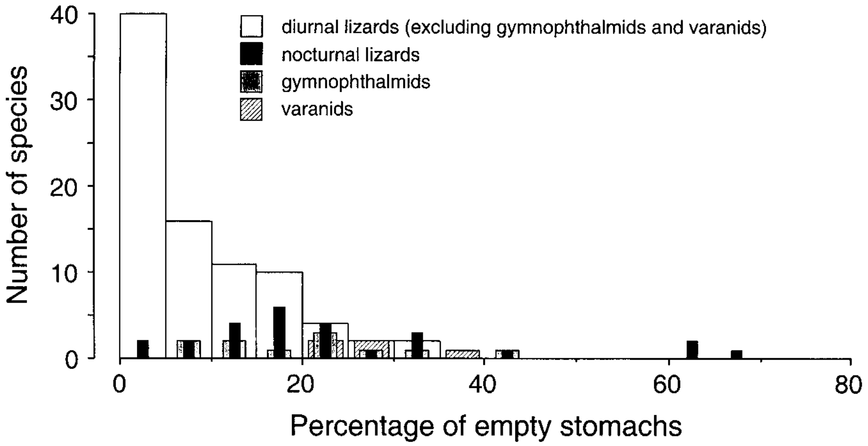

FIG. 1. Histogram of the number of species of lizards with various percentages of empty stomachs.

possibly excepted), the day/night difference in foraging success is likely real and not merely a phylogenetic artifact. The apparent reduction in foraging success of nocturnal lizards might reflect the difficulty of detecting prey in dim light, reduced or erratic activity of insect prey at night, or shorter activity times of geckos relative to diurnal species.

Although nocturnal lizards appear to have relatively low foraging success, their fasts are sometimes broken by feasts, as during termite swarms. Bustard (1967) noted that some geckos feed voraciously after long fasts, and he argued that their storage of fat in bulbous tails was a compensatory adaptation to intermittent feeding. Whether the digestive systems of such geckos atrophy during fasts is unknown: guts of several species of intermittent-feeding snakes and frogs do atrophy during prolonged fasts (Secor et al. 1994, McWilliams et al. 1997), which apparently conserves energy.

Do dietary patterns (Table 2) imply lower rates of growth (production) by nocturnal vs. diurnal lizards? We expect that this will prove to be the case not only because ingestion rates (as indexed by percentage of empty stomachs) of nocturnal lizards appear relatively low, but also because metabolic rates of diurnal and nocturnal lizards in deserts often are surprisingly similar (Nagy and Degen 1988, Nagy and Knight 1989, but see Nagy et al. 1993). Unfortunately, field data to evaluate relative rates of growth and production of diurnal vs. nocturnal taxa are currently inadequate (Andrews 1982).

Trophic level, dietary specialization, and body size

Presumably prey density is relatively low for most top predators, especially large ones. In fact, top predators (*Varanus* and pygopodids in Australia, *Nucras* in the Kalahari; see Plate 1) are more likely to have empty stomachs than are insectivorous lizards (Table 2). Interestingly, *Varanus prasinus* from the South Pacific is insectivorous, and all 29 individuals contained food (Greene 1986). The nocturnal Australian pygopodid *Lialis* (Gekkonidae), which preys on skinks and is an ecological equivalent of a snake, has the highest percentage of empty stomachs of any lizard we examined—in fact, 25 out of 37 stomachs were empty (Appendix)! Curiously, however, *Gambelia wislizeni*, which is a top predator in the southern portion of its range in North America, has a very low incidence of empty stomachs (2.6%, Table 2). Thus, this pattern is not universal and may be somewhat taxon—not trophic level—specific.

The incidence of empty stomachs is unrelated (r^2 = 0.03) to standardized diet breadth (Appendix). Overall, then, dietary specialists are just as likely to have empty stomachs as are dietary generalists. However, specialists on termites show striking variation in feeding success. Several nocturnal Australian geckos are termite specialists (*Diplodactylus conspicillatus, D. pulcher, Rhynchoedura ornata* [see Plate 1]; Pianka and Pianka 1976, Pianka 1986: Appendix E.3), and >40% of all stomachs of these dietary specialists were empty (Table 2). In contrast, several species of diurnal Australian *Ctenotus* skinks that are termite specialists have low to moderate frequencies of empty stomachs: *C. ariadnae* = 20%, *C. grandis* = 6.4%, *C. pantherinus* = 12.4%. No Kalahari gecko is a termite specialist, but the one diurnal lizard (*Heliobolus lugubris*) that specializes on termites rarely had empty stomachs (4.8%). This Kalahari species is a very active forager (Huey and Pianka 1981) and may have access to termites in tunnels or termitaria. Diurnal termite specialists capture termites in their tunnels, in termitaria, or in open foraging trails, and would appear to have more reliable access to termites than nocturnal species, which must capture termites at night when these insects are active aboveground. Termite activity at night may be unreliable (certainly termites swarms are).

Although termite-eating lizards show variable feeding success, ant-eating lizards are uniformly very successful. Three closely related arboreal and diurnal ant specialists (*Tropidurus plica, T. umbra,* and *T. flaviceps*) in the Amazon rain forest never had empty stomachs (Appendix), and diurnal ant specialists in North American and Australian deserts similarly have very low frequencies of empty stomachs (*Phrynosoma platyrhinos* = 0.0%, *Moloch horridus* = 3.4%, respectively).

Incidence of empty stomachs is unrelated (r^2 = 0.02) to body size (mean snout–vent length, SVL). Similarly, change in size during ontogeny seems to be unrelated to incidence of empty stomachs. For example, juvenile and adult *Varanus gouldi* had nearly identical percentages of empty stomachs (22.0% vs. 22.4%, Appendix). However, more detailed comparisons within species would be welcome.

Foraging mode

Lizards often have somewhat polarized foraging modes (Pianka 1966, Vitt and Congdon 1978, Anderson and Karasov 1981, Huey and Pianka 1981, Anderson 1993, Perry and Pianka 1997, Perry 1999): some species are active foragers ("widely foraging"), whereas others are ambush foragers ("sit-and-wait"). Diverse aspects of the biology of lizards are correlated with foraging mode (Vitt and Congdon 1978, Huey and Pianka 1981, Anderson 1993, Perry and Pianka 1997), and foraging mode usually runs along phylogenetic lines (Huey and Pianka 1981, Cooper 1994, Perry 1999). In North America, for example, teiids are widely foraging, whereas as iguanids are typically sit-and-wait. Widely foraging lizards should generally have higher daily energy expenditures (Anderson and Karasov 1981, Nagy et al. 1984), but they might encounter prey at relatively high rates and hence potentially have relatively low frequency of empty stomachs and high net energy gains (Nagy et al. 1984).

We made foraging-mode assignments based mainly on subjective criteria (see Huey and Pianka 1981), but excluded all nocturnal species as well as a few diurnal species for which foraging-mode designations were uncertain. We then examined whether foraging mode was associated with consistent differences in percentages of empty stomachs on each continent.

Sit-and-wait lizards have a significantly lower incidence of empty stomachs than do widely foraging lizards in Australia (3.0 ± 0.79 [$N = 12$ lizard species] vs. 17.5 ± 1.86 [23] respectively, $P < 0.001$) and in South America (6.9 ± 1.50 [20] vs. 17.0 ± 2.27 [19], $P < 0.001$), but not in the Kalahari (2.5 ± 0.05 [5] vs. 7.1 ± 2.40 (7), $P = 0.15$], in Central America (11.4 ± 3.98 [4] vs. 13.5 [1], $P > 0.9$], or North America (1.5 ± 0.71 [8] vs. 1.1 [1], $P > 0.8$]. However, other variables appear to confound these trends. In particular, the high mean for widely foraging lizards in South America is largely driven by gymnopthalmids (20.7%, $N = 10$ species), which have an unusual foraging biology (see *Neotropical lizards,* above). In Australia, the high mean is influenced by varanids (26.5%), which are top carnivores (see *Trophic level, dietary specialization, and body size,* above), and by skinks, which represent 20 of the 52 Australian species.

Kalahari lizards of the family Lacertidae are unusual in having both foraging modes represented, and so a close examination of these lizards provides a phylogenetically controlled comparison (Huey and Pianka 1981). All of these lacertids had low percentages of empty stomachs (all < 5%), except for the wide forager *Nucras tessellata,* which is also a top predator (Pianka 1986), suggesting that foraging mode has little impact in comparisons involving close relatives. Interestingly, a doubly-labeled water study (Nagy et al. 1984) suggested that a wide forager (*Heliobolus lugubris*) had a significantly higher rate of food intake at one site in late spring than did a sympatric sit-and-wait forager (*Pedioplanus lineoocellata*). In terms of frequency of empty stomachs, however, these two species are nearly identical (2.2% for *H. lugubris* vs. 4.8% for *P. lineoocellata*).

Overall, the association between foraging mode and percentage of empty stomachs is inconsistent among continents. If anything, however, wide foragers often have a relatively high frequency of empty stomachs, but this difference is likely confounded by differences in trophic level and by phylogeny.

Concluding remarks

Overall, our analyses demonstrate that the vast majority of lizards have food in their stomachs. This observation, based on a large sample of individuals and species from a very diverse array of habitats on several different continents, strongly suggests that lizards are generally in positive energy balance and thus gaining energy. For most lizards, therefore, life is not "feast vs. famine" but rather a "moveable feast."

A few groups do, however, have a high frequency of empty stomachs. Most conspicuously, nocturnal lizards on three continents are much more likely to have empty stomachs than are diurnal lizards (Fig. 1), and this patterns holds even when comparisons are restricted to nocturnal vs. diurnal geckos. Other patterns (trophic level, dietary specialization, body size, foraging mode) appear relatively idiosyncratic and may be relatively taxon or habitat specific. For example, three species of nocturnal termite specialists (Australian geckos) have quite high frequencies of empty stomachs, but several species of diurnal termite specialists do not (three Australian skinks and one Kalahari lacertid).

We encourage others to compile data on other taxa: such data should be readily available in the literature. Snakes might prove to be particularly interesting, as many of these reptiles appear to be intermittent feeders (Greene 1997; J. A. Rodríguez-Robles, *personal communication*) and thus should have a high frequency of empty stomachs (e.g., Secor et al. 1994, Rodríguez-Robles and Greene 1999). In any case, workers attempting to explore temporal dynamics of net energy gain will ultimately need to use more direct and comprehensive approaches, such as isotopic techniques (Nagy and Knight 1989: 16). However, such data—at least on a scale approaching that analyzed herein—are unlikely to be available for some time, if ever.

ACKNOWLEDGMENTS

This analysis was inspired by a lecture by G. Vermeij, who emphasized the evolutionary importance of energy levels. Field research in North America, Australia, Africa, and the Neotropics was supported by grants or fellowships from the National Science Foundation (E.R. Pianka, L.J. Vitt), the Guggenheim and Fulbright Foundations (E.R. Pianka), and National Geographic Society (R.B. Huey, E.R. Pianka, and C. M. Cavalier). Write up was supported by a fellowship from the Guggenheim Foundation (R.B. Huey). We thank K. Nagy and J. Rodríguez-Robles for discussion.

LITERATURE CITED

Anderson, R. A. 1993. Analysis of foraging in a lizard, *Cnemidophorus tigris.* Pages 83–116 *in* J. W. Wright and L. J. Vitt, editors. Biology of whiptail lizards (genus *Cnemidophorus*). Oklahoma Museum of Natural History, Norman, Oklahoma, USA.

Anderson, R. A., and W. H. Karasov. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia **49**:67–72.

Andrews, R. M. 1982. Patterns of growth in reptiles. Pages 273–320 *in* C. Gans and F. H. Pough, editors. Biology of the Reptilia. Volume 13. Physiology D (Physiological Ecology). Academic Press, London, UK.

Bustard, H. R. 1967. Gekkonid lizards adapt fat storage to desert environments. Science **158**:1197–1198.

Cooper, W. E., Jr. 1994. Prey chemical discrimination, foraging mode, and phylogeny. Pages 95–116 *in* L. J. Vitt and E. R. Pianka, editors. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, New Jersey, USA.

Dunham, A. E., B. W. Grant, and K. L. Overall. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiological Zoology **62**:335–355.

Garland, T., Jr., P. E. Midford, and A. R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. American Zoologist **39**:374–378.

Greene, H. W. 1986. Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. Fieldiana (Zoology) **31**:1–12.

Greene, H. W. 1997. Snakes: the evolution of mystery in nature. University of California Press, Berkeley, California, USA.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, UK.

Huey, R. B., and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology **62**:991–999.

Martins, E. P. 1996. Conducting phylogenetic comparative studies when the phylogeny is not known. Evolution **50**: 12–22.

Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into analyses of interspecific data. American Naturalist **149**:646–667.

McWilliams, S. R., D. Afik, and S. Secor. 1997. Patterns and processes in the vertebrate digestive system. Trends in Ecology and Evolution **12**:420–422.

Nagy, K. A. 1988. Energetics of desert reptiles. Pages 165–186 *in* P. K. Ghosh and I. Prakash, editors. Ecophysiology of desert vertebrates. Scientific Publishers, Jodhpur, India.

Nagy, K. A., and A. A. Degen. 1988. Do desert geckos conserve energy and water by being nocturnal? Physiological Zoology **61**:495–499.

Nagy, K. A., I. A. Girard, and T. K. Brown. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annual Review of Nutrition **19**:247–277.

Nagy, K. A., R. B. Huey, and A. F. Bennett. 1984. Field energetics and foraging mode of Kalahari lacertid lizards. Ecology **65**:588–596.

Nagy, K. A., and M. H. Knight. 1989. Comparative field energetics of a Kalahari skink (*Mabuya striata*) and gecko (*Pachydactylus bibroni*). Copeia 1989: 13–17.

Nagy, K. A., M. K. Seely, and R. Buffenstein. 1993. Surprisingly low field metabolic rate of a diurnal desert gecko, *Rhoptropus afer*. Copeia 1993: 216–219.

Parsons, P. A. 1998. Behavioral variability and limits to evolutionary adaptation under stress. Advances in the Study of Behavior **27**:155–180.

Perry, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. American Naturalist **153**: 98–109.

Perry, G., and E. R. Pianka. 1997. Animal foraging: past, present and future. Trends in Ecology & Evolution **12**:360–364.

Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. Ecology **47**:1055–1059.

Pianka, E. R. 1986. Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton University Press, Princeton, New Jersey, USA.

Pianka, E. R., and H. D. Pianka. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. Copeia 1976: 125–142.

Pond, C. 1981. Storage. Pages 190–210 *in* C. R. Townsend and P. Calow, editors. Physiological ecology: an evolutionary approach to resource use. Sinauer Associates, Sunderland, Massachusetts, USA.

Rodríguez-Robles, J. A., and H. W. Greene. 1999. Food habits of the long-nosed snake (*Rhinocheilus lecontei*), a "specialist" predator? Journal of Zoology, London **248**:489–499.

Secor, S. M., E. D. Stein, and J. Diamond. 1994. Rapid upregulation of snake intestine in response to feeding: a new model of intestinal adaptation. American Journal of Physiology **266**:G695–G705.

Townsend, C. R., and P. Calow. 1981. Physiological ecology: an evolutionary approach to resource use. Sinauer Associates, Sunderland, Massachusetts, USA.

Vermeij, G. 1995. Economics, volcanoes, and Phanerozoic revolutions. Paleobiology **21**:125–152.

Vitt, L. J., and J. Congdon. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. American Naturalist **112**:575–608.

Vitt, L. J., and P. A. Zani. 1996. Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. Canadian Journal of Zoology **74**:1313–1335.

Vitt, L. J., and P. A. Zani. 1998*a*. Ecological relationships among sympatric lizards in a transitional forest in the northern Amazon of Brazil. Journal of Tropical Ecology **12**:63–86.

Vitt, L. J., and P. A. Zani. 1998*b*. Prey use among sympatric lizard species in lowland rain forest of Nicaragua. Journal of Tropical Ecology **14**:537–559.

APPENDIX

The data set summarizing dietary and related data, by lizard species, for the 18 223 individual lizards that we studied, is available is ESA's Electronic Data Archives: *Ecological Archives* E082-001.