

SYMPOSIUM

Locomotion, Energetics, Performance, and Behavior: A Mammalian Perspective on Lizards, and Vice Versa

Theodore Garland, Jr.¹ and Ralph L. Albuquerque

Department of Biology, University of California, Riverside, CA 92506, USA

From the symposium “The Ecology of Exercise: Mechanisms Underlying Individual Variation in Movement Behavior, Activity or Performance” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 4–8, 2017 at New Orleans, Louisiana.

¹E-mail: tgarland@ucr.edu

Synopsis Animals are constrained by their abilities and by interactions with environmental factors, such as low ambient temperatures. These constraints range from physical impossibilities to energetic inefficiencies, and may entail trade-offs. Some of the constraints related to locomotion and activity metabolism can be illustrated through allometric comparisons of mammals and lizards, as representative terrestrial vertebrate endotherms and ectotherms, respectively, because these lineages differ greatly in aerobic metabolic capacities, resting energetic costs, and thermoregulatory patterns. Allometric comparisons are both useful and unavoidable, but “outlier” species (unusual for their clade) can also inform evolutionary scenarios, as they help indicate extremes of possible adaptation within mammalian and saurian levels of organization. We compared mammals and lizards for standard metabolic rate (SMR), maximal oxygen consumption during forced exercise (VO_{2max}), net (incremental) cost of transport (NCT), maximal aerobic speed (MAS), daily movement distance (DMD), daily energy expenditure (DEE) during the active season, and the ecological cost of transport (ECT = percentage of DEE attributable to locomotion). (Snakes were excluded because their limbless locomotion has no counterpart in terrestrial mammals.) We only considered lizard SMR, VO_{2max} , NCT, MAS, and sprint speed data if measured at 35–40 °C. On average, MAS is ~7.4-fold higher in mammals, whereas SMR and VO_{2max} are ~6-fold greater, but values for all three of these traits overlap (or almost overlap) between mammals and lizards, a fact that has not previously been appreciated. Previous studies show that sprint speeds are similar for smaller mammals and lizards, but at larger sizes lizards are not as fast as some mammals. Mammals move ~6-fold further each day than lizards, and DMD is by far the most variable trait considered here, but their NCT is similar. Mammals exceed lizards by ~11.4-fold for DEE. On average for both lineages, the ECT is surprisingly low, somewhat higher for lizards, and positively allometric. If a lizard and mammal of 100 g body mass were both to move their entire DMD at their MAS, they could do so in ~21 and 17 min, respectively, thus de-emphasizing the possible importance of time constraints. We conclude that ecological-energetic constraints related to locomotion are relatively more likely to occur in large, carnivorous lizards. Overall, our comparisons support the idea that the (gradual) evolution of mammalian endothermy did not necessarily require major changes in locomotor energetics, performance, or associated behaviors. Instead, we speculate that the evolution of thermoregulatory responses to low temperatures (e.g., shivering) may have been a key and “difficult” step in this transition.

Introduction

Stemming from Arnold’s (1983) seminal paper, the “ecomorphological paradigm,” as presently construed (Garland and Kelly 2006; Careau and Garland 2012; Lailvaux and Husak 2014; Storz et al. 2015; Orr and Garland 2017), posits that natural and sexual selection act most directly on behavior (what an animal does in a particular situation), that behavior is constrained or limited by organismal

performance abilities (e.g., maximal sprint speed), and that performance (when an animal is maximally motivated) is determined by the interactions among multiple lower-level (subordinate) traits (e.g., maximal heart rate, leg length, muscle fiber type). Our purpose here is to consider some of the constraints that locomotor capacities and costs place on behavior, which range from physical impossibilities to energetic inefficiencies, and may entail trade-offs

(Garland 2014). Our focus is on locomotion and activity metabolism, because virtually all behavior—including many behaviors crucial for Darwinian fitness—depends upon locomotion, and because we have now accumulated a fairly large data base on capacities for locomotor performance, daily movement distances (DMDs) in the field, and various related measures of energetics.

We use allometric comparisons of mammals and lizards (as representative terrestrial vertebrate endotherms and ectotherms) to illustrate possible constraints because the two groups are relatively well-studied and differ greatly in aerobic metabolic capacities, daily energetic costs, and thermoregulatory patterns, but are still similar enough in terms of general ecology and body plan to be comparable (both groups are mostly terrestrial quadrupeds). Such allometric comparisons are useful and unavoidable, but comparisons of “outliers” (species unusual for their clade) can also inform mechanism (Weibel et al. 1991) and evolutionary scenarios, as they help to indicate extremes of possible adaptation within mammalian and saurian lineages.

We compare mammals and lizards for basal or standard metabolic rate (BMR or SMR), the latter only for measurements taken at 35–40°C, which is within the range for most mammals during the active season (i.e., not torpid or hibernating; Ruf and Geiser 2015). (BMR also correlates positively with body temperature among species of mammals, but the correlation is not strong in the range of 35–40°C [White and Seymour 2004].) We also compare maximal rates of oxygen consumption during forced exercise (VO_{2max}) and maximal aerobic speeds (MAS = speed at which VO_{2max} is attained) with lizards restricted to 35–40°C because they vary strongly with temperature within species (John-Alder and Bennett 1981; Hertz et al. 1983; Bennett and John-Alder 1984; Autumn et al. 1994). For consistency, we also retain information on the net cost of transport (NCT) of lizards in this restricted temperature range, even though some studies suggest it does not vary with temperature within species of lizards (John-Alder and Bennett 1981; Bennett and John-Alder 1984; White et al. 2016). Information on the NCT, DMD, and daily energy expenditure (DEE) during the active season is then used to compute the ecological cost of transport (ECT = percentage of DEE attributable to locomotion [Garland 1983a]).

The foregoing performance and energetic measurements that we consider should set boundaries for much of what an animal does, or can do, in a locomotor context (Fig. 1). For example, maximal sprint speed limits how fast an animal can run and might be a major determinant of the outcome of predator–prey interactions

(Foster et al. 2015; Moore and Biewener 2015), presuming that running away is the strategy applied (Bulova 1994; Cooper et al. 2014). Of course, some animals, such as skunks, porcupines, and horned lizards (*Phrynosoma*), rely little on sprinting as part of their antipredator behavior. Their alternate defensive mechanisms have coadapted with their behavior and probably also with other aspects of their morphology, coloration, life history, and ecology (Pianka and Parker 1975; Stankowich and Campbell 2016). (Some lizards even alter their antipredator strategy as a function of body temperature, which affects locomotor abilities [Hertz et al. 1982; Herrel et al. 2007].)

Maximal aerobic capacity and its associated locomotor speed will limit sustained efforts, such as actively foraging for a prolonged time, defending a territory, or moving long distances during migration (Brownscombe et al. 2017; Yap et al. 2017). For example, VO_{2max} and endurance capacity may be higher during the breeding season and consequently allow higher activity intensity associated with increased intraspecific interactions (territory disputes and mating activities) in *Dipsosaurus dorsalis* (John-Alder 1984) and *Sceloporus undulatus* (John-Alder et al. 2009). This correlation suggests that low aerobic capacity might impose a behavioral constraint on activity levels needed for breeding success.

Just as basal or even resting metabolic rate cannot equal maximum aerobic metabolic rate (otherwise no energy would be available for any activity beyond than simply lying down!), the cost of traveling in the wild cannot equal the total DEE. If the cost of locomotion is too high a fraction of DEE, then insufficient energy will be available for other biological functions (Garland et al. 2011b), thus constraining them. The ECT is a useful index of relative locomotor costs (e.g., Christian et al. 1997; Girard 2001).

The comparison of terrestrial mammals and lizards necessarily means painting with a broad brush. One may wonder if this is somehow a “fair” comparison. We think that it is. The first placental and marsupial mammals date from ~175 mya and may have weighed 20–30 g, resembling a modern shrew (Jones et al. 2013; Springer et al. 2017). Living mammals number ~5400 species, but if we exclude monotremes (which have low body temperatures compared with other mammals [Dawson et al. 1979]) as well as bats, whales, and seals (which have no counterparts among lizards), we are left with ~4100 species. Lizards diversification to modern groups occurred ~200 mya, leaving us with ~6263 extant species (excluding 3619 snakes) (Uetz 2016). It may surprise some that extant lizards are more speciose than extant mammals. However, the latter span a much larger range of body sizes (Pough 1980; Meiri 2008;

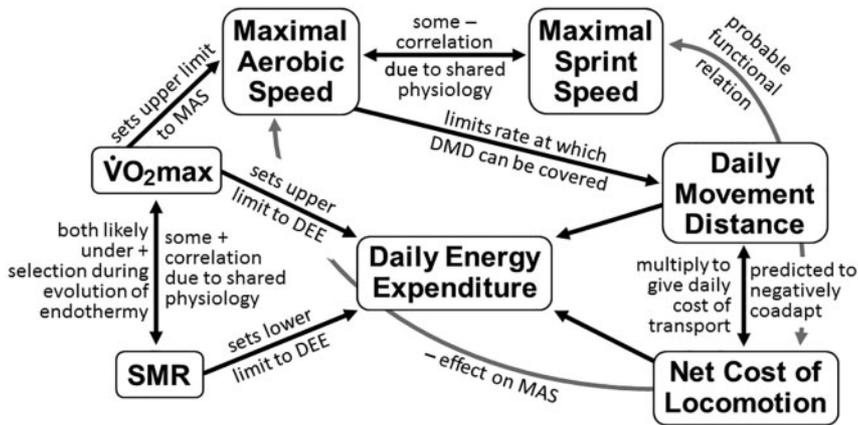


Fig. 1 Interrelationships of the traits considered in the present study, plus maximal sprint speed (see references in the text). For most mammals and lizards, DEE (Fig. 2) is 2- to 3-fold higher than SMR (Fig. 3). VO_{2max} attained during exercise (Fig. 3) sets a theoretical absolute upper limit to DEE, but in practice this metabolic state can only be sustained for minutes, not an entire day. However, the highest sustained DEE of mammals can exceed BMR by several folds (Hammond and Diamond 1997), as for dogs during the Iditarod sled race (Piersma and van Gils 2010), humans in extreme athletic events or under controlled tests (Westerterp 2001; Cooper et al. 2011; Rosenkilde et al. 2015), and rodents challenged by cold, lactation, and/or having to run for food (Speakman and Krol 2010; Zhao et al. 2013). The product of DMD (Fig. 4) and the net cost of locomotion (NCT: Fig. 5), divided by DEE (Fig. 2), is termed the ECT (Garland 1983a), a value that, on average, is relatively small for both mammals and lizards (Table 1). Maximal sprint speeds and maximal aerobic (sustainable) speeds (Fig. 6) likely trade-off to some extent, although this has yet to be demonstrated (Garland et al. 1988), and indeed speed and endurance (as opposed to MAS) do not reliably trade-off in lizards (Albuquerque et al. 2015a). Given the network of interactions among these traits and their physiological and morphological foundations, one would expect that natural or sexual selection acting on any one of them would likely lead to coadaptation of at least some of the others, including antipredator behavior and body size, which has a strong effect on all of these traits (Bauwens et al. 1995; Brashares et al. 2000; Vanhooydonck and Van Damme 2003; Angilletta et al. 2006; Reale et al. 2010; Wallace and Garland 2016). Other aspects of locomotor performance would be expected to exhibit correlated evolution as well, such as a positive correlation between speed and acceleration (Vanhooydonck et al. 2006; Wilson et al. 2013).

O’Gorman and Hone 2012) and, arguably, occupy a greater amount of morphospace and a larger number of niches.

Methods

We gathered data from peer-reviewed articles published in scientific journals, found primarily through Google Scholar and Web of Science. For most of the traits considered here, recent data compilations served as a starting point from which data from later publications were added.

Basal and standard metabolic rates (BMR and SMR, respectively) was measured in the dark, on undisturbed animals, during the non-active period of the day for each species. Major reviews were available for mammals (White et al. 2009; Gillooly et al. 2017); we excluded bats, whales, and seals. For lizards (excluding snakes), the data are presented in Supplementary Table 1.

For mammals, maximal aerobic capacity (VO_{2max}) during forced exercise was taken primarily from Dlugosz et al. (2013), with the addition of several species (or populations) that had been missed in

that compilation (Weibel et al. 1983; MacMillen and Hinds 1992; Baudinette et al. 1993; Williams et al. 2002) (*Trichosurus vulpecula*, 1850 g, 7714.5 mL O_2/h ; *Lontra canadensis*, 11,100 g, 28,092 mL O_2/h ; *Potorus tridactylus*, 1084 g, 5898 mL O_2/h ; *Cavia cobaya*, 913.5 g, 3396 mL O_2/h ; *Dicrostonyx groenlandicus*, 61 g, 450 mL O_2/h ; *Dipodomys ordii*, 56.2 g, 441.6 mL O_2/h ; *Dipodomys panamintinus*, 65.60 g, 444.6 mL O_2/h), but excluding one bat. For lizards, many sources were used (Supplementary Table 2).

Data for the NCT (Taylor et al. 1970; Seeherman et al. 1981) were compiled by White et al. (2016), but we also checked the original sources as we had been building this data base for many years. In addition, we added data from MacMillen and Hinds (1992).

MAS is the speed at which VO_{2max} is attained, and both measures were frequently reported in the same papers. We compiled data from original sources, as presented in Supplementary Table 3.

DMD (Online Supplementary Table 4) was measured by direct observation of marked animals or radiotelemetric fixes, if done for a sufficient portion of the day and including enough data points to allow

an accurate estimation of the distance traveled (Garland 1983a; Goszczynski 1986; Harris and Steudel 1997; Garland 1999; Girard 2001).

DEE was taken only from studies using the doubly labeled water method, with a period of at least 24 h between marking and recapture of the animals (primary sources: Nagy et al. 1999; Nagy and Bradshaw 2000). The full database is found in Supplementary File 5.

The ECT is the minimum energetic cost of locomotion in the field and was calculated as the product of DMD and NCT, divided by DEE (Garland 1983a). Further discussions of the ECT, including its assumptions and limitations, can be found elsewhere (Altmann 1987; Baudinette 1991; Karasov 1992; Girard 2001).

We took a simple approach to statistical analysis: analysis of covariance (ANCOVA) with log-transformed data and body mass as the only covariate. Although body temperature can affect all of the performance and metabolic traits we consider, restricting the lizard data to those gathered at 35–40°C (and excluding snakes) should make them generally directly comparable to those for terrestrial mammals (excluding monotremes, bats, whales, and seals). To test for differences in the allometric slopes of relationships within mammals and lizards, we compared the slopes of the regression lines with standard *F* tests for the interaction between log body mass and a 0–1 dummy variable to code for mammal versus lizard. Although we present estimates of allometric equations along with their standard errors, the standard errors especially should be treated with caution (see next paragraph). In the text below, we present separate equations for mammals and lizards, as these may be of the most use for readers, e.g., if they want to predict the value of a trait for a given body size in one group or the other. For illustrative purposes, we also present values estimated by the regression models with forced parallel slopes (but with different intercepts for mammals and lizards) for a body mass of 100 g (Table 1).

We did not attempt to perform phylogenetically based statistical comparisons (Garland et al. 2005; Rezende and Diniz-Filho 2012; Garamszegi 2014) for two main reasons. First, we are comparing only two clades separated by long divergence times, thus leading to statistical difficulties that reduce statistical power to detect group differences (Garland et al. 1993; Vanhooydonck and Van Damme 1999). Second, both nonphylogenetic and phylogenetic estimates of slopes and group differences are generally non-biased, although the former will not be minimum-variance. As our first main point is simply

Table 1 Comparison of the traits considered in this study for animals of 100 g body mass, using allometric estimates with parallel slopes (i.e., not those shown in the text)

Trait	Units	Mammal	Lizard	Mammal/lizard
SMR	mL O ₂ /h	95.1	16.1	5.93
VO _{2max}	mL O ₂ /h	886.4	147.1	6.03
NCT	kJ/km	2.02	2.30	0.88
MAS	km/h	5.24	0.71	7.38
Sprint speed	km/h	15	15	1.00
DMD	km/day	1.49	0.25	5.96
DEE	kJ/day	117.0	10.3	11.41
ECT	% DEE	2.57	5.51	0.47
Time to Walk DMD	min/day	17.0	20.8	0.82

The ratio of VO_{2max}/SMR is very similar for mammals (9.3) and lizards (9.2).

to compare average values for mammals and lizards, while controlling for variation in body size, not to do statistical tests of whether they differ, the foregoing limitations should not cloud results and interpretation. Our second main point is to examine the extent of overlap (or almost overlap) between mammals and lizards, which can be done to a first approximation by inspection of the data without statistical procedures.

Results and discussion

Sprint speed

As reported originally by (Garland 1983b) for mammals and by (Van Damme and Vanhooydonck 2001) for lizards, maximal sprint speed shows a nonlinear relation with body size, with the fastest species occurring at intermediate body sizes. Whether these overall relations are better fit by a second-degree polynomial (Garland 1983b; Clemente et al. 2009a), a break-point regression (Chappell 1989), or something else (e.g., see Figure 1 in Jones and Lindstedt 1993) is unclear. Addressing this issue further is best deferred to a time when we have estimates of error variance for the data points analyzed, as well as estimates of phylogenetic relationships for both groups (again, with indices of uncertainty), and potentially new statistical tools (see also below under the section “Future directions”). In addition, analyses within lineages of mammals suggests that speed is largely independent of body mass within some of them (Garland 1983b; Djawdan and Garland 1988; Garland et al. 1988).

As shown in Figure 5 of Van Damme and Vanhooydonck (2001) and Figure 5 of Clemente et al. (2009a), sprint speeds of mammals and lizards show

complete overlap at smaller body masses. This similarity coincides with the general similarity in maximal power input from muscles of small mammals and lizards during burst activities (Bennett and Ruben 1979). However, sprint speeds for the largest living lizards in the genus *Varanus* are much lower than for some mammals (Clemente et al. 2009a). Whether this “deficiency” in large lizards is based on metabolic or biomechanical limitations (Christian and Garland 1996; Clemente et al. 2009a), or rather reflects a lack of selection for very fast, large lizards, is unknown.

Even without the use of phylogenetic statistics that may paint a somewhat different picture regarding outliers (Garland and Ives 2000), a number of relatively slow “outlier” species are apparent in the published studies cited in the previous paragraph. In general, these species have alternative means of dealing with predators. For example, moles largely avoid predators that might chase them across ground due to their burrowing habits. Moreover, their specializations for digging likely compromise their sprinting abilities. The porcupine has quills as a means of defense against predators (Stankowich and Campbell 2016), and so does not need speed in that context (nor for obtaining food). Very large mammals (at least as adults), including rhinos and elephants, escape most predators by virtue of their size, and in addition biomechanical factors likely constrain their top speeds (Biewener 2005).

On the positive end of the spectrum, the fastest lizard (34.6 km/h, 230 g, spiny-tailed iguana) is intermediate in size (Garland 1984). For mammals, bipedal kangaroo rats have high speed, endurance, and agility (Djawdan and Garland 1988; MacMillen and Hinds 1992; Djawdan 1993). Received wisdom indicates that the cheetah reigns supreme in terms of terrestrial speed. Garland (1983b) used a value of 110 km/h, but the most accurate timing of this species indicates a maximum speed of 104.4 km/h (Sharp 1997; Wilson et al. 2013), within the range of values reported for some antelope and the American pronghorn (Garland 1983b).

Basal (or standard) and maximal metabolic rates

As expected, both lizards and mammals show a positive allometric relation between metabolic rate and body size, but with slopes less than unity (i.e., mass-specific values increase with body size) (White and Kearney 2013; White and Kearney 2014; Uyeda et al. 2016). The average BMR for 476 species of mammals is 6.0 times higher than the average SMR for 41 lizards measured at 35–40°C, a somewhat

lower difference than commonly cited (e.g., Bennett and Ruben 1979). The pooled within-groups slope for BMR–SMR from ANCOVA was 0.713 ± 0.007 . However, the slope of the allometric relation is slightly steeper ($P=0.001$) for lizards than for mammals, leading to some convergence of average predicted values at larger body sizes, and some overlap is apparent at intermediate body sizes in Fig. 3. (Bats tend to have relatively high BMR [Uyeda et al. 2016], but including them in the above analyses [see also Table 1] changes the numbers only in the second or third decimal place.) Separate allometric equations are as follows:

$$\begin{aligned} \text{Mammals: } \log_{10} \text{BMR} \\ &= 0.567 (\pm 0.019) + 0.707 (\pm 0.007) \\ &\times \log_{10} \text{Mass} \end{aligned}$$

$$\begin{aligned} \text{Lizards: } \log_{10} \text{SMR} \\ &= -0.376 (\pm 0.049) + 0.795 (\pm 0.024) \\ &\times \log_{10} \text{Mass} \end{aligned}$$

The proximate causes of the higher resting metabolic rates of mammals as compared with lizards include larger internal organs, increased mitochondrial volume densities in various tissues, altered membrane composition that may act as a metabolic pacemaker (“leaky membranes”), and increased rates of protein synthesis (e.g., Else and Hulbert 1981; Hulbert and Else 1989; Hulbert and Else 2000; Else et al. 2004; Else et al. 2004; Hulbert et al. 2006; see also White and Kearney 2013). All of these lower-level, subordinate traits also show allometric scaling with body size (e.g., Turner et al. 2006 and references in the previous sentence).

The 84 species of mammals have an average $\text{VO}_{2\text{max}}$ 6.0-fold higher than the 53 lizards. The ANCOVA slope is $0.845 (\pm 0.015)$, higher than for BMR–SMR. Lizards have a significantly lower slope ($P=0.021$), although the largest lizard (6.8 kg) in the dataset is much smaller than the largest mammal (475 kg). Nonetheless, overlap almost occurs, especially at the smaller body sizes, attributable to some small *Varanus* (Clemente et al. 2009b) and one species of whiptail lizard having high $\text{VO}_{2\text{max}}$ (Garland 1993). Further, if one imagines a line extending from the lizard with the highest $\text{VO}_{2\text{max}}$ (in the 15–40 g range), with the pooled within-groups slope from ANCOVA, that line clearly would hit the values for mammals at larger body sizes. Or, imagine a similar line extending downwards along the body mass axis from the mammal with the lowest $\text{VO}_{2\text{max}}$ (~50 kg); again, it would intercept with

some of the higher values for lizards. Separate allometric equations are as follows:

$$\begin{aligned} \text{Mammals: } \log_{10} \text{VO}_{2\text{max}} \\ &= 1.209 (\pm 0.051) + 0.862 (\pm 0.016) \\ &\times \log_{10} \text{Mass} \end{aligned}$$

$$\begin{aligned} \text{Lizards: } \log_{10} \text{VO}_{2\text{max}} \\ &= 0.619 (\pm 0.074) + 0.779 (\pm 0.032) \\ &\times \log_{10} \text{Mass} \end{aligned}$$

Numerous studies have elucidated the mechanistic underpinnings of a high $\text{VO}_{2\text{max}}$, either within lineages or between mammals and lizards, including larger hearts, higher maximal heart rates and blood pressures, non-nucleated erythrocytes, higher blood hemoglobin levels, increased mitochondrial volume densities in heart and skeletal muscles, a muscular diaphragm, and a more elaborate lung structure (e.g., Else and Hulbert 1981; Weibel et al. 1983; Hulbert and Else 1989; Weibel et al. 1991; Jones and Lindstedt 1993; Conley et al. 1995; Else et al. 2004; Hulbert et al. 2006; Hillman et al. 2012).

Net cost of transport

Considering both mammals ($N=91$) and lizards ($N=23$) combined, the NCT scales with body mass to the $0.711 (\pm 0.010)$ power. Complete overlap occurs at all body sizes between lizards and mammals, with no statistically significant difference in the cost of transport between the two lineages (P for elevation difference = 0.097, with lizards having slightly elevated values). Slopes do not differ ($P=0.984$). Separate allometric equations are as follows:

$$\begin{aligned} \text{Mammals: } \log_{10} \text{NCT} \\ &= 0.568 (\pm 0.040) + 0.717 (\pm 0.011) \\ &\times \log_{10} \text{Mass} \end{aligned}$$

$$\begin{aligned} \text{Lizards: } \log_{10} \text{NCT} \\ &= 0.626 (\pm 0.048) + 0.716 (\pm 0.021) \\ &\times \log_{10} \text{Mass} \end{aligned}$$

As discussed elsewhere, nocturnal lizards tend to have low costs of transport (Autumn et al. 1999; Hare et al. 2007; White et al. 2016), but they were excluded from the present analyses due to their low body temperatures.

MAS

The MAS scales as $0.178 (\pm 0.021)$ (ANCOVA slope) for 49 mammals and 19 lizards, with mammals having higher MAS ($P=5 \times 10^{-22}$) by 7.4-fold. Lizards seem to show a shallower slope (Fig. 6), but the difference is not statistically significant ($P=0.180$), and it is mainly driven by two species of relatively small lizards (*Cnemidophorus tigris* (Garland 1993); *Varanus gilleni* (estimated from Bickler and Anderson 1986) that are famous for their active, widely foraging lifestyles. The data for mammals suggest perhaps some curvilinearity downwards at the larger body sizes, but the two largest-bodied mammals in the dataset, both species in the genus *Bos* (wild and domestic cattle), have relatively low MAS and are not known for their athletic prowess. Separate allometric equations are as follows:

$$\begin{aligned} \text{Mammals: } \log_{10} \text{MAS} \\ &= 0.327 (\pm 0.072) + 0.190 (\pm 0.022) \\ &\times \log_{10} \text{Mass} \end{aligned}$$

$$\begin{aligned} \text{Lizards: } \log_{10} \text{MAS} \\ &= -0.363 (\pm 0.137) + 0.109 (\pm 0.061) \\ &\times \log_{10} \text{Mass} \end{aligned}$$

The higher MAS of mammals means that they have the potential to sustain locomotor activity at substantially higher speeds than their saurian counterparts, with important implications for foraging and other activities (e.g., see Bennett and Ruben 1979; Garland et al. 1988; Garland 1993). In general, variation in MAS will be closely associated with variation in $\text{VO}_{2\text{max}}$ (e.g., see Thompson and Knight-Maloney 2017).

DMD

DMD is by far the most variable trait, with two orders of magnitude difference between the smallest and largest values at a given body size (Fig. 4). The pooled scaling slope is 0.177 ± 0.042 , and mammals ($N=125$) travel on average 6.1 times more than lizards ($N=20$) on a daily basis. Mammals and lizards do not differ in slope ($P=0.674$). Within mammals, carnivores generally move longer distances than other species at any body size (not shown in the figure, but apparent on inspection of the data) (Garland 1983a; Goszczynski 1986; Harris and Steudel 1997). Many of the lizards in the sample are smaller than any of the mammals, but the overlap between mammals and lizards is extensive. Separate allometric equations are as follows:

$$\begin{aligned} \text{Mammals: } \log_{10}\text{DMD} \\ &= -0.150 (\pm 0.190) + 0.169 (\pm 0.047) \\ &\times \log_{10}\text{Mass} \end{aligned}$$

$$\begin{aligned} \text{Lizards: } \log_{10}\text{DMD} \\ &= -1.028 (\pm 0.175) + 0.216 (\pm 0.089) \\ &\times \log_{10}\text{Mass} \end{aligned}$$

Interestingly, the pooled scaling exponent for DMD (0.177) is virtually identical to that for MAS (0.178), which makes biological sense. That is, variation in the speed that animals can sustain scales the same way as the distances they typically move in nature, suggesting coadaptation of locomotor behavior (DMD) and locomotor abilities (as indexed by MAS).

DEE

Of the traits we have considered (Fig. 1), the largest average difference between lizards and mammals is for DEE as measured in the field (Fig. 2). Overall, with parallel slopes enforced, DEE scales as mass to the $0.761 (\pm 0.017)$ power, and the 112 species of mammals spend, on average, 11.4 times as much energy per day as the 56 lizard species during the active season. (This differential is on the order of 30-fold if data spanning an entire year are considered [Nagy 2005].) Lizards have a significantly steeper allometric slope ($P = 2 \times 10^{-14}$) than mammals, resulting in some convergence with mammals at larger body sizes. Actual overlap occurs for the sloth (enough said) and porcupine, with the giant panda also being quite low for a mammal. At the small end of the body size range, the golden mole is another mammal with very low DEE (Seymour et al. 1998). Separate allometric equations are as follows:

$$\begin{aligned} \text{Mammals: } \log_{10}\text{DEE} \\ &= 0.767 (\pm 0.049) + 0.679 (\pm 0.017) \\ &\times \log_{10}\text{Mass} \end{aligned}$$

$$\begin{aligned} \text{Lizards: } \log_{10}\text{DEE} \\ &= -0.801 (\pm 0.055) + 0.941 (\pm 0.028) \\ &\times \log_{10}\text{Mass} \end{aligned}$$

ECT

The estimated minimum amount of energy dedicated to locomotion in the field (Garland 1983a) is surprisingly low for both groups, and increases with body mass (Table 2). In addition, lizards have higher

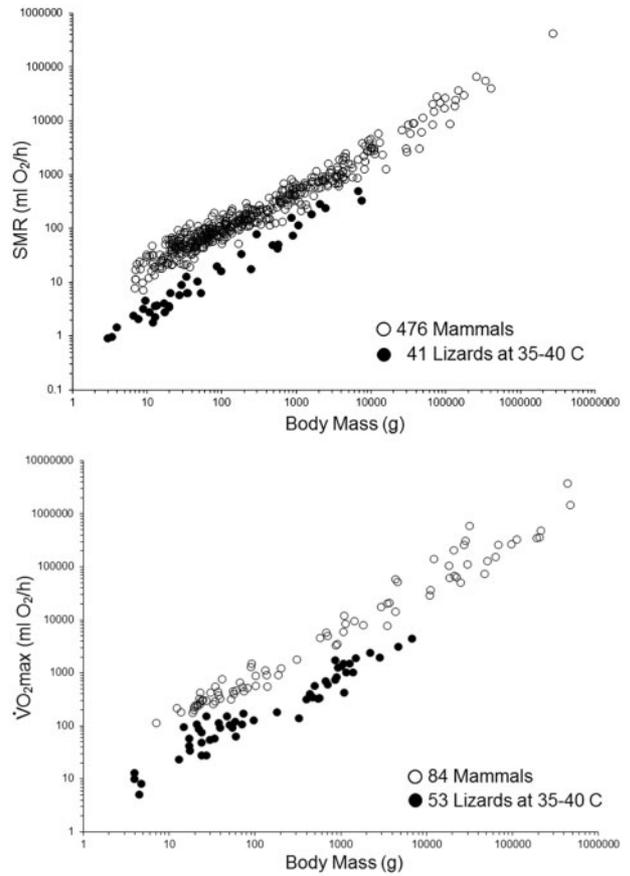


Fig. 2 SMR and maximal (exercise-induced: $\text{VO}_{2\text{max}}$ [Dlugosz et al. 2013]) aerobic metabolic rates average about six-fold higher in mammals than in lizards measured at comparable body temperatures. For SMR, some convergence occurs at larger body sizes, with values for some species overlapping. For $\text{VO}_{2\text{max}}$, some overlap also occurs, especially at smaller body masses. The fact that overlap occurs between mammals and lizards is not widely appreciated for either SMR or $\text{VO}_{2\text{max}}$.

average predicted ECT than mammals (see also Christian et al. 1997). These values should represent the minimum amount of energy spent on locomotion under ideal conditions (e.g., good traction, level substrate, no obstacles, few and non-abrupt changes in direction). Deviations from these conditions in the wild would likely increase the ECT (Altmann 1987; Karasov 1992).

Summary and conclusions

Maximal sprint speeds of mammal and lizards are similar at smaller body sizes, but at larger sizes mammals have a big advantage (no pun intended) (Garland 1983b; Djawdan and Garland 1988; Garland et al. 1988; Bonine and Garland 1999; Van Damme and Vanhooydonck 2001; Clemente et al. 2009a). It would be of considerable interest to

Table 2 Comparison of the ECT (% of DEE) across range of body masses for average mammals and lizards, based on allometric equations that use parallel slopes (i.e., not those shown in the text)

	Body mass (g)				
	1	10	100	1000	10,000
Mammals	1.4	1.9	2.6	3.5	4.7
Lizards	3.0	4.1	5.5	7.5	10.2

These values represent the minimum amount of energy that might be spent on locomotion as animals move about their home ranges or territories on a daily basis. Many exceptions to these average values for ECT are known to exist, such as sloths (Pauli et al. 2016), moles (Seymour et al. 1998), and some carnivores (Girard 2001; Speakman et al. 2015).

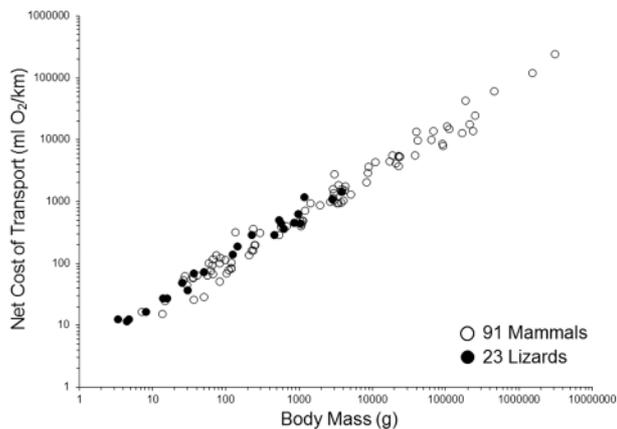


Fig. 3 The NCT is very similar in mammals and lizards across a range of body sizes.

know the maximum speeds attained by the giant (possibly >300 kg), extinct varanid lizard *Varanus (Megalania) priscus*, especially as they may have encountered aboriginal humans (see also Clemente et al. 2009a). At any size, mammals also have a large advantage in terms of VO_{2max} (Fig. 3) and maximal aerobic (sustainable) speeds (Fig. 6). The cost of transport per unit distance moved is similar in the two lineages (Fig. 5), regardless of body size. On average, mammals move further than lizards on a daily basis (Fig. 4) and have much higher DEEs (Fig. 2), and hence food requirements (Nagy 2001). Combining NCT, DMD, and DEE allows calculation of the minimum percent of the DEE that is attributable to locomotor costs (ECT), and this value is surprisingly low in both groups, though higher on average in larger animals and in lizards as compared with mammals (Table 2). Therefore, the “30,000-foot view” (AskTheManager.com 2017) would suggest that ecological-energetic constraints related to

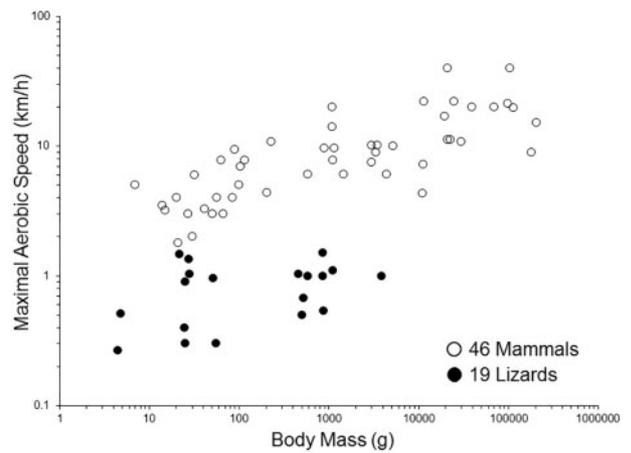


Fig. 4 MAS (speed at which VO_{2max} is attained) averages about 7.4-fold higher in mammals than in lizards measured at comparable body temperatures (35–40 °C), but values almost overlap for some small-bodied species. Thus, mammals can patrol their territories or traverse their home ranges at much higher sustainable speeds.

locomotion are most likely in large, carnivorous lizards (see also Christian et al. 1997) because the cost of moving about is relatively high, whereas both maximal aerobic and maximal sprint speeds are relatively low. Thus, we might expect these animals to adopt strategies for energy conservation and/or to compensate for their relatively low maximal speeds, such as the switch from widely foraging to sit-and-wait predatory behavior seen in Komodo dragons relative to most other varanid lizards.

On average, MAS is ~7-fold higher in mammals (Fig. 6) and DMD is ~5-fold higher. If animals were to cover their DMD while moving at their maximal aerobic speed, then mammals and lizards of 100 g body mass would take about 15 and 21 min, respectively, to do so. Thus, at least for smaller body sizes, daily movements would not appear to be limited by available time, except perhaps when environmental conditions are extreme. However, the difference in speed of movement at the MAS could affect visibility by predators and/or the ability of animals to perceive their environment. On the other hand, many animals, especially smaller ones, do not typically move at constant speeds, but rather use intermittent locomotion (Girard et al. 2001; Trouilloud et al. 2004; Stojan-Dolar and Heymann 2010; and references therein).

Endothermic homeothermy is the epitome of a complex trait (Woods et al. 2015; Garland et al. 2016), and interest in its evolutionary origins played a major role in the development of evolutionary physiology (Bennett and Ruben 1979; Bennett and Ruben 1986; Garland and Carter 1994). Interest in the evolution of endothermy remains a “hot” topic in comparative, ecological, and evolutionary

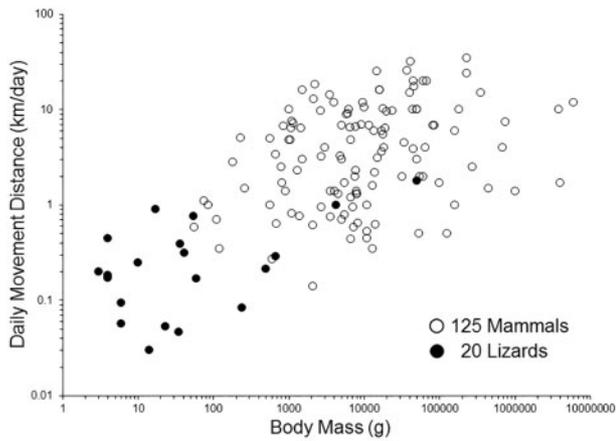


Fig. 5 Daily movements distances (Garland 1983a) are highly variable within both mammals and lizards (see also Table 1), and values broadly overlap between these groups, but on average they are about 6-fold higher in mammals. See text for allometric equations with pooled slope from ANCOVA.

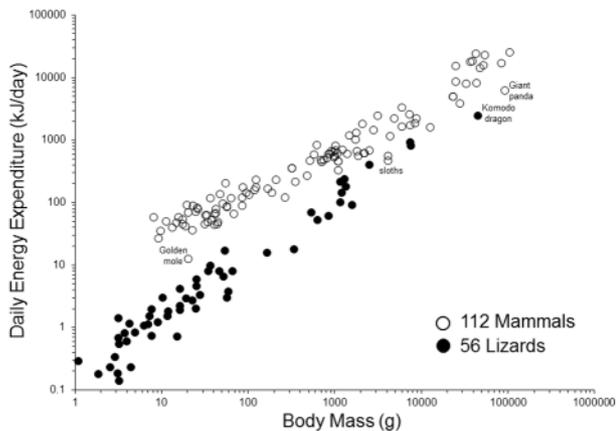


Fig. 6 Field metabolic rates during the active season (measured by doubly-labeled water) average about 11.4-fold higher in mammals than in lizards, but the slope is significantly steeper for lizards and overlap occurs at the larger body sizes. The average difference between mammals and lizards is closer to 30-fold if calculated on an annual basis for temperate-zone species (Nagy 2005).

physiology (Hayes and Garland 1995; Farmer 2000; Koteja 2000; Nespolo et al. 2011; Nespolo et al. 2011; Nespolo and Roff 2014; Wone et al. 2015; Farmer 2016; Killen et al. 2016; Tattersall et al. 2016; Nespolo et al. 2017; Nicol 2017). Taken together, our results suggest that the evolution of mammalian endothermy did not necessarily require major changes in locomotor energetics, performance, or associated behaviors. Rather, gradual changes in such traits as standard (Dawson et al. 1979) and maximal aerobic metabolic rates seem likely to have occurred. Moreover, in terms of metabolic rate and locomotor performance, the evolution of mammalian endothermy may not have

necessitated major changes. Finally, as noted by (Nicol 2017), extant monotremes illustrate mosaic evolution, and hence may be crucial in understanding the evolution of endothermy. Most likely, endothermy evolved with lots of coadaptation across levels of biological organization, ranging from subcellular to morphological to behavioral and life history traits, but not all changes occurred simultaneously, and probably multiple solutions (Garland et al. 2011a; Losos 2011; Travisano and Shaw 2013; Wallace and Garland 2016) (but see Projecto-Garcia et al. 2013) appeared in different lineages (Hillenius and Ruben 2004).

Future directions

The comparisons presented here and the network of interacting traits shown in Fig. 1 suggests various avenues for future research:

(1) Comparisons of mammals and lizards living in sympatry would allow control for environmental effects, which may have large and confounding influences on such traits as DMD and DEE. This would allow direct determination of the extent of overlap in such traits.

(2) Within either mammals or lizards, many of the traits presented here or in previous literature comparisons (Van Damme and Vanhooydonck 2001 for maximal sprint speeds) could be analyzed in relation to habitat, ecology, diet, mating system, life history traits, etc. to test various functional and adaptive hypotheses (Garland et al. 2005; Rezende and Diniz-Filho 2012). For example, maximal sprint speed is likely to vary in relation to diet, foraging mode, habitat, and life history traits (Garland et al. 1988; Djawdan 1993; Van Damme and Vanhooydonck 2001; Vanhooydonck and Van Damme 2003; Clemente et al. 2009a). Some of the relations may be somewhat unexpected, as in the positive relationship between brain size and aerobic capacity (Raichlen and Gordon 2011; Kolb et al. 2013). It should also be noted that clades of mammals or lizards may show grade shifts (Ferguson et al. 1996; Rezende and Diniz-Filho 2012; Garland 2014), such that suites of traits differ as compared with other lineages, even when controlling for body size and other ecological indicators of variation in the selective regime (e.g., Pontzer et al. 2014).

(3) Following from (2), various hypotheses about coadaptation could be tested. For example, one might expect that DMD, MAS, VO_{2max} , and NCL would have been under some sort of correlational selection in relation to diet, foraging strategy, and other aspects of behavioral ecology (Altmann 1987; e.g., see Garland 1999; Verwajen and Van Damme 2008; Albuquerque et al. 2015b; Wallace and Garland

2016). One might also expect coadaptation of the elements that affect DEE, much as sloths (and other arboreal folivores) appear to have a suite of adaptations related to their lifestyle and overall low rates of energy expenditure (Pauli et al. 2016). More generally, relative to birds and mammals, vertebrate ectotherms can be viewed as low-energy specialists (Pough 1980). For animals that have low activity levels either habitually or in relation to seasonality (e.g., because of hibernation), one could predict low plasticity of exercise capacities to avoid deterioration by detraining effects. Indeed, lizards may be somewhat less plastic than mammals in this regard (e.g., Garland et al. 1987; O'Connor et al. 2011; but see Husak et al. 2015). A related question is whether they exercise to keep fit (Halsey 2016).

(4) Mechanistically based trade-offs might be expected to occur between maximal sprint and aerobic speeds (or other measures related to stamina), though these have been hard to find so far (Garland et al. 1988; Vanhooydonck et al. 2001; Albuquerque et al. 2015a) (see also Vanhooydonck and Van Damme 2001; Calsbeek 2017). Also deserving of much further study is the mechanistic basis of lineage or species differences in such traits as sprint speed (Bonine and Garland 1999; Schaeffer and Lindstedt 2013; Vanhooydonck et al. 2014), BMR (Starostová et al. 2009; Raichlen et al. 2010; White and Kearney 2013), and $VO_{2\max}$ (Hillman et al. 2012; Killen et al. 2016; Gillooly et al. 2017).

(5) The extent and frequency to which animals use their maximal capacities in the wild has generated considerable interest (Hertz et al. 1988; Irschick and Losos 1998; Irschick and Garland 2001; Irschick et al. 2005; Husak 2006; Irschick and Higham 2016), but many questions remain, including whether general patterns emerge in relation to body size or among clades of vertebrates.

(6) For any of these questions, future analyses could apply phylogenetically based statistical procedures, though we do not believe they would alter our primary conclusions. Perhaps of greater importance would be refinement of the various datasets to include information on error variances, such as standard errors for each datum. Potentially, phylogenetically based measurement error models (Ives et al. 2007) could be developed that would allow predictive estimation (cf. Garland and Ives 2000) of the extent of overlap between mammals and lizards if one had access to much larger samples of species. The number of species included here, although substantial for some traits, still represents a relatively small fraction of the number of extant species (see Introduction), and it is inevitable that as more species are measured the extent of overlap between mammals and lizards will increase.

(7) Further insights to the evolution of mammalian endothermy may come from attempts to understand the origins and neurobiology of the metabolic (and behavioral) responses to low ambient temperature. Another avenue that may prove fruitful is modeling from both the genetic (Nespolo and Roff 2014) and explicitly mechanistic (Brice 2010) perspectives.

Acknowledgments

We thank the organizers of this symposium for the invitation to participate. The mammal-lizard comparisons that form the basis of this contribution were first presented at the First World Congress of Herpetology in 1989.

Funding

R.L.A. is supported by Brazilian Coordenação de Aperfeiçoamento de Pessoal de Nível Superior process 8935-13-0.

Supplementary data

Supplementary data available at *ICB* online.

References

- Albuquerque RL, Bonine KE, Garland T Jr. 2015a. Speed and endurance do not trade off in phrynosomatid lizards. *Physiol Biochem Zool* 88:634–47.
- Albuquerque RL, Sanchez G, Garland T Jr. 2015b. Relationship between maximal oxygen consumption and home range area in mammals. *Physiol Biochem Zool* 88:660–7.
- Altmann SA. 1987. The impact of locomotor energetics on mammalian foraging. *J Zool (Lond)* 211:215–25.
- Angilletta MJ Jr, Bennett AF, Guderley H, Navas CA, Seebacher F, Wilson RS. 2006. Coadaptation: a unifying principle in evolutionary thermal biology. *Physiol Biochem Zool* 79:282–94.
- AskTheManager.com. 2017. The 25 most annoying business phrases. Ask Manag. (<http://askthemanager.com/2008/11/the-25-most-annoying-business-phrases/>) [date last accessed March 29, 2017].
- Autumn K, Jindrich D, DeNardo D, Mueller R. 1999. Locomotor performance at low temperature and the evolution of nocturnality in geckos. *Evolution* 53:580–99.
- Autumn K, Weinstein RB, Full RJ. 1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiol Zool* 67:238–62.
- Baudinette RV. 1991. The energetics and cardiorespiratory correlates of mammalian terrestrial locomotion. *J Exp Biol* 160:209–31.
- Baudinette RV, Halpern EA, Hinds DS. 1993. Energetic cost of locomotion as a function of ambient temperature and during growth in the marsupial *Potorous tridactylus*. *J Exp Biol* 174:81–95.

- Bauwens D, Garland T Jr, Castilla AM, Van Damme R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution* 49:848–63.
- Bennett AF, John-Alder HB. 1984. The effect of body temperature on the locomotory energetics of lizards. *J Comp Physiol B* 155:21–7.
- Bennett AF, Ruben JA. 1979. Endothermy and activity in vertebrates. *Science* 206:649–54.
- Bennett AF, Ruben JA. 1986. The metabolic and thermoregulatory status of therapsids. In: Hotton N, MacLean PD, Roth LJ, Roth EC, editors. *The ecology and biology of mammal-like reptiles*. Washington, D.C.: Smithsonian Institution. p. 207–18.
- Bickler PE, Anderson RA. 1986. Ventilation, gas exchange, and aerobic scope in a small monitor lizard, *Varanus gil- leni*. *Physiol Zool* 76–83.
- Biewener AA. 2005. Biomechanical consequences of scaling. *J Exp Biol* 208:1665–76.
- Bonine KE, Garland T Jr. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *J Zool (Lond)* 248:255–65.
- Brashares J, Garland T Jr, Arcese P. 2000. Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. *Behav Ecol* 11:452–63.
- Brice P. 2010. Quantifying aspects of the evolution of endothermy. *Aust Zool* 35:349–62.
- Brownscombe JW, Cooke SJ, Algera D, Burnett NJ, Eliason EJ, Danylchuk AJ, Hinch SG, Farrell AP. 2017. The ecology of exercise in wild fish - integrating concepts of individual physiological capacity, behaviour and fitness through diverse case studies. *Integr Comp Biol* 57:281–92.
- Bulova SJ. 1994. Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. *Copeia* 1994:980–92.
- Calsbeek R. 2017. Performance tradeoffs, ontogenetic conflict, and multisport athletes: how is an Ironman triathlete Like a frog? *Integr Comp Biol* 57:207–16.
- Careau V, Garland T Jr. 2012. Performance, personality, and energetics: correlation, causation, and mechanism. *Physiol Biochem Zool* 85:543–71.
- Chappell R. 1989. Fitting bent lines to data, with applications to allometry. *J Theor Biol* 138:235–56.
- Christian A, Garland T Jr. 1996. Scaling of limb proportions in monitor lizards (Squamata: Varanidae). *J Herpetol*: 219–30.
- Christian KA, Baudinette RV, Pamula Y. 1997. Energetic costs of activity by lizards in the field. *Funct Ecol* 11:392–97.
- Clemente CJ, Thompson GG, Withers PC. 2009a. Evolutionary relationships of sprint speed in Australian varanid lizards. *J Zool (Lond)* 278:270–80.
- Clemente CJ, Withers PC, Thompson GG. 2009b. Metabolic rate and endurance capacity in Australian varanid lizards (Squamata: Varanidae: *Varanus*). *Biol J Linn Soc* 97:664–76.
- Conley KE, Christian KA, Hoppeler H, Weibel ER. 1995. Heart mitochondrial properties and aerobic capacity are similarly related in a mammal and a reptile. *J Exp Biol* 198:739–46.
- Cooper JA, Nguyen DD, Ruby BC, Schoeller DA. 2011. Maximal sustained levels of energy expenditure in humans during exercise. *Med Sci Sports Exerc* 43:2359–67.
- Cooper WE, Pyron RA, Garland T Jr. 2014. Island tameness: living on islands reduces flight initiation distance. *Proc R Soc Lond B Biol Sci* 281:20133019.
- Dawson TJ, Grant TR, Fanning D. 1979. Standard metabolism of monotremes and the evolution of homeothermy. *Aust J Zool* 27:511–5.
- Djawdan M. 1993. Locomotor performance of bipedal and quadrupedal heteromyid rodents. *Funct Ecol* 7:195–202.
- Djawdan M, Garland T Jr. 1988. Maximal running speeds of bipedal and quadrupedal rodents. *J Mammal* 69:765–72.
- Dlugosz EM, Chappell MA, Meek TH, Szafranska PA, Zub K, Konarzewski M, Jones JH, Bicudo JEPW, Nespolo RF, Careau V et al. 2013. Phylogenetic analysis of mammalian maximal oxygen consumption during exercise. *J Exp Biol* 216:4712–21.
- Else PL, Hulbert AJ. 1981. Comparison of the “mammal machine” and the “reptile machine”: energy production. *Am J Physiol Regul Integr Comp Physiol* 240:R3–9.
- Else PL, Turner N, Hulbert AJ. 2004. The evolution of endothermy: role for membranes and molecular activity. *Physiol Biochem Zool* 77:950–8.
- Farmer CG. 2000. Parental care: the key to understanding endothermy and other convergent features in birds and mammals. *Am Nat* 155:326–34.
- Farmer CG. 2016. Hot-blooded lizard illuminates endothermy origins. *J Exp Biol* 219:909–10.
- Ferguson SH, Virgl JA, Lariviere S. 1996. Evolution of delayed implantation and associated grade shifts in life history traits of North American carnivores. *Ecoscience* 3:7–17.
- Foster KL, Collins CE, Higham TE, Garland T Jr. 2015. Determinants of lizard escape performance: decision, motivation, ability, and opportunity. In: Cooper WE, Blumstein DT, editors. *Escaping from predators: an integrative view of escape decisions*. Cambridge: Cambridge University Press. p. 287–321.
- Garamszegi LZ, editor. 2014. *Modern phylogenetic comparative methods and their application in evolutionary biology*. Berlin, Heidelberg: Springer. (<http://link.springer.com/content/pdf/10.1007/978-3-662-43550-2.pdf>) [date last accessed August 22, 2014].
- Garland T Jr. 1983a. Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am Nat* 121:571–87.
- Garland T Jr. 1983b. The relation between maximal running speed and body mass in terrestrial mammals. *J Zool (Lond)* 199:157–70.
- Garland T Jr. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. *Am J Physiol Regul. Integr Comp Physiol* 247:R806–15.
- Garland T Jr. 1993. Locomotor performance and activity metabolism of *Cnemidophorus tigris* in relation to natural behaviors. In: Wright JW, Vitt LJ, editors. *Biology of whiptail lizards: genus Cnemidophorus*. Norman (OK): Oklahoma Museum of Natural History and University of Oklahoma. p. 163–210.
- Garland T Jr. 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Anim Behav* 57:77–83.
- Garland T Jr. 2014. Quick guide: trade-offs. *Curr Biol* 24:R60–1.

- Garland T Jr, Bennett AF, Rezende EL. 2005. Phylogenetic approaches in comparative physiology. *J Exp Biol* 208:3015–35.
- Garland T Jr, Carter PA. 1994. Evolutionary physiology. *Annu Rev Physiol* 56:579–621.
- Garland T Jr, Else PL, Hulbert AJ, Tap P. 1987. Effects of endurance training and captivity on activity metabolism of lizards. *Am J Physiol Regul Integr Comp Physiol* 252:R450–6.
- Garland T Jr, Geiser F, Baudinette RV. 1988. Comparative locomotor performance of marsupial and placental mammals. *J Zool (Lond)* 215:505–22.
- Garland T Jr, Ives AR. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am Nat* 155:346–64.
- Garland T Jr, Kelly SA. 2006. Phenotypic plasticity and experimental evolution. *J Exp Biol* 209:2344–61.
- Garland T Jr, Kelly SA, Malisch JL, Kolb EM, Hannon RM, Keeney BK, Van Cleave SL, Middleton KM. 2011a. How to run far: multiple solutions and sex-specific responses to selective breeding for high voluntary activity levels. *Proc R Soc Lond B Biol Sci* 278:574–81.
- Garland T Jr, Schutz H, Chappell MA, Keeney BK, Meek TH, Copes LE, Acosta W, Drenowatz C, Maciel RC, van Dijk G et al. 2011b. The biological control of voluntary exercise, spontaneous physical activity and daily energy expenditure in relation to obesity: human and rodent perspectives. *J Exp Biol* 214:206–29.
- Garland T Jr, Zhao M, Saltzman W. 2016. Hormones and the evolution of complex traits: insights from artificial selection on behavior. *Integr Comp Biol* 56:207–24.
- Garland T Jr, Dickerman AW, Janis CM, Jones JA. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst Biol* 42:265–92.
- Gillooly JF, Gomez JP, Mavrodiev EV. 2017. A broad-scale comparison of aerobic activity levels in vertebrates: endotherms versus ectotherms. *Proc R Soc Lond B Biol Sci* 284:20162328.
- Girard I. 2001. Field cost of activity in the kit fox, *Vulpes macrotis*. *Physiol Biochem Zool* 74:191–202.
- Girard I, McAleer MW, Rhodes JS, Garland T Jr. 2001. Selection for high voluntary wheel-running increases speed and intermittency in house mice (*Mus domesticus*). *J Exp Biol* 204:4311–20.
- Goszczynski J. 1986. Locomotor activity of terrestrial predators and its consequences. *Acta Theriol* 31:79–95.
- Halsey LG. 2016. Do animals exercise to keep fit? *J Anim Ecol* 85:614–20.
- Hammond KA, Diamond J. 1997. Maximal sustained energy budgets in humans and animals. *Nature* 386:457–62.
- Hare KM, Pledger S, Thompson MB, Miller JH, Daugherty CH. 2007. Low cost of locomotion in lizards that are active at low temperatures. *Physiol Biochem Zool* 80:46–58.
- Harris MA, Steudel K. 1997. Ecological correlates of hind-limb length in the Carnivora. *J Zool (Lond)* 241:381–408.
- Hayes JP, Garland T Jr. 1995. The evolution of endothermy: testing the aerobic capacity model. *Evolution* 836–47.
- Herrel A, James RS, Van Damme R. 2007. Fight versus flight: physiological basis for temperature-dependent behavioral shifts in lizards. *J Exp Biol* 210:1762–7.
- Hertz PE, Huey RB, Garland T Jr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles Olympians or Boy Scouts? *Am Zool* 28:927–38.
- Hertz PE, Huey RB, Nevo E. 1982. Fight versus flight: body temperature influences defensive responses of lizards. *Anim Behav* 30:676–9.
- Hertz PE, Huey RB, Nevo E. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* 1075–84.
- Hillenius WJ, Ruben JA. 2004. The evolution of endothermy in terrestrial vertebrates: Who? When? Why? *Physiol Biochem Zool* 77:1019–42.
- Hillman SS, Hancock TV, Hedrick MS. 2012. A comparative meta-analysis of maximal aerobic metabolism of vertebrates: implications for respiratory and cardiovascular limits to gas exchange. *J Comp Physiol B* 183:167–79.
- Hulbert AJ, Else PL. 1989. Evolution of mammalian endothermic metabolism: mitochondrial activity and cell composition. *Am J Physiol Regul Integr Comp Physiol* 256:R63–9.
- Hulbert AJ, Else PL. 2000. Mechanisms underlying the cost of living in animals. *Annu Rev Physiol* 62:207–35.
- Hulbert AJ, Turner N, Hinde J, Else P, Guderley H. 2006. How might you compare mitochondria from different tissues and different species? *J Comp Physiol B* 176:93–105.
- Husak JF. 2006. Does survival depend on how fast you can run or how fast you do run? *Funct Ecol* 20:1080–6.
- Husak JF, Keith AR, Wittry BN. 2015. Making Olympic lizards: the effects of specialised exercise training on performance. *J Exp Biol* 218:899–906.
- Irschick DJ, Garland T Jr. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu Rev Ecol Syst* 32:367–96.
- Irschick DJ, Herrel A, Vanhooydonck B, Huyghe K, Damme van R. 2005. Locomotor compensation creates a mismatch between laboratory and field estimates of escape speed in lizards: a cautionary tale for performance-to-fitness studies. *Evolution* 59:1579–87.
- Irschick DJ, Higham TE. 2016. Animal athletes: an ecological and evolutionary approach. Oxford (NY): Oxford University Press.
- Irschick DJ, Losos JB. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* 52:219–26.
- Ives AR, Midford PE, Garland T Jr. 2007. Within-species variation and measurement error in phylogenetic comparative methods. *Syst Biol* 56:252–70.
- John-Alder HB. 1984. Seasonal variations in activity, aerobic energetic capacities, and plasma thyroid hormones (T3 and T4) in an iguanid lizard. *J Comp Physiol B* 154:409–19.
- John-Alder HB, Bennett AF. 1981. Thermal dependence of endurance and locomotory energetics in a lizard. *Am J Physiol* 241:R342–9.
- John-Alder HB, Cox RM, Haenel GJ, Smith LC. 2009. Hormones, performance and fitness: natural history and endocrine experiments on a lizard (*Sceloporus undulatus*). *Integr Comp Biol* 49:393–407.
- Jones JH, Lindstedt SL. 1993. Limits to maximal performance. *Annu Rev Physiol* 55:547–69.
- Jones ME, Anderson CL, Hipsley CA, Müller J, Evans SE, Schoch RR. 2013. Integration of molecules and new fossils

- supports a Triassic origin for *Lepidosauria* (lizards, snakes, and tuatara). *BMC Evol Biol* 13:21.
- Karasov WH. 1992. Daily energy expenditure and the cost of activity in mammals. *Am Zool* 32:238–48.
- Killen SS, Glazier DS, Rezende EL, Clark TD, Atkinson D, Willener AS, Halsey LG, Kearney M, Bronstein JL. 2016. Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *Am Nat* 187:592–606.
- Kolb EM, Rezende EL, Holness L, Radtke A, Lee SK, Obenaus A, Garland T Jr. 2013. Mice selectively bred for high voluntary wheel running have larger midbrains: support for the mosaic model of brain evolution. *J Exp Biol* 216:515–23.
- Koteja P. 2000. Energy assimilation, parental care and the evolution of endothermy. *Proc R Soc Lond B Biol Sci* 267:479–84.
- Lailvaux SP, Husak JF. 2014. The life history of whole-organism performance. *Q Rev Biol* 89:285–318.
- Losos JB. 2011. Convergence, adaptation, and constraint. *Evolution* 65:1827–40.
- MacMillen RE, Hinds DS. 1992. Standard, cold-induced, and exercise-induced metabolism of rodents. In: Tomasi TE, Horton TH, editors. *Mammalian energetics: interdisciplinary views of metabolism and reproduction*. Ithaca (NY): Comstock Publishing Associates. p. 16–33.
- Meiri S. 2008. Evolution and ecology of lizard body sizes. *Glob Ecol Biogeogr* 17:724–34.
- Moore TY, Biewener AA. 2015. Outrun or outmaneuver: predator–prey interactions as a model system for integrating biomechanical studies in a broader ecological and evolutionary context. *Integr Comp Biol* 55:1188–97.
- Nagy KA. 2001. Food requirements of wild animals: predictive equations for free-living mammals, reptiles, and birds. *Nutr Abstr Rev Ser B Livest Feeds Feed* 71:21R–31R.
- Nagy KA. 2005. Field metabolic rate and body size. *J Exp Biol* 208:1621–5.
- Nagy KA, Bradshaw SD. 2000. Scaling of energy and water fluxes in free-living arid-zone Australian marsupials. *J Mammal* 81:962–70.
- Nagy KA, Girard IA, Brown TK. 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annu Rev Nutr* 19:247–77.
- Nespolo RF, Bacigalupe LD, Figueroa CC, Koteja P, Opazo JC. 2011. Using new tools to solve an old problem: the evolution of endothermy in vertebrates. *Trends Ecol Evol* 26:414–23.
- Nespolo RF, Roff DA. 2014. Testing the aerobic model for the evolution of endothermy: implications of using present correlations to infer past evolution. *Am Nat* 183:74–83.
- Nespolo RF, Solano-Iguaran JJ, Bozinovic F. 2017. Phylogenetic analysis supports the aerobic-capacity model for the evolution of endothermy. *Am Nat* 189:13–27.
- Nicol SC. 2017. Energy homeostasis in monotremes. *Front Neurosci* 11:195.
- O'Connor JL, McBrayer LD, Higham TE, Husak JF, Moore IT, Rostal DC. 2011. Effects of training and testosterone on muscle fiber types and locomotor performance in male six-lined racerunners (*Aspidoscelis sexlineata*). *Physiol Biochem Zool* 84:394–405.
- O'Gorman EJ, Hone DWE. 2012. Body size distribution of the dinosaurs. *PLoS One* 7:e51925.
- Orr TJ, Garland T Jr. 2017. Complex reproductive traits and whole-organism performance. *Integr Comp Biol* 57:407–22.
- Pauli JN, Peery MZ, Fountain ED, Karasov WH. 2016. Arboreal folivores limit their energetic output, all the way to slothfulness. *Am Nat* 188:196–204.
- Pianka ER, Parker WS. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. *Copeia* 1975:141–62.
- Piersma T, van Gils JA. 2010. *The flexible phenotype: a body-centred integration of ecology, physiology, and behaviour*. Oxford (NY): Oxford University Press.
- Pontzer H, Raichlen DA, Gordon AD, Schroepfer-Walker KK, Hare B, O'Neill MC, Muldoon KM, Dunsworth HM, Wood BM, Isler K et al. 2014. Primate energy expenditure and life history. *Proc Natl Acad Sci U S A* 111:1433–7.
- Pough FH. 1980. The advantages of ectothermy for tetrapods. *Am Nat* 115:92–112.
- Projecto-Garcia J, Natarajan C, Moriyama H, Weber RE, Fago A, Cheviron ZA, Dudley R, McGuire JA, Witt CC, Storz JF. 2013. Repeated elevational transitions in hemoglobin function during the evolution of Andean hummingbirds. *Proc Natl Acad Sci U S A* 110:20669–74.
- Raichlen DA, Gordon AD. 2011. Relationship between exercise capacity and brain size in mammals. *PLoS One* 6:e20601.
- Raichlen DA, Gordon AD, Muchlinski MN, Snodgrass JJ. 2010. Causes and significance of variation in mammalian basal metabolism. *J Comp Physiol B* 180:301–11.
- Reale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos Trans R Soc B Biol Sci* 365:4051–63.
- Rezende EL, Diniz-Filho JAF. 2012. Phylogenetic analyses: comparing species to infer adaptations and physiological mechanisms. *Compr Physiol* 2:639–74.
- Rosenkilde M, Morville T, Andersen PR, Kjaer K, Rasmussen H, Holst JJ, Dela F, Westerterp K, Sjo din A, Helge JW. 2015. Inability to match energy intake with energy expenditure at sustained near-maximal rates of energy expenditure in older men during a 14-d cycling expedition. *Am J Clin Nutr* 102:1398–405.
- Ruf T, Geiser F. 2015. Daily torpor and hibernation in birds and mammals. *Biol Rev* 90:891–926.
- Schaeffer PJ, Lindstedt SL. 2013. How animals move: comparative lessons on animal locomotion. *Compr Physiol* 3:291–314.
- Seeherman HJ, Richard Taylor C, Maloij GM, Armstrong RB. 1981. Design of the mammalian respiratory system. II. Measuring maximum aerobic capacity. *Respir Physiol* 44:11–23.
- Seymour RS, Withers PC, Weathers WW. 1998. Energetics of burrowing, running, and free-living in the Namib Desert golden mole (*Eremitalpa namibensis*). *J Zool (Lond)* 244:107–17.
- Sharp NCC. 1997. Timed running speed of a cheetah (*Acinonyx jubatus*). *J Zool (Lond)* 241:493–4.
- Speakman JR, Gorman ML, Mills MG, Raath JP. 2015. Wild dogs and kleptoparasitism: some misunderstandings. *Afr J Ecol* 54:125–7.

- Speakman JR, Krol E. 2010. Limits to sustained energy intake. XIII. Recent progress and future perspectives. *J Exp Biol* 214:230–41.
- Springer MS, Emerling CA, Meredith RW, Janečka JE, Eizirik E, Murphy WJ. 2017. Waking the undead: implications of a soft explosive model for the timing of placental mammal diversification. *Mol Phylogenet Evol* 106:86–102.
- Stankowich T, Campbell LA. 2016. Living in the danger zone: exposure to predators and the evolution of spines and body armor in mammals. *Evolution* 70:1501–11.
- Starostová Z, Kubička L, Konarzewski M, Kozłowski J, Kratochvíl L. 2009. Cell size but not genome size affects scaling of metabolic rate in *Eyelid Geckos*. *Am Nat* 174:E100–5.
- Stojan-Dolar M, Heymann EW. 2010. Functions of intermittent locomotion in *Mustached Tamarins (Saguinus mystax)*. *Int J Primatol* 31:677–92.
- Storz JF, Bridgham JT, Kelly SA, Garland T Jr. 2015. Genetic approaches in comparative and evolutionary physiology. *Am J Physiol Regul Integr Comp Physiol* 309:R197–214.
- Tattersall GJ, Leite CAC, Sanders CE, Cadena V, Andrade DV, Abe AS, Milsom WK. 2016. Seasonal reproductive endothermy in *Tegu lizards*. *Sci Adv* 2:e1500951.
- Taylor CR, Schmidt-Nielsen K, Raab JL. 1970. Scaling of energetic cost of running to body size in mammals. *Am J Physiol* 219:1104–7.
- Thompson MA, Knight-Maloney M. 2017. Physiological and biomechanical mechanisms of distance-specific human running performance. *Integr Comp Biol* 57:293–300.
- Travisano M, Shaw RG. 2013. Lost in the map. *Evolution* 67:305–14.
- Trouilloud W, Delisle A, Kramer DL. 2004. Head raising during foraging and pausing during intermittent locomotion as components of antipredator vigilance in chipmunks. *Anim Behav* 67:789–97.
- Turner N, Haga KL, Else PL, Hulbert AJ. 2006. Scaling of Na⁺, K⁺-ATPase molecular activity and membrane fatty acid composition in mammalian and avian hearts. *Physiol Biochem Zool* 79:522–33.
- Uetz P. 2016. Species Statistics Aug 2016. (<http://www.reptile-database.org/db-info/SpeciesStat.html>) [date last accessed March 30, 2017].
- Uyeda JC, Pennell MW, Miller ET, Maia R, McClain CR. 2016. The evolution of energetic scaling across the vertebrate tree of life. *Proc Natl Acad Sci U S A* published online (doi:10.1086/692326).
- Van Damme R, Vanhooydonck B. 2001. Origins of interspecific variation in lizard sprint capacity. *Funct Ecol* 15:186–202.
- Vanhooydonck B, Herrel A, Damme RV, Irschick DJ. 2006. The quick and the fast: the evolution of acceleration capacity in *Anolis* lizards. *Evolution* 60:2137–47.
- Vanhooydonck B, James RS, Tallis J, Aerts P, Tadic Z, Tolley KA, Measey GJ, Herrel A. 2014. Is the whole more than the sum of its parts? Evolutionary trade-offs between burst and sustained locomotion in lacertid lizards. *Proc R Soc Lond B Biol Sci* 281:20132677.
- Vanhooydonck B, Van Damme R. 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evol Ecol Res* 1:785–805.
- Vanhooydonck B, Van Damme R. 2001. Evolutionary trade-offs in locomotor capacities in lacertid lizards: are splendid sprinters clumsy climbers? *J Evol Biol* 14:46–54.
- Vanhooydonck B, Van Damme R. 2003. Relationships between locomotor performance, microhabitat use and antipredator behaviour in lacertid lizards. *Funct Ecol* 17:160–9.
- Vanhooydonck B, Van Damme R, Van Dooren TJ, Bauwens D. 2001. Proximate causes of intraspecific variation in locomotor performance in the lizard *Gallotia galloti*. *Physiol Biochem Zool* 74:937–45.
- Verwaijen D, Van Damme R. 2008. Foraging mode and locomotor capacities in *Lacertidae*. *Amphib-reptil* 29:197–206.
- Wallace IJ, Garland T Jr. 2016. Mobility as an emergent property of biological organization: insights from experimental evolution. *Evol Anthropol* 25:98–104.
- Weibel ER, Richard Taylor C, O'Neil JJ, Leith DE, Gehr P, Hoppeler H, Langman V, Baudinette RV. 1983. Maximal oxygen consumption and pulmonary diffusing capacity: a direct comparison of physiologic and morphometric measurements in canids. *Respir Physiol* 54:173–88.
- Weibel ER, Taylor CR, Hoppeler H. 1991. The concept of symmorphosis: a testable hypothesis of structure-function relationship. *Proc Natl Acad Sci U S A* 88:10357–61.
- Westerterp KR. 2001. Limits to sustainable human metabolic rate. *J Exp Biol* 204:3183–7.
- White CR, Alton LA, Crispin TS, Halsey LG. 2016. Phylogenetic comparisons of pedestrian locomotion costs: confirmations and new insights. *Ecol Evol* 6:6712–20.
- White CR, Blackburn TM, Seymour RS. 2009. Phylogenetically informed analysis of the allometry of mammalian basal metabolic rate supports neither geometric nor quarter-power scaling. *Evolution* 63:2658–67.
- White CR, Kearney MR. 2013. Determinants of inter-specific variation in basal metabolic rate. *J Comp Physiol B* 183:1–26.
- White CR, Kearney MR. 2014. Metabolic scaling in animals: methods, empirical results, and theoretical explanations. *Compr Physiol* 4:231–56.
- White CR, Seymour RS. 2004. Does basal metabolic rate contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, ecological, and life-history variables. *Physiol Biochem Zool* 77:929–41.
- Williams TM, Ben-David M, Noren S, Rutishauser M, McDonald K, Heyward W. 2002. Running energetics of the North American river otter: do short legs necessarily reduce efficiency on land? *Comp Biochem Physiol A Mol Integr Physiol* 133:203–12.
- Wilson AM, Lowe JC, Roskilly K, Hudson PE, Golabek KA, McNutt JW. 2013. Locomotion dynamics of hunting in wild cheetahs. *Nature* 498:185–9.
- Wone BWM, Madsen P, Donovan ER, Labocha MK, Sears MW, Downs CJ, Sorensen DA, Hayes JP. 2015. A strong response to selection on mass-independent maximal metabolic rate without a correlated response in basal metabolic rate. *Heredity* 114:419–27.
- Woods HA, Martin LB, Ghalambor CK. 2015. Conclusions: the central role of the organism in biology. In: Martin LB, Ghalambor CK, Woods AH, editors. *Integrative*

- organismal biology. Hoboken (NJ): John Wiley & Sons, Inc. p. 309–17.
- Yap KN, Serota MW, Williams TD. 2017. The physiology of exercise in free-living animals: what can we learn from current model systems? *Integr Comp Biol* 57:195–206.
- Zhao Z-J, Krol E, Moille S, Gamo Y, Speakman JR. 2013. Limits to sustained energy intake. XV. Effects of wheel running on the energy budget during lactation. *J Exp Biol* 216:2316–27.