Relationship between Maximal Oxygen Consumption ($\dot{V}O_2max$) and Home Range Area in Mammals

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ABSTRACT

Home range is defined as the area traversed during normal daily activities, such as foraging, avoiding predators, and social or antagonistic behaviors. All else being equal, larger home ranges should be associated with longer daily movement distances and/or higher average movement speeds. The maximal rate of oxygen consumption ($\dot{V}O_2max$) generally sets an upper limit to the intensity of work (e.g., speed of locomotion) that an animal can sustain without fatigue. Therefore, home range area and $\dot{V}O_2max$ are predicted to evolve in concert (coadapt). We gathered literature data on home range and $\dot{V}O_2max$ for 55 species of mammals. We computed residuals from log-log (allometric) regressions on body mass with two different regression models: ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS). Residuals were weakly positively related for both the OLS ($r = 0.278$, one-tailed $P < 0.05$) and PGLS ($r = 0.210$, $P > 0.05$) regressions. For $\dot{V}O_2max$, the PGLS regression model had a slightly higher likelihood than the OLS model, but the situation was reversed for home range area. In addition, for both home range area and $\dot{V}O_2max$, models that fit better than either OLS or PGLS were obtained by modeling residual variation with the Ornstein-Uhlenbeck process to mimic stabilizing selection (RegOU), indicating that phylogenetic signal is present in both size-adjusted traits, consistent with findings of previous studies. (However, residuals from the RegOU models cannot be tested for correlation due to mathematical complexities.) We conclude that the best estimate of the residual correlation is probably somewhere between these two values reported above. Possible reasons for the low correlation between residual home range area and $\dot{V}O_2max$ are discussed.

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Introduction

The idea that physiological performance abilities should evolve in a correlated fashion (coadapt) with aspects of an organism's behavioral ecology is a central tenant of ecological and evolutionary physiology (Garland and Carter 1994; Garland and Losos 1994; Angilletta et al. 2006). For example, among species of *Anolis* lizards, maximal sprint speed measured in the laboratory correlates positively with both escape speed and feeding speed measured in the field (Irschick and Losos 1998). Also among lizard species, treadmill endurance capacities are positively correlated with daily movement distance, the percentage of time spent moving, and the number of moves per minute (Garland 1999). Other than those two studies, we are not aware of any that have demonstrated a cross-species correlation between quantitative measures of locomotor behavior in the field and aspects of exercise abilities through phylogenetically based statistical analyses. Therefore, the purpose of this study was to take advantage of a recent comparative analysis of mammalian maximal oxygen consumption ($\dot{V}O_2max$; Dlugosz et al. 2013) to test for a positive association with home range size, a widely reported measure of field locomotor behavior in mammals (Kelt and Van Vuren 2001; Mysterud et al. 2001).

As defined by Burt (1943), home range is the area traversed by an animal in its normal activities of food gathering, mating, and caring for young. All else being equal, a larger home range area would imply an increase in the distance moved per unit time (e.g., per day), the amount of time spent moving, or both. For terrestrial locomotion, it is less costly to cover a greater distance by increasing speed rather than increasing the amount of time spent moving at a given speed (e.g., Rezende et al. 2009 and references therein). Moving faster to cover a greater distance would also minimize the amount of time spent exposed to predators or other environmental hazards, such as high temperatures. The speed of locomotion (intensity of activity) that can be sustained by an animal for a prolonged period of time is limited by its aerobic capacity, which, in terrestrial vertebrates, is typically measured as the maximal rate of oxygen consumption during forced treadmill exercise (Seeherman et al. 1981). In general, $\dot{V}O_2max$ defines the upper limit to the rate of work that can be sustained for more than a brief period. If a larger home range area implies a higher average rate of movement, then a

positive correlation between home range area and $\dot{V}O_2$max would be expected.

To test this prediction in an evolutionary framework, we gathered literature data for 55 species of mammals. We computed residuals from log-log regressions on body mass and then tested the residuals for correlation by use of both conventional and phylogenetically informed statistical methods (Rezende and Diniz-Filho 2012).

Methods

All of the $\dot{V}O_2$max data were obtained from Dlugosz et al. (2013). We used various Internet search tools (especially Google, Google Scholar, and Web of Science) to obtain home range data for as many species as possible that were also included in the study by Dlugosz et al. (2013).

As indicated in the appendix, available online, we found usable home range data for 55 species. Home range area can be affected by several methodological factors. For example, precision of location data and whether the data are constrained to occur on a predefined grid will vary among techniques, for example, traps versus radio telemetry. Also, the different ways to calculate the home range area from location data can result in different area values, even if calculated from the same data set. For example, whereas inclusive boundary strip adds half the distance between traps as part of the home range, the minimum convex polygon method would consider only the area inside the polygon created from connecting the outermost points. Therefore, we also noted the method used to locate animals (direct observation, trapping, and telemetry [we considered radio, satellite, and radioactive telemetry as one category]), the area calculation method (minimum convex polygon, kernel, inclusive/exclusive boundary strips, and 95% probability ellipses), the season in which the animals were captured (fall, spring, summer, winter, and all year [we considered the study all year if it included all seasons or both winter and summer]), the sex (males, females, pooled), and duration of the study in months. These were used as cofactors when computing residual home range area. When body mass was not reported in the original home range study, it was taken from another article with an average for the species used, or the mass from Dlugosz et al. (2013) was used. For more details on how the data were treated, refer to the appendix.

In Mesquite, version 2.75, we trimmed the phylogenetic tree of Dlugosz et al. (2013) to 55 species (tips) to match the species with home range data, including the Arctic fox (*Alopex lagopus*), which was inadvertently omitted from the analyses presented in that article. Following Dlugosz et al. (2013), branch lengths were set by the arbitrary method of Pagel (1992; fig. 1). The phylogeny was exported from Mesquite as a PDI file and then imported to the DOS PDDIST program to create the phylogenetic variance-covariance matrix (Garland and Ives 2000).

In Matlab, version 6.1, we used the Regressionv2.m program of Lavin et al. (2008) to regress $\log_{10} \dot{V}O_2$max and $\log_{10}$ home range area on $\log_{10}$ body mass using ordinary least squares (OLS), phylogenetic generalized least squares (PGLS), and a phylogenetic regression model that allows the branches to vary in length according to an Ornstein-Uhlenbeck process to mimic stabilizing selection on the residuals (RegOU). These models are discussed in detail in Lavin et al. (2008; see also Rezende and Diniz-Filho 2012). Briefly, the OLS method analyzes the data assuming a star phylogeny with contemporaneous tips (usually called conventional or nonphylogenetic analysis), PGLS uses the phylogenetic tree as input, and RegOU allows the nodes of the tree to move between the root and the tips of the tree and hence the tree varies continuously between a star and the original tree or even a more hierarchical tree. In the RegOU model, a parameter named d is estimated by restricted maximum likelihood, simultaneously with estimation of the regression parameters, to determine the optimal amount of stretching or compressing of the tree as the nodes move between the root and the tips (Garland and Ives 2000; Blomberg et al. 2003). A d value higher than 1 means that the nodes of the tree were pushed closer to the tips (i.e., making the tree more hierarchical), while a value smaller than 1 indicates that the nodes were pulled toward the root, making it somewhat closer to a star phylogeny. In the limit, d can be estimated as 0, which indicates that a star phylogeny best fits the regression residuals. Any estimated d value greater than 0 indicates the presence of phylogenetic signal in the residuals.

The residuals obtained from the $\dot{V}O_2$max and home range regressions for OLS and PGLS models were then correlated (one for each regression model) in SPSS, version 22.0. We did not use residuals from the RegOU models because they are not strictly comparable when the estimated d values differ. For home range area, we computed two sets of regressions, one including body mass plus all the cofactors listed above and another set including only body mass so that it would be directly comparable to the $\dot{V}O_2$max regressions. When correlating 55 residual data points, the nominal degrees of freedom would be 53, with a corresponding critical value of 0.224 for a one-tailed test. However, it is appropriate to reduce degrees of freedom to account for the parameters estimated when computing the regression models used to calculate residuals. For $\dot{V}O_2$max, only body mass was used as an independent variable, but for the full model used with home range area, an additional 10 dummy variables were included to account for variation related to calculation method, season, and so on. The exact number of degrees of freedom that should be subtracted is not entirely obvious, so we also consider significance levels as if we had 43 df, for which the one-tailed critical value would be 0.248.

In principle, a better approach to test for a relation between two variables could be to include one (e.g., $\dot{V}O_2$max) as an additional independent variable in a multiple regression model predicting the other (e.g., home range size; e.g., see Freckleton 2002). That would solve certain statistical issues, including the calculation of degrees of freedom, and also allow use of the more flexible RegOU model. Unfortunately, multiple regressions can be unreliable when the correlation between independent variables is strong (collinearity or multicollinearity). In this case, log body mass (for home range area) and log $\dot{V}O_2$max have a
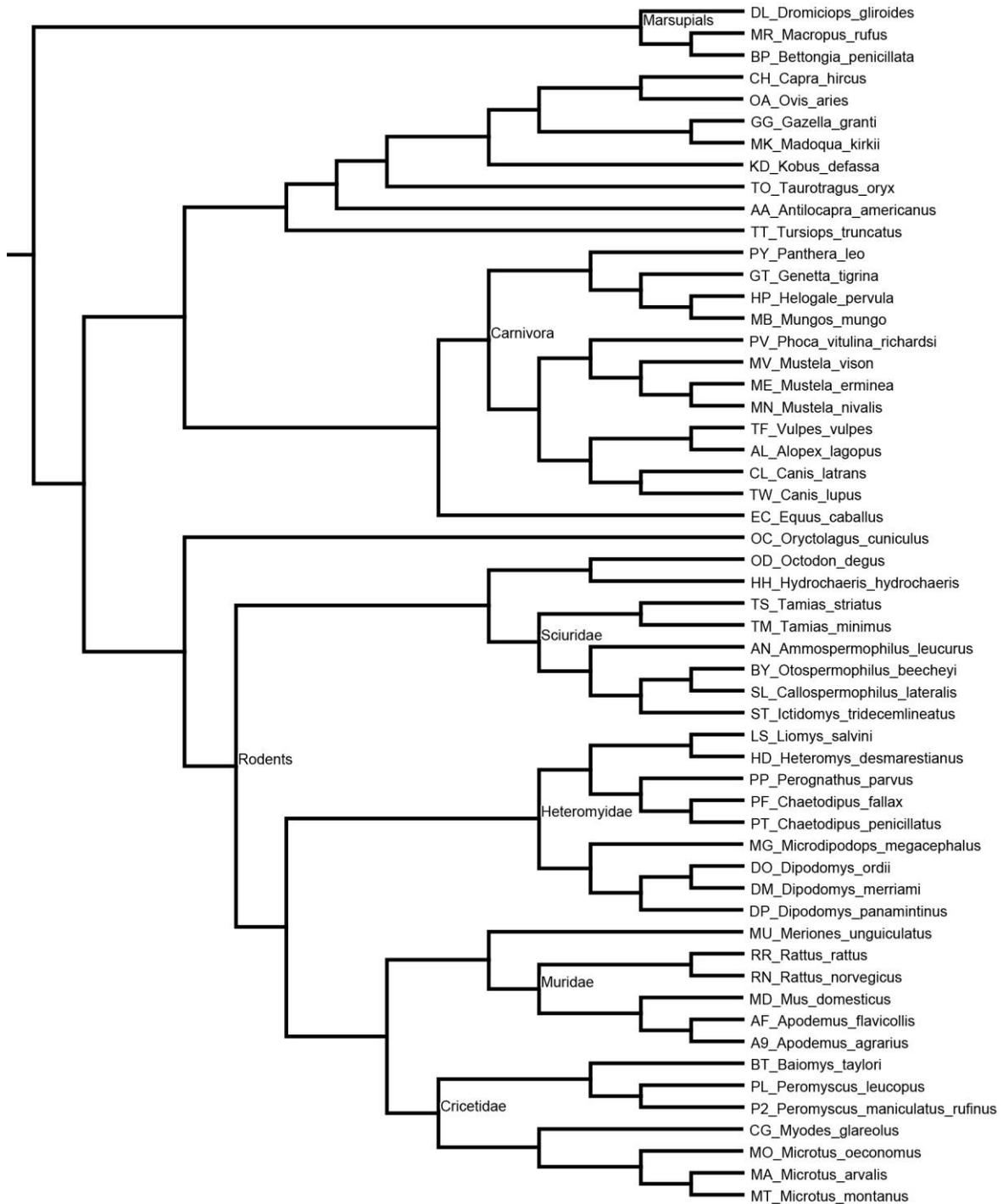
Figure 1. Phylogeny used to compute phylogenetic regressions (phylogenetic generalized least squares and RegOU). This tree was trimmed from the original provided by Dlugosz et al. (2013), and we added *Alopex lagopus*, which was unintentionally omitted in their article. Branch lengths were then set using the arbitrary method of Pagel (1992), following Dlugosz et al. (2013). The two-character codes at the start of the scientific names correspond to codes in the file of raw data provided in the appendix, available online.
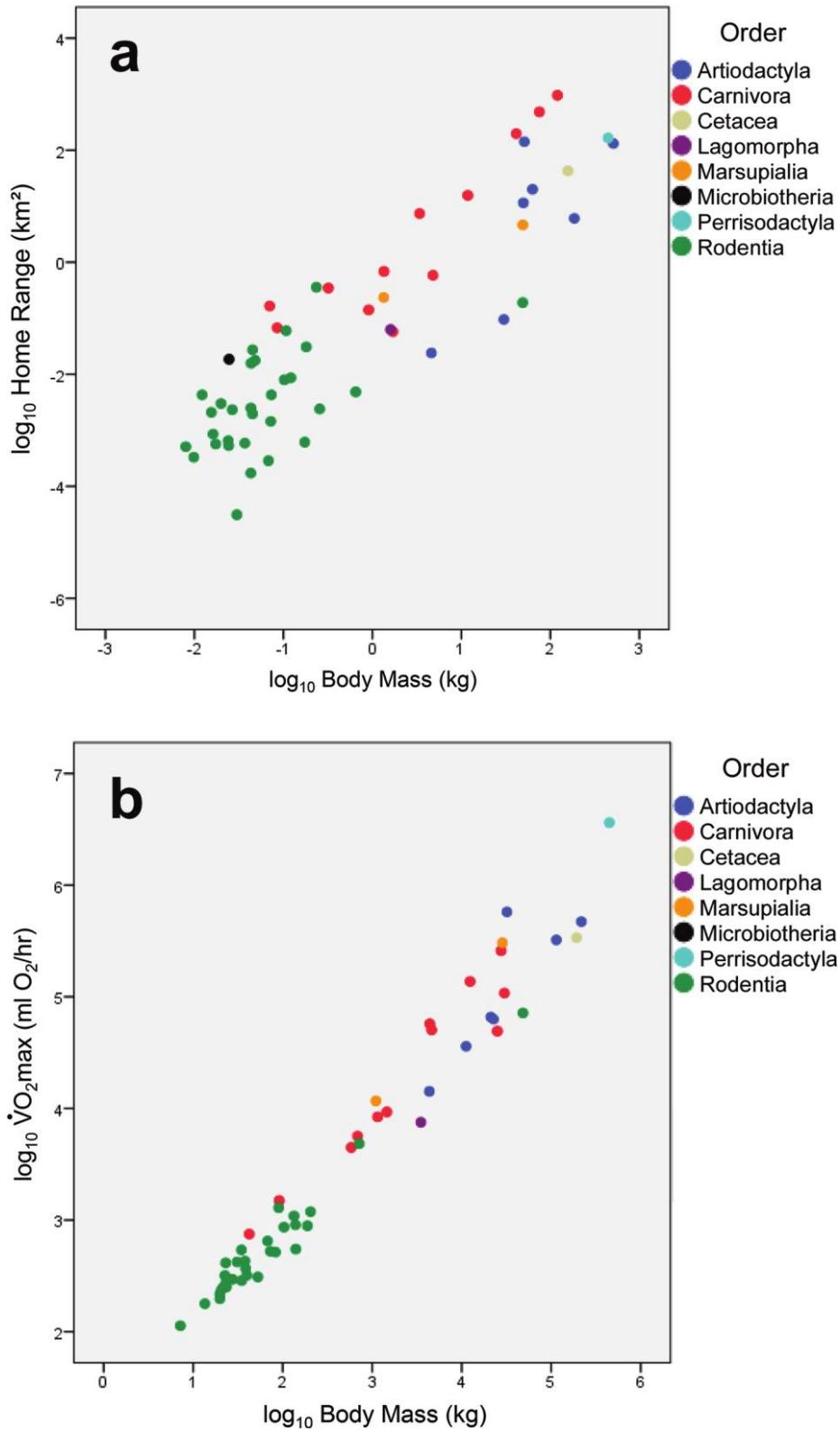
Figure 2. Scatterplots of $\log_{10}$ home range area (*a*) and $\log_{10}$ $\dot{V}O_2$max (*b*) versus $\log_{10}$ body mass for 55 species of mammals.

correlation of 0.972. Adding log $\dot{V}_{O_2}$max to the multiple regression model for log home range area results in a very high variance inflation factor (VIF) of 21.360 for log body mass and 21.798 for log $\dot{V}_{O_2}$max. Must statistical sources warn strongly about VIF values above 10, and some warn about values of even 4 or 5. Therefore, we not comfortable with the estimated partial correlations or P values for log $\dot{V}_{O_2}$max in this analysis. In addition, we have separate estimates of body mass for the two traits of interest, and the multiple regression approach would accommodate only one, perhaps an average, but that would induce additional error into the estimate of body mass.

Results

Figure 2a shows a scatterplot of home range area with body mass. As shown in table 1, the ln maximum likelihood for the RegOU multiple regression (-60.1488) was high enough to be considered significantly better ($P = 0.0159$ and $P = 0.0016$, respectively) than the OLS (-63.0550) or PGLS (-65.1521) models, based on a ln likelihood ratio test with 1 df to account for the additional parameter estimated in the RegOU model (Lavin et al. 2008; e.g., see Gartner et al. 2010). Hence, the tree used in the best-fitting model was intermediate between a star and the original tree (estimated OU parameter, $d = 0.337$), and residual home range area contains statistically significant phylogenetic signal. The foregoing comparisons are based on full models predicting home range, which included additional cofactors and covariates related to methodology (see "Methods"; appendix). For the models that used only body mass as an independent variable, the estimated d value in the RegOU model was 0, indicating that a star phylogeny better fit the data than did the hierarchical tree shown in figure 1. We then compared the full model fit by RegOU (ln maximum likelihood = -60.1488) with the minimal OLS model (only log body mass as an independent variable, ln maximum likelihood =

-70.9329) and found that twice the difference in ln likelihoods (21.5682) would be considered statistically significant with 12 df ($P = 0.0427$). Therefore, we conclude that the full RegOU model is the best fitting for home range area.

Figure 2b shows that, for a given body mass, $\dot{V}_{O_2}$max is much less variable than home range area (fig. 2a). For the $\dot{V}_{O_2}$max regressions (table 1), the ln maximum likelihood for the RegOU regression (9.9644) was high enough to be considered significantly better ($P = 0.0029$ and $P = 0.0016$, respectively) than the OLS (5.5224) or PGLS (6.8137) models, based on a ln likelihood ratio test with 1 df. So, as for home range area, residual $\dot{V}_{O_2}$max contains significant phylogenetic signal but not as much as would be implied by the tree shown in figure 1, similar to the findings of Dlugosz et al. (2013) for the larger data set.

The correlation of OLS residuals (fig. 3a) was positive ($r = 0.278$) and statistically significant (one-tailed $P < 0.05$ with either 53 or 43 df). The correlation of residuals from the PGLS models was lower and statistically nonsignificant ($r = 0.210$, one-tailed $P > 0.05$). Note that for home range area, the OLS model fits the data somewhat better than the PGLS model, based on a comparison of the likelihoods (table 1), whereas for $\dot{V}_{O_2}$max the converse is true.

Discussion

Contrary to our expectation, we found only weak evidence for a positive correlation between residual home range area and $\dot{V}_{O_2}$max. Several explanations are possible, and they are not mutually exclusive.

One possibility is that the data include too much measurement error (in the broad sense of Ives et al. 2007), which obscures any correlation. Methods for calculating home range area are much more variable than for measurement of $\dot{V}_{O_2}$max, and this difference could partly account for the much greater

Table 1: Parameter estimates for regressions of $\log_{10} \dot{V}_{O_2}$max (mL O_2/h) and $\log_{10}$ home range area (km^2) on $\log_{10}$ body mass (kg)

Dependent variable and model	d	y-intercept	SE	Slope	SE	ln maximum likelihood	Mean squared error	SE of estimate	R^{2a}
Home range:									
OLS	...	-5.3312	1.2661	1.3204	.1303	-63.0550	.7593	.8714	.8390
PGLS	...	-4.7801	1.5022	1.1421	.1360	-65.1521	.8195	.9053	.7684
RegOU	.3369	-5.0512	1.2501	1.2625	.1267	-60.1488	.6832	.8266	.7996
$\dot{V}_{O_2}$max:									
OLS	...	1.2264	.0673	.8686	.0224	5.5224	.0497	.2229	.9660
PGLS	...	1.2900	.1807	.8392	.0285	6.8137	.0474	.2178	.9425
RegOU	.4768	1.2597	.0992	.8489	.0271	9.9644	.0425	.2061	.9488

Note. For the home range regressions, we also included covariates and cofactors related to methodological variation (see "Methods"; those additional parameter estimates are not shown here). The ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) regression models were used to compute residuals, which were then tested for correlation (see "Results"; fig. 3). For both dependent variables, the best-fitting models, based on ln maximum likelihood ratio tests, were the RegOU models (see "Results"). d is the Ornstein-Uhlenbeck transformation parameter that estimates the best-fitting amount of stretching or compressing of branch lengths (see "Methods"). For both traits, these values are significantly greater than 0, based on likelihood ratio tests comparing RegOU with PGLS models, thus indicating the presence of phylogenetic signal in the residuals. SE = standard error.

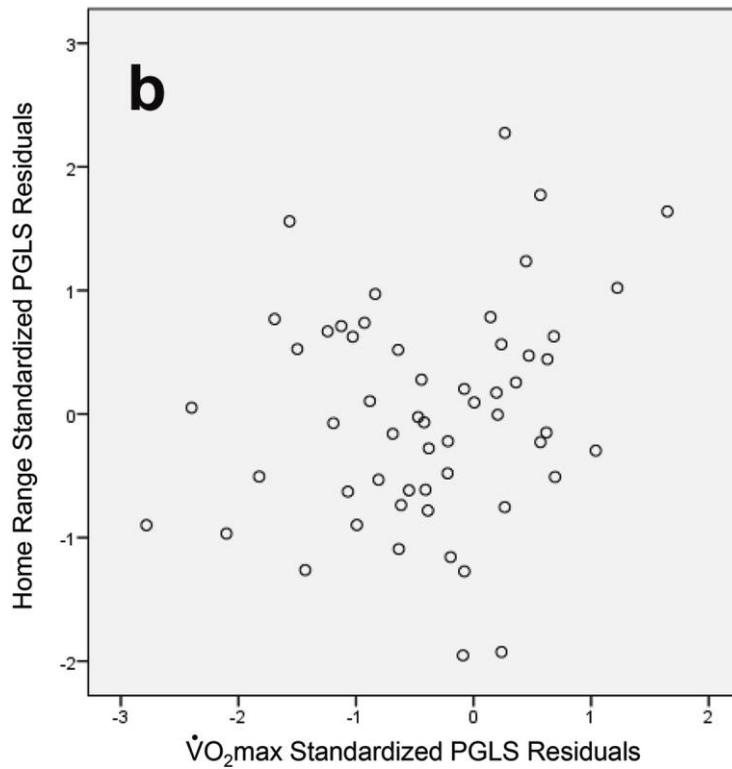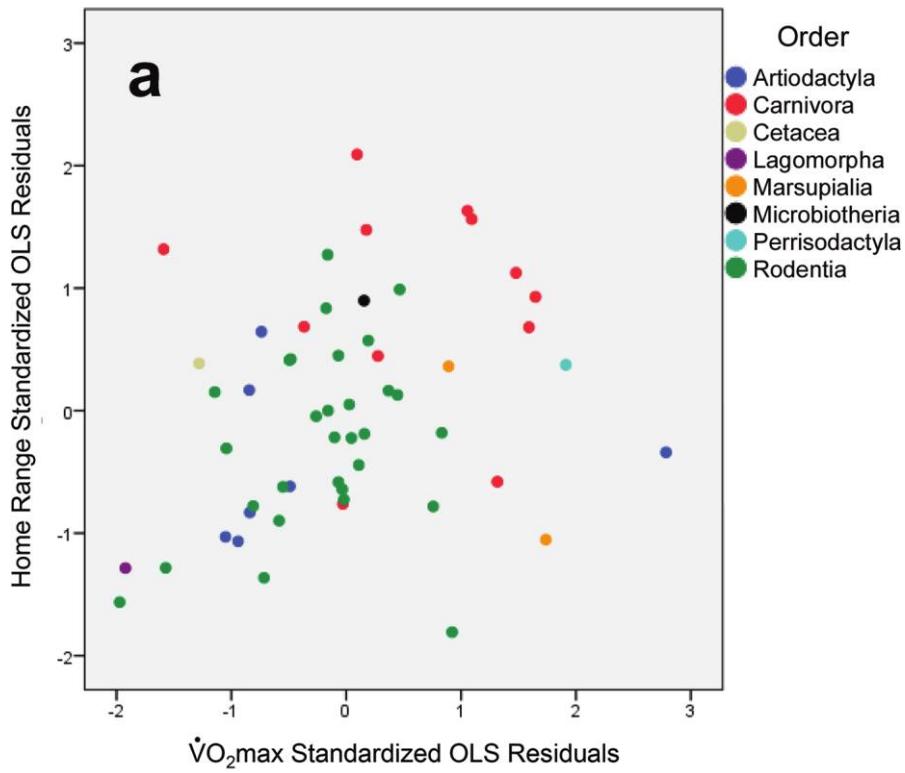[a]Values are not comparable between OLS and the phylogenetic models.

Figure 3. Scatterplots of residual $\log_{10}$ home range area versus residual $\log_{10}$ $\dot{V}O_2$max based on conventional ordinary least squares (OLS) regressions (*a*) and phylogenetic generalized least squares (PGLS) models (*b*). For *a* the correlation using all data points ($r = 0.278$) is statistically significant, but for *b* it is not ($r = 0.212$).

variability of home range area at any given body mass (fig. 2). Indeed, the phylogenetic RegOU model that included additional independent variables to partially account for measurement-related variation fit the home range data significantly better. Many studies have reported variation in home range size, adjusting for variation in body mass, among populations of the same species of mammal (McNab 1963; Grant et al. 1992; Herfindal et al. 2005). Because the home range and $\dot{V}O_2$max data analyzed here did not come from the same populations of each species, population differences likely contributed to the measurement error in our data, as this also refers to some aspects of real biological variation in the trait being studied (Ives et al. 2007). Similarly, variation related to age, sex, or season could have diluted the true correlation between home range area and $\dot{V}O_2$max (e.g., see Lindstedt et al. 1986; Mysterud et al. 2001).

The d values observed in RegOU models indicate how the tree was altered to best fit the data in the statistical models. For both home range area and $\dot{V}O_2$max, the estimated d was significantly greater than 0, indicating that the variance-covariance matrix of the residuals was not the identity matrix or, equivalently, that the best-fitting phylogenetic tree was not a star. At the same time, the d values were less than 1, indicating that the altered tree is somewhat less hierarchical than the one shown in figure 1 (i.e., the nodes of the tree were pulled toward the root, making the tree less hierarchical). Thus, for this set of species, phylogenetic signal is not as strong for home range area as it is for $\dot{V}O_2$max, a result consistent with the overall pattern documented previously (Blomberg et al. 2003). Whether this result means that home range is more biologically variable or more evolutionarily labile than $\dot{V}O_2$max cannot be addressed without a detailed consideration of measurement error in the broad sense (Blomberg et al. 2003; Ives et al. 2007; Revell et al. 2008), which is not possible with the data presently available.

Although we have emphasized that measurement error of various types may have obscured a true correlation between home range size and $\dot{V}O_2$max, it is important to note that other studies have successfully identified interspecific correlates of home range size and $\dot{V}O_2$max, or related measures, with phylogenetically informed analyses. For example, $\dot{V}O_2$max has been shown to correlate positively with brain size among species of mammals (Raichlen and Gordon 2011). Kelly et al. (2006) reported positive correlations between residual home range area and both residual hind-limb length and residual metatarsal/femur ratio in both Carnivora and ungulates (although the home range–leg length correlation failed to reach statistical significance in the ungulate sample). Among species of lizards, treadmill endurance capacity is positively related to daily movement distance, the percentage of time spent moving, and the number of moves per minute (Garland 1999). Bowman et al. (2002) found that dispersal distance and distance moved after translocation in mammals also correlate with home range area, after controlling for body size, although this study used only conventional regression and correlation analyses. Harris and Steudel (1997) observed that residual hind-limb length in Carnivora was not correlated with home range or daily move-ment distance (contra Kelly et al. 2006) but was related to prey capture mode. Hence, we do not believe that the lack of correlation we observed reflects only high measurement error in the data for home range area and/or $\dot{V}O_2$max.

Finally, we note that the somewhat different correlations observed with the residuals obtained from conventional and phylogenetic analyses provide another example of how ignoring phylogenetic relationships can affect results (Garland et al. 1993, 2005; Rezende and Diniz-Filho 2012; White and Kearney 2014; references therein). As an example closely related to this study, Harris and Steudel (1997) reported a positive correlation ($r = 0.263$, two-tailed $P = 0.0597$) between home range area and residual hind-limb length that became "insignificant" with use of phylogenetically independent contrasts. Examination of our data (fig. 3a) indicates that the more positive correlation in the nonphylogenetic analysis may be largely attributable to Carnivora tending to have both large home ranges and high $\dot{V}O_2$max for their body size.

Future Directions

Home range area is not necessarily the same as an animal's territory, which is a smaller area, inside the home range, that is actively defended against conspecifics and/or interspecific intruders (Burt 1943; Grant et al. 1992). Possibly, a tighter relationship exists between $\dot{V}O_2$max and territory size, given that the movements and attention dedicated to the territory may generally be more intense than for the home range as a whole. Unfortunately, information on territory size is much less available.

Alternatively, daily movement distance (Garland 1983) or possibly average movement speed or some other metric (e.g., see Garland 1999; Perry 1999) might have a tighter relationship with $\dot{V}O_2$max than the area of the home range. Some animals might have a small home range area but be more active and move more frequently inside that area, possibly close to the maximum aerobic capacity (e.g., squirrels), thus requiring a higher $\dot{V}O_2$max, all else being equal. Movement distances and speeds, like home range area, will also be affected by such ecological factors as substrate availability, habitat type, productivity, density of conspecifics and other species, and so on, which were not considered here. It will also be of interest to test for a relationship between $\dot{V}O_2$max and dispersal distance in mammals (Bowman et al. 2002). Finally, as more data become available, it will be important to test possible clade differences in relationships, as may be the case with Carnivora (see fig. 3a).

Acknowledgments

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