

A phylogenetic test of the relationship between saltation and habitat openness in gerbils (Gerbillinae, Rodentia)

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Abstract Saltation is movement by means of hopping on two legs, or jumping on four. This locomotory mode is common in various taxa, including desert rodents, that inhabit open, arid environments and is associated with the elongation of hind feet and tails. Many adaptive hypotheses have been proposed to explain why saltation is common in open habitats, including considering it as a strategy for antipredation and/or energy conservation. Yet, the association between saltation ability (i.e., leap distance) and habitat openness has not been demonstrated statistically within any taxonomic group. Here, I use phylogenetic generalized least squares analyses (PGLS) to statistically test the association between indices of saltation, with those of habitat openness, in gerbils. I find that habitat openness is significantly (positively) correlated with relative hind foot length (RHFL), but not with relative tail length (RTL), indicating that gerbil species living in more open environments, have proportionately greater RHFL (and by inference greater leap distance). This supports the hypothesis that increased saltatorial ability is adaptive to more open habitats. The association between RHFL, RTL, in addition to relative ear length (REL) with indices of habitat temperature, was also tested. Temperature was found to be significantly (positively) correlated with RTL, in accordance with Allen's rule (indicating that gerbils from warmer habitats have proportionately

greater RTL), but not with RHFL or REL. These results indicate that, in gerbils, different appendages may be responding to different environmental adaptive pressures (i.e., saltatorial ability vs. thermoregulation).

Keywords Allen's rule · Desert adaptation · Relative hind foot length · Relative ear length · Relative tail length

Introduction

Saltatorial locomotion is movement by means of leaping, which includes bipedal hopping (i.e., ricocheting) as in kangaroos, and quadrupedal jumping (i.e., springing), as in rabbits (Martin et al. 2011; Feldhamer et al. 2015). Saltation is associated with the elongation of the most distal segments of the hind limb, including the tibia and the hind foot (which is accompanied by enlarged, elastic tendons), and a lengthened tail, which often develops a terminal tuft (Eisenberg 1963a, b; Breed 1975; Nikolai and Bramble 1983; Dempster and Perrin 1990; Martin et al. 2011; Feldhamer et al. 2015). During high amplitude hopping or jumping, an enlarged hind foot, with the attendant tendons, confers an advantage in leaping ability, by increasing propulsion, through the amplified storage and release of elastic energy; while in the air, a long tail acts as a counter balance and improves maneuverability (Berman 1985; Alexander and Vernon 1975; Mares 2009; Martin et al. 2011).

An increase in relative hind foot length (RHFL) (and relative tail length (RTL)) is observed in both bipedal hoppers and quadrupedal jumpers (Berman 1985; Alexander and Vernon 1975; Mares 2009). Although this general pattern holds in saltatorial species from most rodent families, the bones associated with the elongation of the foot (e.g., phalanges or

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metatarsals) often varies (Berman 1985; Hildebrand 1988). Both bipedal and quadrupedal saltation is associated with increased hind foot length (relative to the body and the fore foot) because in both locomotory modes, the hind foot provides the main source of thrust to propel the body off the ground (Eisenberg 1963a, b; Price 1978; Martin et al. 2011; Taraborelli et al. 2003). In bipeds, saltation is achieved exclusively by the hind feet, both of which strike the ground next to each other, together; quadrupeds saltate the same way, with the difference being that there is an alternation between the hind feet and the fore feet striking the ground simultaneously (Pinkham 1973; Martin et al. 2011; Taraborelli et al. 2003).

Saltation is common in desert environments—regions that receive low and unpredictable rainfall, and as a result, are sparsely vegetated and open (Louw and Seely 1982; Sowell 2001; Hickman et al. 2004). In addition to saltatorial locomotion, desert rodents (e.g., jerboas, gerbils, hopping mice, springhares, kangaroo rats) share many other convergent adaptations, including auditory bullar hypertrophy and increased nasal passage complexity (Mares 1975, 1976; Berman 1985; Djawdan 1993; Mares 1993a, b; Ojeda et al. 1999; Shenbrot et al. 1999; Sowell 2001; Rocha et al. 2007; Ward 2009; Wu et al. 2014). An enlarged tympanic bulla is a common mammalian adaptation to subterranean life and is common in desert rodents, where it aids in sound amplification in open environments, where sound dissipates quickly (Howell 1932; Lay 1972; Webster and Webster 1975; Prakash and Ghosh 2012). Out of the five rodent families that saltate, only one (jumping mice) inhabits productive regions; all others inhabit arid, open habitats, suggesting an adaptive value for this locomotory mode in such regions (Berman 1985).

A common adaptive explanation for the prevalence of saltation in desert rodents is its usefulness as an antipredator strategy in open habitats, allowing them to escape predators by moving quickly and unpredictably (Eisenberg 1975; Harris 1984; Dempster and Perrin 1990). Another prevailing explanation for the frequency of this gait in deserts is that saltation increases stride length, relative to walking, and is thus energy efficient, making it adaptive for long-distance travel (Berman 1985; Hall 2008; but see Thompson (1985), who found similar locomotory energetic costs in saltatorial and quadrupedal heteromyids of equal mass). This energy efficiency is important because resources in desert environments are low, patchily distributed, and often separated by long distances; a saltatorial gait allows for the use of open microhabitats by facilitating the acquisition of resources with the lowest expenditure of metabolic energy (about half of the metabolic cost of walking) (Berman 1985; Ezcurra et al. 2006).

Precise comparative data on leaping distance of saltatorial rodents is not yet available; however, increased relative length, and specialization, of the hind foot is correlated with increased leap length, in various rodent taxa (Berman 1985; Rogovin et al. 1992; Kotler et al. 1994; Taraborelli et al.

2003). According to Kaup (1975) and Berman (1985), long-distance leaps are adaptive to very open deserts, where distances between resource patches are large, and consequently, the most specialized (bipedal) saltatorial rodents, with the greatest RHFL, the jerboas, reside in such deserts (i.e., North Africa and central Asia). On the other hand, short-distance leaps are adaptive to heavily vegetated and productive regions, because they are more maneuverable, and thus, among the least specialized (quadrupedal) saltatorial rodents, the jumping mice, reside in such areas (Kaup 1975; Berman 1985). Based on this observation, increased RHFL (and the attendant increase in leap distance) is expected to be more adaptive to more arid (and thus more open) regions. To date, this adaptive prediction has not been statistically confirmed within any taxonomic group.

Gerbils (subfamily Gerbillinae) are an ideal group to test the aforementioned hypothesis (see below). This taxonomic group consists of 103 species (16 genera) of murid rodents that primarily inhabit deserts and open habitats, throughout Africa and Asia (Nowak 1999; Vaughan et al. 2011; Musser and Carleton 2005). Although not as specialized for leaping as bipedal saltatorial desert rodents (e.g., jerboas and kangaroo rats), gerbils are also saltatorial, often employing a quadrupedal jumping gait, with different genera exhibiting different gradations of springing ability (Eisenberg 1963a, b; Dempster and Perrin 1990; Nowak 1999; Vaughan et al. 2011; Musser and Carleton 2005). Most gerbils have long and narrow hind feet, in addition to lengthy tails, which are modifications for saltation (Nowak 1999; Vaughan et al. 2011). Although most live in arid and open regions, a fair number of gerbil species inhabit mesic habitats, including grasslands and savanna woodlands (Carleton and Musser 1984; Nowak 1999).

In this study, I use a phylogenetic framework to test the correlation between indices of saltatorial locomotion (RHFL and RTL) with indices of habitat openness (e.g., aridity) in gerbils from various arid and mesic regions. Gerbils are a good system to test this association because they (1) are among the most diverse desert-dwelling mammal clades (they are the most diverse mammal subfamily in the Palearctic Desert), thus improving the power of the statistical analyses; (2) inhabit habitats with a wide variation in openness and aridity; (3) exhibit a large range of variation in relative hind foot and tail lengths (as well as degrees of saltatorial ability); and (4) subfamily-level molecular phylogenies have recently been estimated (e.g., Chevret and Dobigny 2005; Alhajeri et al. 2015). My main prediction is that species living in more arid and open habitats will have proportionally greater hind foot and tail lengths (and that these two morphological traits are correlated with each other), assuming that both these traits are associated with increased leap distance (see above).

Allen's rule (1877), an ecogeographic pattern of positive association between appendage length and temperature, in

endotherms (often explained in terms of adaptation for thermoregulation), may also influence relative hind foot and tail lengths. Thus, I also test the correlation between habitat temperature and the lengths of the hind foot, tail, and the ear (i.e., REL). In accordance to Allen's rule, I predict some degree of positive association between the relative lengths of these three appendages with environmental temperature.

Materials and methods

Data collection

I compiled morphological data for adults of each gerbil species from the literature for head-body length, tail length, hind foot length, and ear length (all in millimeters). Most of the morphological data came from Kingdon et al. (2013), Smith et al. (2010), and Monadjem et al. (2015), supplemented by various other sources (Electronic Supplementary Table S1). Field guides were preferred because they are often based on a large number of individuals, followed by primary literature, and finally, information from museum skin tags, in the latter case when available, more than one skin tag was examined. As in most rodents, sexual dimorphism is uncommon in gerbils (e.g., Nowak 1999; Smith et al. 2010; Kingdon et al. 2013; Monadjem et al. 2015), and thus pooled data from both males and females was used. Values for RHFL, RTL, and REL were calculated by dividing hind foot, tail, and ear lengths with head-body length. A squared transformation was applied to RTL and REL values prior to comparative analyses, to meet their assumptions of normality; raw RHFL values were used, as they were normally distributed. Normality was assessed by visual inspection of the distribution of the variables in R (R Development Core Team 2015) using the base package.

For each gerbil species, I extracted the standard 19 bioclimatic variables (BIO1–19; Electronic Supplementary Table S1) from the WorldClim database (www.worldclim.org; Hijmans et al. 2005) at a spatial resolution of 2.5 min, using DIVA-GIS 7.5 (Hijmans et al. 2012). I obtained the range of each species from the International Union for Conservation of Nature Red List (IUCN 2015), which I used to calculate the average for each bioclimatic variable, following Alhajeri et al. (2015). In order to meet the assumptions of normality of subsequent statistical analyses, BIO1, BIO5, BIO9, BIO10, and BIO11 were squared transformed, and BIO4, BIO7, and BIO12–19 were log-transformed; the remaining bioclimatic variables (BIO2, BIO3, BIO6, and BIO8) were not transformed. Prior to the log transformations, species with a value of zero for BIO14, BIO17, BIO18, and BIO19 were replaced with a small number ($=0.0000001$), which is much smaller than the lowest value of all variables.

The final dataset used in the comparative analyses includes 90.3 % of the species (93 out of 103), and 100 % of the genera

(all 16) of gerbils recognized in Wilson and Reeder (2005). The gerbil species missing from this dataset did not have reliable morphological data in the literature and/or lacked range data in IUCN. The final data matrix appears in the Electronic Supplementary Table S1.

Comparative analyses

In all subsequent comparative analyses, I account for the phylogenetic non-independence of gerbil species by applying phylogenetic correction, using phylogenetic generalized least squares analyses (PGLS). The PGLS was based on the most recently published, and most extensively sampled, subfamily-level gerbil chronogram by Alhajeri et al. (2015). Two versions of the chronogram were used in PGLS: (1) an unmodified 54 species chronogram from Alhajeri et al. (2015), where only species missing data were removed (pruned) and (2) a modified 93 species chronogram, where an additional 39 species with morphological data were grafted onto their closest relatives based on the taxonomy of Musser and Carleton (2005) (Electronic Supplementary Fig. S1). Polytomies created by the grafted species were randomly resolved prior to PGLS, since this method requires a fully bifurcating tree. PGLS was conducted using the Caper library (Orme et al. 2013) in R.

In order to test the association between saltation and habitat openness, I tested the phylogenetically corrected linear relationship between relative hind foot and tail lengths with three indices of habitat openness. The first habitat openness index tested was annual precipitation (BIO12), which is among the most commonly used indices of habitat productivity and aridity in general.

I also used an index of overall precipitation to estimate habitat openness, based on all precipitation bioclimatic variables (BIO12–BIO19), which represent annual trends, seasonality, and limiting factors. Because BIO12–BIO19 are all derived from monthly rainfall values, they are highly correlated, and thus, a principal component analyses (PCA) was conducted to reduce their dimensionality and extract independent factors that describe major trends in habitat precipitation. Only the first two principal components (PCs) were analyzed in PGLS, because only these two components had eigenvalues greater than values generated by the broken stick model (Legendre and Legendre 1998) as implemented in the Vegan library (Oksanen et al. 2015) in R. I rotated the PCs using the VARIMAX criterion (Kaiser 1958), as implemented in the Psych library (Revelle 2015) in R, in order to improve their interpretation. I used a conservative, but arbitrary, cutoff loading value of 0.8 to indicate variables with high loading on the PC axes, in order to facilitate interpretation by limiting discussed variables to the most important ones.

The third proxy of habitat openness used was the aridity index (AI), based on the formula of de Martonne (1942) (see

modification in Alhajeri et al. 2015), which takes into account annual precipitation (BIO12), precipitation of the driest quarter (BIO12), mean annual temperature (BIO1), and mean temperature of the driest quarter (BIO9). The AI is a unitless variable, with lower values indicating increased aridity (Baltas 2007). Unlike the first two indices of habitat openness which rely on precipitation data alone, the AI estimates water availability (and consequently primary productivity and habitat openness) using both temperature and precipitation variables. It may be useful to include temperature, since low temperatures have the potential to lower productivity (and thus increase habitat openness) by reducing the rate of photosynthesis (Yom-Tov and Geffen 2006). The AI values for most species were obtained from Alhajeri et al. (2015), and supplemented by newly collected data; the reader is directed to the aforementioned paper for a detailed description of the calculation of the AI. As in Arroyo et al. (2006) and Alhajeri et al. (2015), in order to meet the assumptions of normality of PGLS, the AI was also log transformed, after the calculation of the index from the raw data. While raw AI scores are usually positive, log-transformed data included negative values, which are interpreted here as indicating the most arid regions.

In addition to conducting the analyses on all gerbil species (mesic and desert), I repeated the aforementioned analyses on only desert species, since the adaptive hypotheses (see Introduction) are related to deserts, and thus, the latter are expected to more strongly exhibit the pattern of association between saltation and habitat openness. I followed the same procedure to classify desert versus mesic species as discussed in Alhajeri et al. (2015), which is based on the species distributions from IUCN (2015) (Electronic Supplementary Table S1).

I examined the conformity of gerbils to Allen's rule by testing the phylogenetically corrected linear relationship between relative hind foot, tail, and ear lengths with two indices of habitat temperature: (1) mean annual temperature (BIO1) and (2) an index of temperature based on all temperature bioclimatic variables (BIO1–BIO11). As in above, since BIO1–BIO11 are all derived from monthly temperature values, they are highly correlated, and thus were reduced using PCA and rotated using VARIMAX. Only PC1 and PC2 satisfied the broken-stick criterion and were thus subsequently analyzed in PGLS.

I also used PGLS to test the hypothesis that relative hind foot and tail lengths are (strongly) correlated, because they are both associated with saltation. The association between RHFL and RTL with REL was also tested. Since REL is not associated with saltation, the correlation between RTL and RHFL is expected to be stronger than either is to REL (since RHFLs and RTLs are not functionally linked with RELs).

Results

Correlation between saltation and habitat openness

VARIMAX-rotated PC1–2 of the precipitation bioclimatic variables (BIO12–19) explained 82 % of the variation (43 and 39 % for PC1 and PC2 respectively; Table 1). Annual precipitation (BIO12), precipitation of the wettest month (BIO13), and precipitation of wettest quarter (BIO16) loaded most strongly (all in the positive direction) on PC1 (all loadings ≥ 0.8 ; Table 1). On PC2, the variables that loaded most strongly on the positive direction were precipitation of the driest month (BIO14), precipitation of the driest quarter (BIO17), and precipitation of the coldest quarter (BIO19); precipitation seasonality (BIO15) loaded most strongly in the negative direction (all loadings $\geq |0.8|$; Table 1).

The fact that the PC1 of the precipitation variables represents both the annual trend in precipitation (increased annual precipitation) and environmental extremes (increased precipitation of the wettest month and wettest quarter) but not seasonality (e.g., coefficient of variation of precipitation), suggests that this axis may mostly represent primary productivity, and thus a reasonable index of habitat openness. Similarly, the PC2 of the precipitation variables represents limiting factors (increased precipitation of the driest month, driest quarter, and coldest quarter) as well as reduced precipitation seasonality (i.e., it loads negatively on the axis), or increased environmental predictability, which implies more constant environments and therefore might also be an adequate alternative index of habitat openness. Both PC1 and PC2 of the precipitation variables were used as proxies of habitat openness (in addition to the annual precipitation and the AI).

A significant negative relationship was found between RHFL and annual precipitation in all four datasets (54 species phylogeny, 93 species phylogeny, desert and mesic gerbils, and desert gerbils alone), in the PGLS analysis ($b = -0.0192$ to -0.0142 , $R^2_{adj} = 0.1837$ – 0.3403 , all $P < 0.0003$; Table 2, Fig. 1a). Similarly, PGLS indicated a weak, significant, relationship between RHFL and PC1 of the precipitation bioclimatic variables in all four datasets ($b = -0.0144$ to -0.0110 , $R^2_{adj} = 0.1554$ – 0.3241 , all $P < 0.0003$; Table 2, Fig. 1b). Out of the four datasets, only the PGLS conducted with the 54 species phylogeny, using only desert gerbils, showed a significant, negative, relationship between RHFL and PC2 of the precipitation bioclimatic variables ($b = -0.0142$, $R^2_{adj} = 0.1345$, $P = 0.0173$); all other datasets showed no correlation (all $P > 0.1505$; Table 2, Fig. 1c). With the exception of the 54 species phylogeny dataset, using both desert and mesic gerbils, which showed no significant correlation ($P = 0.0506$), all three other datasets showed a significant negative correlation between RHFL and the AI ($b = -0.0105$ to -0.0041 , $R^2_{adj} = 0.0395$ – 0.1837 , all $P < 0.0312$; Table 2, Fig. 1d).

Table 1 PCA of the temperature (BIO1–11) and precipitation (BIO12–19) bioclimatic variables

Temperature variables	PC1	PC2	Precipitation variables	PC1	PC2
BIO1	0.73	0.68	BIO12	0.95	0.14
BIO2	−0.18	0.60	BIO13	0.98	−0.11
BIO3	0.95	−0.02	BIO14	0.26	0.85
BIO4	− 0.97	0.13	BIO15	0.01	− 0.80
BIO5	0.04	0.99	BIO16	0.98	−0.06
BIO6	0.90	0.33	BIO17	0.12	0.93
BIO7	− 0.94	0.25	BIO18	0.70	0.21
BIO8	0.69	0.45	BIO19	−0.13	0.87
BIO9	0.17	0.59	% Exp. variance	0.43	0.39
BIO10	0.17	0.96			
BIO11	0.87	0.35			
% Exp. Variance	0.49	0.33			

The analysis was performed separately on temperature and precipitation variables. PCs were VARIMAX rotated; high loadings (≥ 0.8) are indicated in bold. Units and descriptions of BIO1–19 appear in Table S1

There was no significant relationship between RTL and all four examined climatic variables (annual precipitation, PC1 and PC2 of the precipitation bioclimatic variables, and the AI) in all four data sets (all $P > 0.1358$; Table 2).

Relative hind foot, tail, and ear lengths were all positively correlated with each other in the PGLS analyses conducted on both the 54 and the 93 species trees ($b = 0.0100$ to 6.1911 , $R^2_{adj} = 0.0719$ – 0.2008 , all $P < 0.0061$; not all data shown, Fig. 2a, b, c).

Allen's rule

The VARIMAX-rotated PC1–2 of the temperature bioclimatic variables (BIO1–11) explained 82 % of the variation (49 and 33 % for PC1 and PC2 respectively; Table 1). The variables that loaded most strongly on the positive direction of PC1 were isothermality (BIO3), minimum temperature of the coldest month (BIO6), and the mean temperature of the coldest quarter (BIO11); temperature seasonality (BIO4) and the annual range in temperature (BIO7) loaded most strongly in the negative direction (all loadings $\geq |0.8|$; Table 1). The maximum temperature of the warmest month (BIO5) and the mean temperature of the warmest quarter (BIO10) loaded most strongly in the positive direction on PC2 (all loadings ≥ 0.8 ; Table 1).

PC1 represents both limiting factors (increased minimum temperature of the coldest month and increased mean temperature of the coldest quarter), as well as temperature fluctuations (increased isothermality, reduced temperature seasonality, and reduced annual range in temperature). Isothermality is a measure of the year-long temperature evenness, based on the magnitude of the day-to-night temperature oscillation, in comparison to the summer-to-winter oscillation (O'Donnell and Ignizio 2012), and thus might be associated with the limit of tolerance of the species to the environmental temperatures.

PC2 represents only temperature extremes (increased maximum temperature of the warmest month and mean temperature of the warmest quarter). Both PC1 and PC2 of the temperature variables, which represent different aspects of the experienced environmental temperature, were used as alternative measures of environmental temperature (in addition to mean annual temperature).

There was no significant relationship between RHFL and all three examined climatic variables (mean annual temperature in addition to the PC1 and PC2 of the temperature bioclimatic variables) in the PGLS analyses conducted on both the 54 and the 93 species trees (all $P > 0.3684$; Table 3, Fig. 3a). RTL was significantly, positively, correlated with all three examined temperature climatic variables in both trees ($b = 0.0198$ to 0.1412 , $R^2_{adj} = 0.0198$ – 0.3279 , all $P \leq 0.0001$; Table 3, Fig. 3b), except for the PC1 conducted in the 54 species phylogeny, which showed no significant correlation ($P = 0.1601$; Table 3). REL was not significantly correlated with all three examined climatic variables in both trees (all $P > 0.0805$; Table 3, Fig. 3c), except for a very weak, significant negative correlation, with the PC1 of the temperature bioclimatic variables in the 93 species tree ($b = -0.0013$, $R^2_{adj} = 0.0433$, $P = 0.0254$; Table 3).

Discussion

Bipedality—especially bipedal saltation—is rife in desert mammals (Mares 1976; Cerling 1992; Djawdan 1993; Archer et al. 1999; Burk and Springer 2000; Cerling et al. 2011; Wu et al. 2014) which led many to prescribe an adaptive value to this locomotory mode to open environments, especially in rodents (Hatt 1932; Savage and Russell 1983; Eisenberg 1975). Quadrupedal saltation is also common in

Table 2 Summary of the PGLS analyses between the morphological and the precipitation bioclimatic variables, in addition to the AI, as described in the “Materials and methods” section

		54 species phylogeny						93 species phylogeny					
		Desert and mesic gerbils			Desert gerbils only			Desert and mesic gerbils			Desert gerbils only		
		<i>b</i>	R^2_{adj}	<i>P</i> value	<i>b</i>	R^2_{adj}	<i>P</i> value	<i>b</i>	R^2_{adj}	<i>P</i> value	<i>b</i>	R^2_{adj}	<i>P</i> value
Relative hind foot length	vs. Prec. (BIO12)	-0.0192	0.2959	<0.0001	-0.0174	0.3403	0.0001	-0.0142	0.1837	<0.0001	-0.0145	0.2052	0.0003
	PC1 (BIO12–19)	-0.0130	0.2069	0.0003	-0.0144	0.3241	0.0002	-0.0110	0.1554	0.0001	-0.0125	0.2091	0.0003
	PC2 (BIO12–19)	-0.0008	-0.0183	0.8273	-0.0142	0.1345	0.0173	0.0034	0.0118	0.1505	0.0013	-0.0170	0.7344
	Aridity index	-0.0044	0.0537	0.0506	-0.0105	0.1837	0.0059	-0.0041	0.0395	0.0312	-0.0082	0.0888	0.0163
Relative tail length	vs. Prec. (BIO12)	-0.0116	-0.0186	0.8568	-0.0039	-0.0302	0.9571	-0.0225	-0.0083	0.6231	-0.0082	-0.0188	0.8838
	PC1 (BIO12–19)	0.0052	-0.0190	0.9207	0.0217	-0.0262	0.7201	0.0007	-0.0110	0.9862	0.0219	-0.0151	0.6455
	PC2 (BIO12–19)	-0.0499	0.0024	0.2934	-0.0622	-0.0143	0.4754	-0.0008	-0.0110	0.9791	0.0249	-0.0145	0.6254
	Aridity index	0.0458	0.0239	0.1358	-0.0231	-0.0251	0.6843	0.0350	0.0089	0.1801	-0.0146	-0.0172	0.7492

Units and descriptions of BIO12–19 and the AI appear in Table S1. The units and descriptions for the morphological variables appear in the “Materials and methods” section. Variables were transformed prior to PGLS as described in the “Materials and methods” section. Loadings and explained variance for the PCs appear in Table 1. PGLS analysis corrects for phylogeny using the trees in Fig. S1. In the analysis conducted in desert gerbils, only 35 desert species in the 54 species phylogeny and 54 desert species in the 93 species phylogeny were analyzed. Significant *P* values are in bold *b* coefficient estimate, R^2_{adj} adjusted R-squared value

desert mammals (Taraborelli et al. 2003; Prakash and Ghosh 2012; Kingdon et al. 2013), although it is less often studied.

Despite many proposed adaptive hypotheses to explain why saltation is common in open, arid environments (e.g., antipredation (Eisenberg 1975), energy conservation (Hall 2008); see “Introduction” section), this observation is based mostly on anecdotal evidence and/or comparisons of distantly related taxa (e.g., desert rodents from different families, Mares 1975; Berman 1985; Ojeda et al. 1999). To date, the direct association between saltation and habitat openness has not been demonstrated statistically, within any taxonomic group.

Wu et al. (2014) recently used a phylogenetic approach (ancestral state reconstruction) to test a similar adaptive hypothesis to the one explored in this study—that bipedalism is adaptive to open arid environments in jerboas (bipedal saltators) and their close relatives (other dipodoids). To that end, they tested whether the timing of the evolution of bipedalism (using RHFL as a proxy) was associated with the aridification of their habitats—they found no support for this hypothesis in their taxa, as early jerboas seem to have evolved bipedalism under humid, forested environments (Wu et al. 2014). As all jerboas are bipedal saltators, their result runs counter to the broader hypothesis: saltation in general, have evolved as an adaptation to arid, open habitats—although they do not rule out the possibility that bipedal saltation could have been co-opted later on for desert environments (Wu et al. 2014).

Here, I test an associated hypothesis: increased saltatorial ability is associated with increased habitat openness—I find some support for this hypothesis in the interspecific comparisons within the quadrupedal saltatorial clade, Gerbillinae.

The results of this study were consistent across trees (54 vs. 93 species), datasets (all gerbils vs. desert gerbils only), habitat openness indices (BIO12, PC1, PC2, and AI), and temperature indices (BIO1, PC1, and PC2). This may indicate that the results are unaffected by the choice of tree, exclusion of mesic species, and the choice of habitat openness/temperature index. In other words, the only differences were in the strength of the associations (and whether or not they were significant), but never in the direction of significant correlations. This may reflect the fact that the only difference between the trees is the sample size (and the resultant statistical power) that the pattern applies to both desert and non-desert habitats, and/or that the habitat openness and temperature indices are all positively correlated (separately), considering that they were derived from the same monthly temperature and rainfall values. Thus, in the discussion below, I refer only to the overall trends, across all analyses, and do not dwell on the minor discrepancies in the strength of the support in the different analyses, which are ambiguous.

I find that gerbils living in more open environments (based on the four examined proxies) had significantly greater RHFLs (the main studied saltation index) than those living

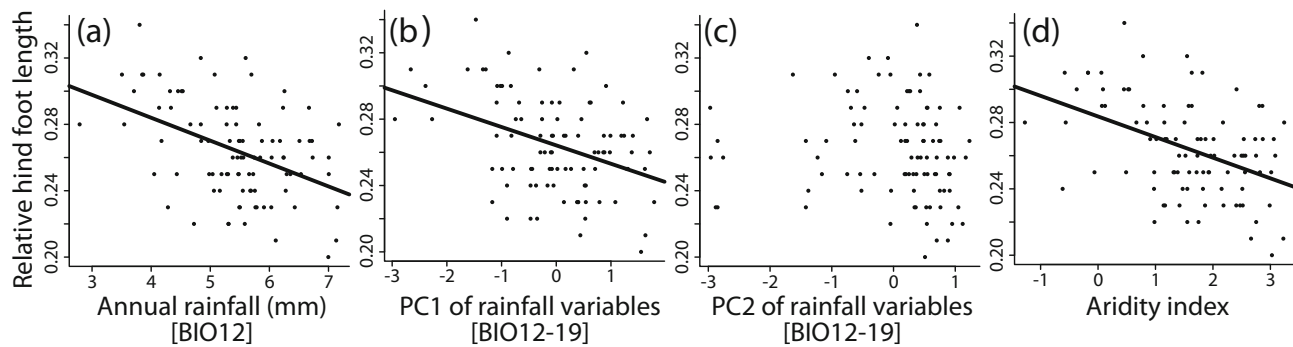


Fig. 1 Linear regressions between RHFL and **a** annual rainfall (BIO12), **b** PC1 of rainfall variables (BIO12–19), **c** PC2 of rainfall variables (BIO12–19), **d** the AI. These plots include all 93 gerbil species. The units and the transformations for all the variables are as indicated in the

“Materials and methods” section. Descriptions of BIO12–19 appear in Table S1. The loadings and explained variance of the PCs appear in Table 1. A best-fit (standard regression) line is shown only for significant PGLS relationships. Full output of statistical analyses is in Table 2

in more mesic and thus less open regions. This result is in accordance with the general observation made by Kaup (1975), that rodents living in the most open deserts (e.g., dipodoids in North African and Asian deserts) tend to be more saltatorial than those that live in intermediately open deserts (e.g., springhares and kangaroo rats in central African and North American deserts, respectively), which in turn are more saltatorial than those that live in more vegetated, productive regions (e.g., jumping mice).

Saltation may also be associated with body mass, and the latter may in turn be associated with climate (i.e., in accordance with Bergmann’s rule). While the conformance of this subfamily to Bergmann’s rule has not been tested before, the order Rodentia does not seem to conform to this ecogeographic trend (Meiri and Dayan 2003; Alhajeri and Steppan 2015). The potential influence of body mass variation (and allometry) on the association between saltation and habitat openness is a potentially interesting avenue to pursue in a subsequent study.

The second examined saltation index, RTL, was not correlated with any of the four studied habitat openness indices—a pattern that is inconsistent with the hypothesis that increased saltation is adaptive to more open environments. One possible

explanation for this lack of association could be that all gerbils have relatively long tails (Nowak 1999; Smith et al. 2010; Kingdon et al. 2013; Monadjem et al. 2015). Unlike the hind feet of saltatorial species, where a relative increase in this appendage results in increased leap distance through increased thrust (Eisenberg 1963a, b; Alexander and Vernon 1975; Taraborelli et al. 2003); the tails function mostly to maintain balance (Mares 1999; Vaughan et al. 2011), where a proportional increase in their lengths does not necessarily lead to an increase in saltatorial ability (or a proportional increase in balance). Thus, unlike RHFL that seems to respond in a continuous fashion to increased habitat openness, interspecific variation in RTL may represent two adaptive optima: (relatively) enlarged tails in saltatorial species (i.e., all gerbil species) vs. non-enlarged tails in non-saltatorial species (not sampled in this study). Moreover, the interspecific variation in the RTL of gerbils seems to respond to other adaptive pressures, including thermoregulation, in response to different environmental temperatures (see below). The thermoregulatory functional role of tails, has been experimentally demonstrated in various rodents, including the laboratory rat (e.g., Little and Stoner 1968;

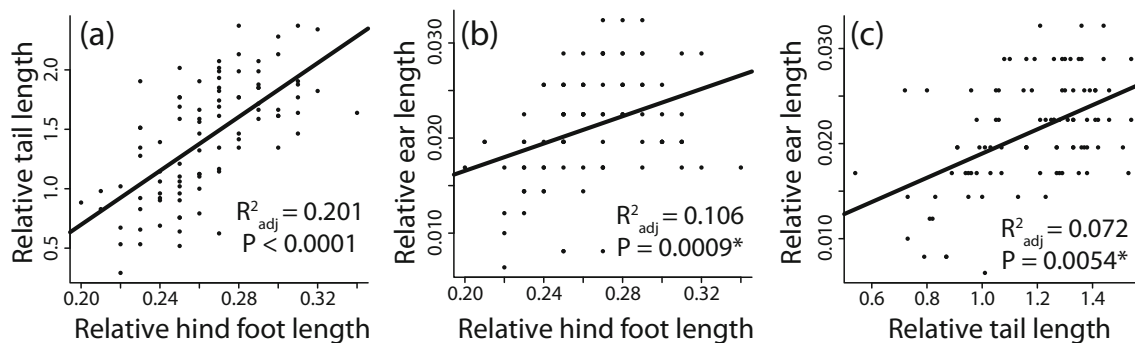


Fig. 2 Linear regressions between **a** RHFL and RTL, **b** RHFL and REL, **c** RTL and REL. Output of PGLS statistical analyses appears on the plots. R^2_{adj} = adjusted R-squared value (adjusted for the number of explanatory

terms in the model relative to the number of data points, which is more conservative than the unadjusted R^2). See the legend of Fig. 1 for more information

Table 3 Summary of PGLS analyses between the morphological variables and the temperature bioclimatic variables described in the “Materials and methods” section

			54 species phylogeny			93 species phylogeny		
			<i>b</i>	R^2_{adj}	<i>P</i> value	<i>b</i>	R^2_{adj}	<i>P</i> value
Relative hind foot length	vs.	Temp. (BIO1)	−0.0001	−0.0177	0.7775	−0.0002	−0.0068	0.5386
		PC1 (BIO1–11)	−0.0020	−0.0130	0.5753	−0.0013	−0.0088	0.6545
		PC2 (BIO1–11)	−0.0006	−0.0182	0.8220	−0.0019	−0.0020	0.3684
Relative tail length	vs.	Temp. (BIO1)	0.0202	0.2857	<0.0001	0.0198	0.1983	<0.0001
		PC1 (BIO1–11)	0.0666	0.0191	0.1601	0.0852	0.0446	0.0237
		PC2 (BIO1–11)	0.1412	0.3279	<0.0001	0.1073	0.1486	0.0001
Relative ear length	vs.	Temp. (BIO1)	0.0000	−0.0166	0.7152	0.0000	−0.0110	0.9657
		PC1 (BIO1–11)	−0.0013	0.0395	0.0805	−0.0013	0.0433	0.0254
		PC2 (BIO1–11)	0.0002	−0.0150	0.6439	0.0000	−0.0109	0.9478

Units and descriptions of BIO1–11 appear in Table S1. See the legend of Table 2 for more information

Dawson and Keber 1979), in addition to muskrats, beavers, deer mice, and kangaroo rats (Whittow 2013 and references therein).

There was some support for Allen’s rule in the interspecific variation of the RTLs of gerbils, where species living in warmer climates (based on all three examined indices) had significantly greater RTLs than those living in cooler climates. Relative hind foot and ear lengths were not positively correlated with any of examined habitat temperature indices—a pattern inconsistent with Allen’s rule. The discrepancy in the observed positive correlation with habitat temperature, suggests that out of these three appendages, only RTL may be responding to the adaptive demand for thermoregulation via heat dissipation.

Bidau et al. (2011) recently tested the observance of Allen’s rule in the RTLs of *Ctenomys* (tuco-tucos), a subterranean genus of rodents, and found that this group does not follow this trend (and even some evidence for the converse of this rule in some of the examined variables). Begall et al. (2007) classifies *Ctenomys* as subterranean (species that spend the majority of their life in self-constructed burrows), whereas

the gerbil genera were listed as non-subterranean. This ecological difference could explain why *Ctenomys* do not seem to follow Allen’s rule, while gerbils do—the former live most of their lives in burrows, which have constant temperature and overall climate (Bidau et al. 2011), while the latter spend a significant amount of time aboveground and are primarily diurnal (Nowak 1999), and consequently, require a means to thermoregulate and to adapt to the overall climatic variability.

The tail, feet, and ears of the laboratory rat are naked; in response to heat stress, an unfurred skin surface allows for easier and more efficient heat dissipation by means of radiation, conduction, and convection via the dilation of cutaneous blood vessels in exposed vascularized surfaces (Stricker and Hainsworth 1971; Tsuchiya 2001; Vaughan et al. 2011). However, all three of these appendages are furred in most gerbil species; species living in cold environments tend to have densely furred tails, ears, and feet for insulation from the cold, whereas species living in warmer regions tend to have thinly furred tails and ears (sometimes the latter is bare) to facilitate heat dissipation, but densely furred feet to improve traction on sand and

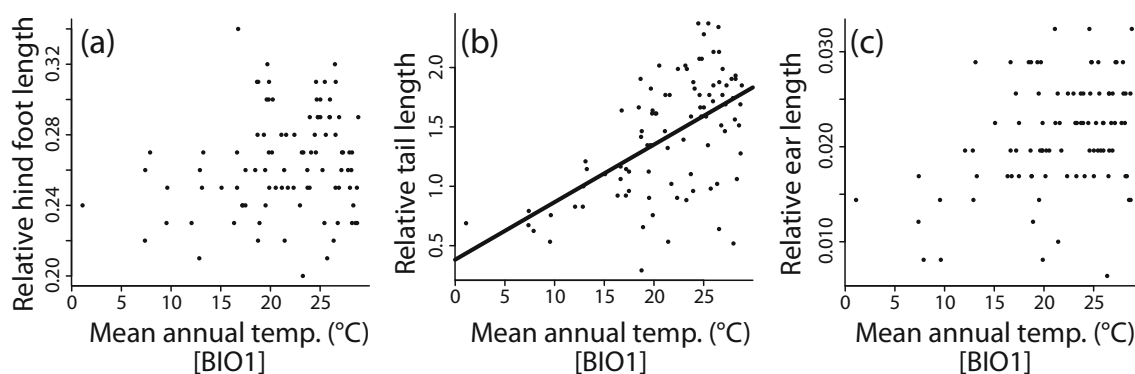


Fig. 3 Linear regressions between mean annual temperature (BIO1) and **a** RHFL, **b** RTL, **c** REL. Full output of statistical analyses is in Table 3. See the legend of Fig. 1 for more information

insulation from the hot desert surface (McManus and Zurich 1972; Nowak 1999; Smith et al. 2010; Kingdon et al. 2013; Monadjem et al. 2015). The interspecific variation in fur development, across habitats, may partly explain why the tails seem to vary according to Allen's rule (i.e., because they are often thinly furred hot environments) while the hind feet do not (i.e., because they are mostly furred in all gerbils); however, it does not explain why the ears do not vary according to Allen's rule (i.e., because they are often unfurred or thinly furred in hot environments). This discrepancy may be due to the fact that gerbil ears are not extensively vascularized (a topic that is not well studied) as in other clades (e.g., desert jackrabbits; see below), and thus are not adapted for the function of thermoregulation.

The results of this study indicate that despite being partially furred (which impedes heat dissipation), gerbil tails seem to be important in thermoregulation by functioning as a heat dissipation structure. Heat dissipation in warm climates may be enhanced by multiple associated thermoregulatory adaptations, including a reduction in fur thickness and an elongation in the RTL, the latter increasing the surface area in which heat dissipation can take place (Allen 1877).

In addition to the elongation of the tail, many mammals have a similar pattern of hind foot and tail elongation in warm climates. For example, the large and well-vascularized ears of jackrabbits provide a large surface area to radiate and release most of the excess heat (including metabolic heat) to the environment, facilitating cooling (Hill and Veghte 1976; Hill et al. 1980). Similarly, foxes living in hot deserts (e.g., the fennec and the swift fox) often exhibit both large and thinly furred ears, and long legs, both of which aid in heat dissipation, in accordance with Allen's rule (Feldhamer et al. 2015). However, based on the interspecific variation in the dimensions of the hind feet and ears of gerbils, this does not seem to be the case in this clade. In hot conditions, in addition to cutaneous vasodilatation (in their tails), some gerbil species (e.g., the Mongolian gerbil) also employ self-grooming behavior for thermoregulation, where body surfaces are covered with saliva, and like sweat, it is associated with evaporative cooling (Thiessen 1988; Grant and Thiessen 1989); this process is common in many other rodents, including the laboratory rat (Stricker and Hainsworth 1971; Vaughan et al. 2011).

The hind feet and ears of gerbils might be constrained from responding to environmental temperature by being more strongly adapted to factors other than heat dissipation, such as saltation in the former (see above) and sound perception in the latter (see below). Just as how saltation is adaptive to open habitats, for the reasons discussed above, the increase in the REL (and/or the tympanic bulla) is also adaptive to open habitats (Prakash and Ghosh 2012). In open habitats, sound dissipates quickly (Lay 1972; Webster and Webster 1975), and a proportional increase in the REL (common in jerboas) and/or

the tympanic bulla (common in kangaroo rats and mice) both increase the detection of low amplitude sounds, which aids in detecting desert predators earlier (Howell 1932; Prakash and Ghosh 2012). Here, I found no significant negative association between REL and any of the four examined habitat openness indices (which would indicate increased REL in more open habitats) (Electronic Supplementary Table S2). Thus, it seems that gerbils mostly improve their detection of low amplitude sounds in their desert environments, not with the proportionate enlargement of the pinnae, but through proportionate bullar inflation, as demonstrated in Lay (1972) and Alhajeri et al. (2015). The size of the pinnae might be constrained within a certain range in gerbils, for a reason that is not immediately clear.

The fact that the relative hind foot, tail, and ear lengths of gerbils were all positively correlated with each other suggests some degree of positive allometric scaling with the head-and-body length. Alternatively, all three morphological variables could be associated if they are all correlated with a third variable, such as an unexamined environmental variable. Among these correlations, the strongest association was between RTL and RHFL, which suggests that the evolution of these two traits is functionally linked to some extent (i.e., through being associated with saltation). However, despite this positive association, I found no correlation between habitat openness and RTL, while the former was associated with RHFL (see above).

To conclude, there seems to be some statistical support for the hypothesis that increased leaping ability is adaptive to increased habitat openness (in gerbils); a pattern that, thus far, was based on anecdotal evidence across divergent mammalian clades. There also appears to be some support for Allen's rule in gerbils. Hence, different appendages in gerbils seem to be responding to different environmental adaptive pressures; RHFL seems to be associated with habitat openness but not with habitat temperature, whereas RTL seems to be associated with the latter, but not the former. REL variation does not seem to be associated with either habitat openness or temperature. This pattern indicates that gerbil species living in more open environments tend to have relatively longer hind feet (and inferentially greater leaping ability), but not necessarily relatively longer tails (or ears). Moreover, it seems that, out of all the examined appendages, Allen's rule only applies to the tails of gerbils, where species living in warmer environments have relatively longer tails.

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