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Predicting life-history trade-offs with whole-organism performance

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Abstract

Whole-organism performance traits are key intermediaries between the organism and the environment. Because performance traits are energetically costly to both build and maintain, performance will compete with other life-history traits over a limited pool of acquired energetic resources at any given time, potentially leading to trade-offs in performance expression. Although these trade-offs can have important implications for organismal fitness we currently lack a conceptual framework for predicting both where trade-offs might be expected, and which traits may be especially prone to trade-offs with other fitness-related life-history traits. We propose such a framework based on an estimate of the energetic requirements of locomotion in vertebrates, the ecological cost of transport. By analysing existing data on mammalian energetic budgets and life-history, we found that species with higher costs of locomotion also tended to be those with "slow" life histories that invest relatively less in current reproduction than "fast" life-history species. We discuss the potential implications of ectothermy for masking such relationships, and how this framework might be expanded upon in the future.

Introduction

The central tenet of life-history theory is that allocation to particular fitness-enhancing traits depends upon the size of the pool of acquired resources, such that limited resource pools drive trade-offs among traits as investment in one impinges upon the expression of others (Tomkins et al. 2004). Any and all traits that depend upon that pool of acquired energetic resources will thus be subject to such trade-offs unless they are "protected" and thus always prioritized. As such, the expression of certain traits can be constrained, reduced, or potentially even checked entirely under resource-limited conditions if investment in competing traits is promoted. Traits that are subject to such trade-offs must therefore incur significant energetic cost at a minimum.

Because of the focus of life-history on the scheduling of key events linked to fitness, "traditional" life-history phenotypes include traits such as gestation period, age at sexual maturity, or longevity. Trade-offs among these traits are common, and changes in life-history strategy involving one or some of these often prompt changes in others (e.g. Reznick and Endler 1982; Reznick et al. 2004). However, other traits that influence fitness (or key fitness components such as survival) are also part of the integrated organismal phenotype (Ghalambor et al. 2003), and thus prone to trade-offs with other life-history traits. Whole-organism performance capacities (which refer to dynamic, ecologically relevant traits including running, biting, and flying; Bennett and Huey 1990; Lailvaux and Irschick 2006) not only impact survival via their effects on dispersal (Phillips et al. 2006), predator-prey interactions (Miles 2004; Husak 2006b; Husak 2006a), and foraging (Huey et al. 1984; Aguirre et al. 2002), but are also key determinants of the outcomes of male combat interactions in many animal species (e.g. Husak et al. 2006b; Lailvaux and Irschick 2007; Condon and Lailvaux 2016) and thus affect reproductive success as well (Husak et al. 2006a; Husak and Fox 2008; Husak et al. 2009).

Recent years have seen increased recognition of the status of whole-organism performance capacities as life-history traits (reviewed in Lailvaux and Husak 2014). Studies from a variety of animal species show that the expression of performance traits such as endurance or sprinting can be reduced by the concomitant expression of other traits that constitute an important source of energetic expenditure. For example, experimental immune activation caused sprint speed to decline by 13% within 4 hours in the lizard *Psammodromus algirus* (Zamora-Camacho et al. 2014). In the lizard *Zootoca vivipara*, however, a similar decline in endurance ability was seen only in pregnant females that were already under energetic stress, and not in individuals with greater available resource pools (Meylan et al. 2013). From the reciprocal perspective, forcing individual *Anolis carolinensis* lizards to invest in locomotor endurance by training them on a treadmill over several

weeks not only increased their endurance capacities (Husak et al. 2015), but also prompted changes in growth rate, fecundity, and immune function in trained individuals, particularly when combined with a dietary restriction regime (Husak et al. 2016). Although these individual studies are intriguing and strongly suggest that performance traits are prone to life-history trade-offs, we currently lack a framework for predicting the circumstances under which performance traits might trade-off with other life-history traits and in which species.

Dietary restriction is an effective technique for exposing resource allocation trade-offs which might otherwise be masked by high resource availability or acquisition, because the allocation limitations and trade-offs among traits that vary in the costs of their optimal expression become more apparent when less energetic resources are available for investment (Glazier 1999; Zera and Harshman 2001). It follows, therefore, that more expensive traits prompt trade-offs to a greater number or extent than cheaper ones. However, whether or not a trait is expensive depends not only on the available resource pool, but also on the baseline rate of energetic expenditure (Clark 2012). For example, an organism that pays greater costs during daily physiological functions might experience more allocation-driven trade-offs than a related organism with cheaper daily energetic expenditure, all else being equal, because higher energetic expenditure depletes the acquired resource pool available for allocation to other various traits.

Because the energetic costs of building and maintaining performance traits are very likely to be trait-specific (Lailvaux and Husak 2014), quantifying those costs therefore poses a significant challenge (Husak and Lailvaux, this issue). Not only do we need to have some estimate of the average energetic costs of using a specific performance trait in a given species, but we must be able to express those costs as a fraction of the overall daily energetic costs paid by the individuals if we are to determine how expensive those costs are with respect to other potential resource investments. Studies considering energy budgets alone imply that the energetic costs of activity in nature can be high; for example, field metabolic rates can be 2-2.5 times those of basal metabolic rates in mammals, and more than 5 times as high in some birds, with the bulk of those costs being attributed to activity (reviewed in McNab 2002). More recently, researchers have begun producing fine-grained estimates of the costs of transport in free-living animals through the use of GPS and remote-sensing technology. For example, Williams et al. (2014) quantified the costs of hunting in free ranging mountain lions wearing SMART (species movement, acceleration, and radio-tracking) collars and showed that that the energetic costs of locating prey (what they called the “pre-kill hunting costs”) accounted for 10-20% of their total energy costs in nature. Similarly, Hubel et al. (2016) found that the energetic costs of hunting in wild dogs, though overestimated in the past, are nonetheless large. However, although remote sensing in particular promises to grant us ever-more

insight into the energetic costs of performance in nature, we are still a long way off from doing so for substantial numbers of animal taxa.

Garland (1983) defined the *ecological cost of transport* (ECT) for a given species as the percentage of that species' daily energetic expenditure that is accounted for by the energetic costs of movement. Although arguably less accurate than newer methods such as SMART sensing, a species' ECT is nonetheless a useful metric of the cost of locomotor performance in particular. Existing ECT data for mammals are both extremely variable and, for the most part, low, and although carnivores exhibit the highest ECT (~20-30%%, roughly consistent with the SMART collar data) likely driven by higher costs of movement incurred during foraging, ECTs for non-carnivorous mammals tend to be lower. Although typically calculated at the species level for use in comparative analyses, ECT is still useful in testing for trade-offs and in theory could be applied at the individual level as well.

Energy budgets of animals are dynamic, and can vary with regard to age, sex, and season. The costliest average energetic expenditure after activity is reproduction, particularly for small mammals (Speakman 2008). Costs of reproduction are also variable, but tend to be especially high for female eutherian mammals, primarily driven by the energetic requirements of lactation (Prentice and Prentice 1988). Within eutherians generally, a given bout of reproduction increases metabolic rates overall by around 25%, with the majority of that increase (80%) being attributable to lactation alone (McNab 2002). Thus, species with larger litter sizes or weaning periods might be especially limited in the amount of energetic resources that they can allocate towards performance. Existing evidence also suggests that species with low basal metabolic rates exhibit greater increases in energetic expenditure during pregnancy (and, probably, lactation), than do species with higher basal metabolic rates (McNab 2002). In other words, pregnancy and lactation require very high rates of metabolism, and consequently a high basal rate of metabolism facilitates a high reproductive output. These high costs of reproduction require that animals either time their reproductive output to coincide with periods of high environmental resource availability, or allocate existing resources away from other physiological tasks and towards reproduction.

In this paper, we combine energetic data relating to activity and life-history data on a variety of species of mammals from seven mammalian orders to test the hypothesis that these two major components of animal energy budgets (namely locomotor performance and reproduction) trade off against each other. Specifically, we predict that mammal species that spend a large proportion of their daily energy budgets on locomotion (as quantified by ECT) exhibit lower reproductive outputs, as captured by a suite of reproductive life-history traits. Although there is no reason to believe that

such a trade-off might be exclusive to mammals, the requisite data to test this hypothesis are lacking for many other animal taxa, and we thus focus on mammals here.

Materials and Methods

Data collection and phylogeny

Garland (1983) defined ECT as:

$$ECT\ (\%\ DEE) = 100\ x\ \frac{DMD\ (\frac{km}{day})x\ (ICL\ (\frac{J}{km})}{DEE\ (\frac{J}{day})}$$

where DMD = daily movement distance; ICL = incremental cost of locomotion (i.e. the slope of the relationship between metabolic output and speed); and DEE = daily energetic expenditure. We collected life-history data (gestation length, lifespan, age at weaning, age at female reproductive maturity, and litter size) and data on daily movement distance, incremental cost of locomotion and daily energetic expenditure, as well as mass from the literature (see supplementary material) for a total of 72 mammal species. Calculating ECT requires all three pieces of information from each species, yet one or more are often lacking – in particular, DEE is not always known. We drew the DMD data from Garland (1983), and relied on allometric equations given by Garland (1983) for DMD and ICL, and by White and Seymour (2005) for DEE to predict values for species in cases where they were unknown (but always based on known body mass). Similarly, although we strived to use empirical data as far as possible in the current analysis, several of the species for which we calculated ECT lack corresponding data for one or more life-history variables of interest.

Missing data are a non-trivial issue for comparative analyses, typically necessitating the exclusion from the dataset of those taxa that lack data for one or more variables, which ultimately reduces sample size and power. In addition to life-history, we also included basal metabolic rate (BMR) as a predictor variable in the current analysis. Relevant data on BMR for the taxa of interest are even sparser than the life-history data. Consequently, to take advantage of multivariate phylogenetic comparative methods (which require no missing data) we have also relied on allometric equations to interpolate missing datapoints for the current dataset based on body mass as well based on existing equations for scaling of mammalian life-history variables (Hoffman 1993; Purvis and Harvey 1995). This dataset therefore constitutes a mix of empirical and interpolated data (although the majority of the data are real data; see supplementary material). Although including interpolated datapoints is not ideal, doing so allows us to test our central prediction with multivariate methods and reasonable statistical power. We nonetheless emphasise the semi-

artificial nature of the dataset, and urge caution in interpretation of our findings that arise from it. The phylogeny and branch lengths used were derived from a recent comprehensive mammalian phylogeny by Binenda-Emonds and others (2007).

Phylogenetically corrected PCA

Allometric relationships among life-history traits tend to be log-linear. We therefore log-transformed all life-history data prior to analyses (as in Swanson and Dantzer 2014). We used phylogenetically informed principal components analysis (Revell 2009) to derive multivariate axes describing variation among the tested life-history traits, which we then tested against ECT.

Phylogenetically corrected regressions

We tested for a relationship between the derived PC axes and ECT by performing phylogenetic least-squares (PGLS) regression with PC axes as the predictor variables, and ECT as the dependent variable. We performed the regression twice; first with the maximum likelihood estimate of λ, and then again with λ fixed to zero (simulating no phylogenetic influence, equivalent to a standard ordinary least-squares regression). We then calculated the sample-size corrected Akaike Information Criteria (AICc) for the regressions with and without phylogenetic influence to determine the best fit regression model. All analyses were conducted in R v 3.3.2 using the packages *ape* (Paradis et al. 2004), *picante* (Kembel et al. 2010), and *geiger* (Harmon et al. 2008).

Results

The phylogenetic PCA returned three PCA axes accounting for 48.2%, 14.6%, and 12.8% of the variation in the overall life-history dataset respectively. PC1 recapitulates the classic fast-slow life history continuum, with individuals exhibiting small body size and BMR; large litter sizes; short gestation times, time to sexual maturity lifespans; and small offspring sizes loading highly on PC1, whereas low loadings on PC1 corresponded to larger, long-lived species with high absolute BMRs and generally low reproductive outputs. PC2 and PC3 explained variation in species that did not fit this pattern, but accounted for far less variation both individually and collectively than did PC1 (Table 1). The model including the maximum likelihood estimate of λ was a better fit than the model with lambda fixed to zero as indicated by a lower AICc (ΔAICc = 10.9, P = 0.004), indicating significant phylogenetic signal in the data. That model showed a significant relationship only between PC1 and

ECT (Figure 1a); no such relationships existed between ECT and PC2 (Figure 1b) or ECT and PC3 (Figure 1c).

Discussion

Energetically expensive traits are expected to trade-off against other traits whose expression is dependent on the same pool of acquired resources. However, determining the true cost of a trait requires examining energetic expenditure within the context of the organism, and in particular relative to the costs that organism pays for expressing other life-history traits (Husak and Lailvaux in press). We used Garland's (1983) ecological cost of transport (ECT), which expresses the daily cost of locomotion as a percentage of total daily energetic expenditure, to test for a trade-off between locomotor performance and a suite of life-history traits, which collectively represent the slow-fast life-history continuum (Swanson and Dantzer 2014; but see Bielby and others 2007). Based on the classic trade-off between reproduction and other life-history traits, we tested the prediction that mammal species with high ECTs would exhibit correspondingly lower reproductive outputs, and thus slower life histories.

Our prediction was supported by analysis of life-history and ECT across several mammalian orders. We found a significant negative relationship between ECT and the major multivariate life-history axis (PC1; Figure 1) which corresponds to the slow-fast life histories (Table 1): that is, species with high scores on PC1 are those with high reproductive outputs, but small body size and metabolic rate, and short lifespan. Our analysis shows that these "fast" life-history species that invest heavily in reproduction tend also to be those that spend less energy on a day-to-day basis on locomotion. This pattern holds only for PC1 (Figure 1a), and thus deviations from this major life-history pattern (described by PC2 and PC3 respectively) are unrelated to ECT in the current dataset (Figure 1b and c). Based on this broad-scale comparison, then, we find support for a potential trade-off between performance and reproductive investment as represented by overall life-history strategy.

The costs of reproduction for many mammals are substantial (Gittleman and Thompson 1988). However, those costs are not experienced equally by all species. The largest animal in our dataset is the elephant *Loxodonta africana* - a mammal at the slow end of the slow-fast continuum - whereas the smallest is a rodent (*Dipodomys deserti*). Smaller animals pay disproportionately high costs of reproduction (which alone may account for the trend seen in Figure 1a), but also face constraints on rates of resource acquisition that larger animals do not (reviewed in Speakman 2008). For example, the *central limitation hypothesis* posits that small mammals such as rodents are limited in the rate at which they can acquire resources by the capacity of the alimentary canal to absorb

food (Hammond and Diamond 1997). There is evidence from studies on rodents in particular that this upper limit to food intake cannot be exceeded (Hammond and Diamond 1994); for example, when an energetically demanding task such as lactation is combined with additional costs of locomotor activity, female house mice (*Mus domesticus*) that were forced to run on wheels through the first 12 days of lactation killed some of their offspring rather than increasing food intake to pay for the extra locomotor expense (Perrigo 1987). Thus, smaller mammals may be especially prone to life-history trade-offs with reproduction not necessarily (or not only) because of their relatively high costs of reproduction, but because of their relatively limited food intake/nutrient uptake rates.

Although one strategy used by animals that invest heavily in current reproduction is to trade-off that investment against future reproductive effort (Williams 1966; Stearns 1992; Charnov 1993; Charlesworth 1994), our analysis indicates that high reproductive investment might constrain energetic expenditure on locomotor performance as well. However, the coarse-grained nature of our analysis does not offer any insight into the timing of those costs and trade-offs, nor into the potential intraspecific variation in those costs. Indeed, the taxon-specific and dynamic character of animal energetic budgets has implications for the identity and timing of specific life-history trade-offs that might impact on overall fitness in various animal taxa. Specifically, it implies that trade-offs between whole-organism performance capacities and other life-history traits will not only depend on the energetic costs of both the performance trait and of other traits involved in that trade-off, but they may also be realized only at certain times of year, and more readily in one sex or the other (that is, the sex that tends to bear the brunt of the energetic burden on reproduction, which is usually the female). This variation raises a number of questions into which our dataset offers little insight, and an important future direction will be to test whether the costs paid specifically by females, for example, constrain male locomotor investment sufficiently to be manifest at the species level, or if intersexual variation in life-history strategy leads to variation in patterns of trade-offs as well.

Our dataset pertains only to mammals, and therefore does not address potential trade-offs between performance and life-history in non-mammalian species. However, evidence from the literature suggests that energetic constraints on performance investment might be widespread. For example, birds do not lactate but nonetheless similarly increase their metabolic expenditures ~ 3x when feeding their young (in this case, this increased expenditure likely applies to both parents if there is biparental care as opposed to only the female in mammals) (McNab 2002), although empirical data are required to determine whether such expenditures are large enough to impinge on performance. The extant variation in bird performance, however, offers scope for more directed tests of a performance/life-history trade-offs. For instance, most flightless birds have lower BMRs

than volant birds, probably in part because the pectoral muscles, which consume large amounts of energy and contribute to heat balance, are greatly reduced (McNab 1994). One possibility is thus that flightless birds that invest less in expensive flight muscle would face fewer constraints on allocation towards reproduction, and may thus exhibit increased reproductive output. However, it is also possible that flight activity or maintenance of the flight "machinery" can be altered to reduce costs (i.e., have high performance without high metabolic rates; Nudds and Bryant 2002) or is not the greatest expense in these animals; for example, an analysis of 22 species of birds by Daan and others (1990) found that more than 50% of the variation in BMR is accounted for by the heart and kidneys alone. Similarly, the energetics of both life-history (Adolph and Porter 1993) and some aspects of locomotion (Bennett and John-Alder 1984) in ectotherms such as lizards are dependent on temperature variation, and lizards also pay their own costs of thermoregulation that are distinct from the metabolic costs levied on endotherms (Huey and Slatkin 1976). Thus, trade-offs between performance and life-history traits might be masked by thermal variation in lizards, even if only through constraints on activity times rather than deviations from thermal optima (Adolph and Porter 1993). Nevertheless, there is substantial variation among lizard species in endurance capacity (Garland 1999), for example, and there does appear to be a trade-off between endurance capacity and relative clutch mass in lizards, similar to that seen in mammals (Husak and Lailvaux this issue), perhaps because their relatively small size puts a limit on energy acquisition as described above for small mammals.

Our finding here has several caveats. Firstly, our dataset constitutes a mix of empirical and predicted data, and these results should thus be interpreted with appropriate caution. Second, because our data set focusses only on terrestrial mammals, and includes no bats or marine mammals, we cannot generalize our results beyond terrestrial locomotion. Of the three major modes of locomotion (i.e. swimming, flying, and terrestrial movement), walking/running is the most expensive (Schmidt-Nielsen 1972). As such, it is perhaps unsurprising that we find trade-offs between life-history and terrestrial locomotion here. However, evidence suggests that marine mammals strive to minimize the costs of locomotion just as terrestrial mammals do (Williams et al. 1992; Weihs 2002), and previous studies note that female elephant seals, for example, reduce their activity and remain within a few meters of the site of parturition while lactating (Costa et al. 1986). Thus, it may be premature to dismiss the relatively cheaper costs of non-terrestrial locomotion as generally insufficient to drive trade-offs with other life-history traits. Finally, it is important to acknowledge the existence of individual heterogeneity in both reproductive rates and the costs of reproduction, particularly in long-lived vertebrates, which means that not all individuals within a species might realize the same life-history trajectories over the course of their entire lifetimes

(Chambert et al. 2013). This is also likely to hold true for whole-organism performance, which exhibits plastic aging trajectories in disparate taxa (e.g. Lailvaux et al. 2011; Lailvaux et al. 2014; Mark et al. 2017).

In conclusion, we show a negative relationship between reproductive investment, as captured by a suite of life-history traits, and proportion of daily energetic expenditure accounted for by locomotion in mammals. We interpret this tentatively as evidence for a trade-off between whole-organism performance and "fast" life-history strategies, such that smaller species with larger litter sizes, more frequent reproduction, and shorter life spans are constrained (through either resource allocation or acquisition) in their capacity to invest in locomotor performance. Future studies interested in trade-offs between performance and other life-history traits might therefore focus on animals at the fast end of the life-history continuum such as small rodents.

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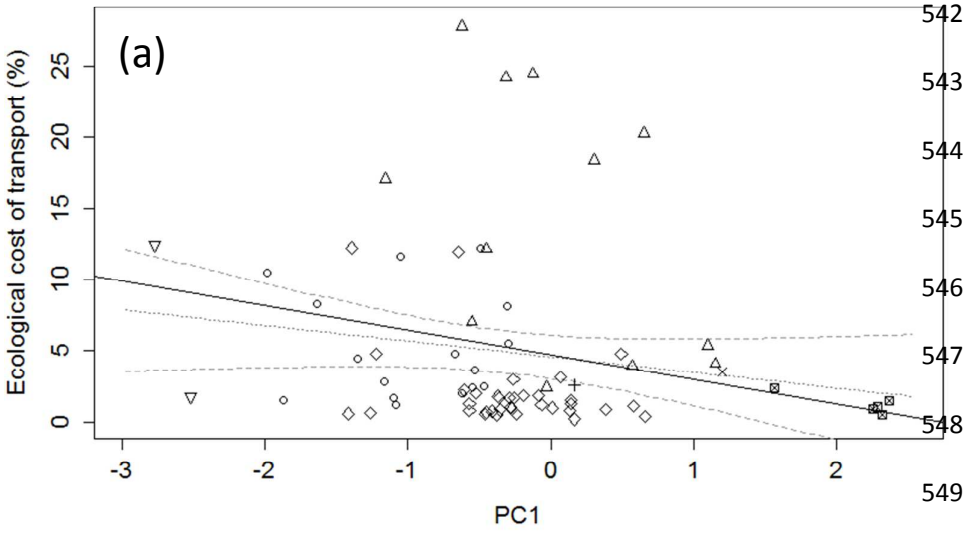
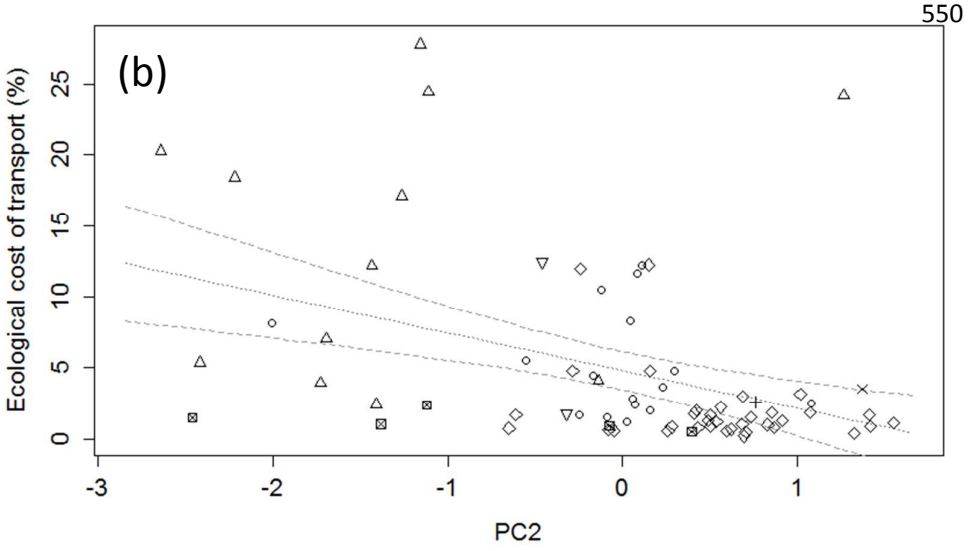
Table 1: Loadings of life-history variables on phylogenetically corrected PCA axes and the percentage of life-history variation explained by each axis.

Life-history trait	PC1	PC2	PC3
% variation explained	48.2	14.6	12.8
Mass	-0.921	-0.08	0.095
Gestation length	-0.79	-0.095	-0.23
Maximum lifespan	-0.58	-0.22	-0.68
Age at female reproductive maturity	-0.56	0.47	0.28
Age at weaning	-0.48	-0.47	0.53
Litter size	0.422	-0.71	0.05
Basal metabolic rate	-0.921	-0.08	0.095

Figure 1: (a) Regression plot of the relationship between ecological cost of transport (ECT) and PC1 from a phylogenetic principal components analysis of life-history traits (β= -1.73, t = -2.017, P= 0.047). There was no significant relationship between ECT and either (b) PC2 (β= -0.006, t = -0.7, P= 0.49) or (c) PC2 (β= -0.003, t = -0.43, P= 0.67). PC axes are scaled by their respective standard deviations. The solid line in (a) is the best-fit line from the phylogenetic regression, whereas the dotted lines represent the best-fit lines from standard univariate regressions. The 95% confidence intervals on those regressions are delimited by the dashed lines. R^2 for the full model =0.12. Symbols used: triangles =carnivores; triangles = proboscidae; circles = artiodactyls; crossed squares = rodents; diamonds = primates; crosses = eulipotyphla; plus signs = diprotodontia.


(a)
Ecological cost of transport (%)
0
5
10
15
20
25
-3
-2
-1
0
1
2
PC1
542
543
544
545
546
547
548
549


(b)
Ecological cost of transport (%)
0
5
10
15
20
25
-3
-2
-1
0
1
PC2
550

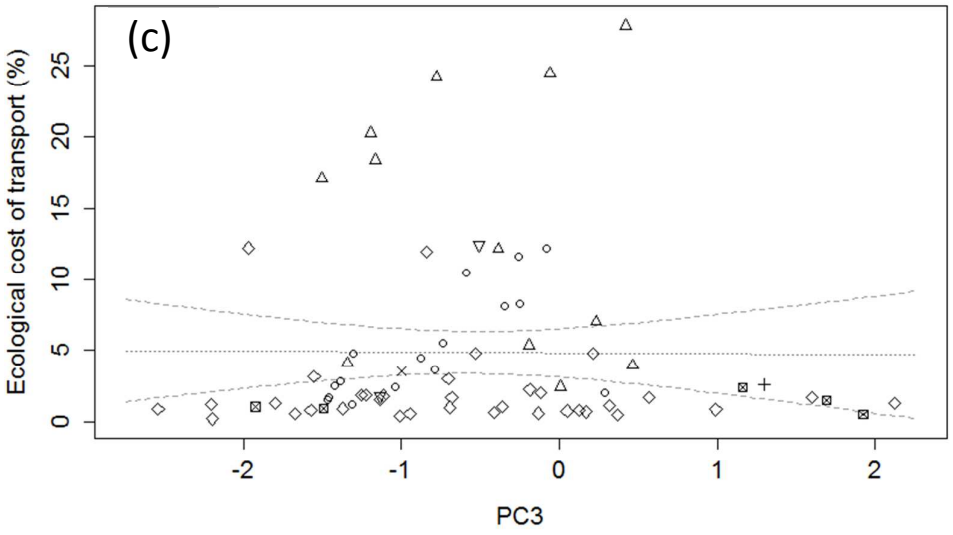
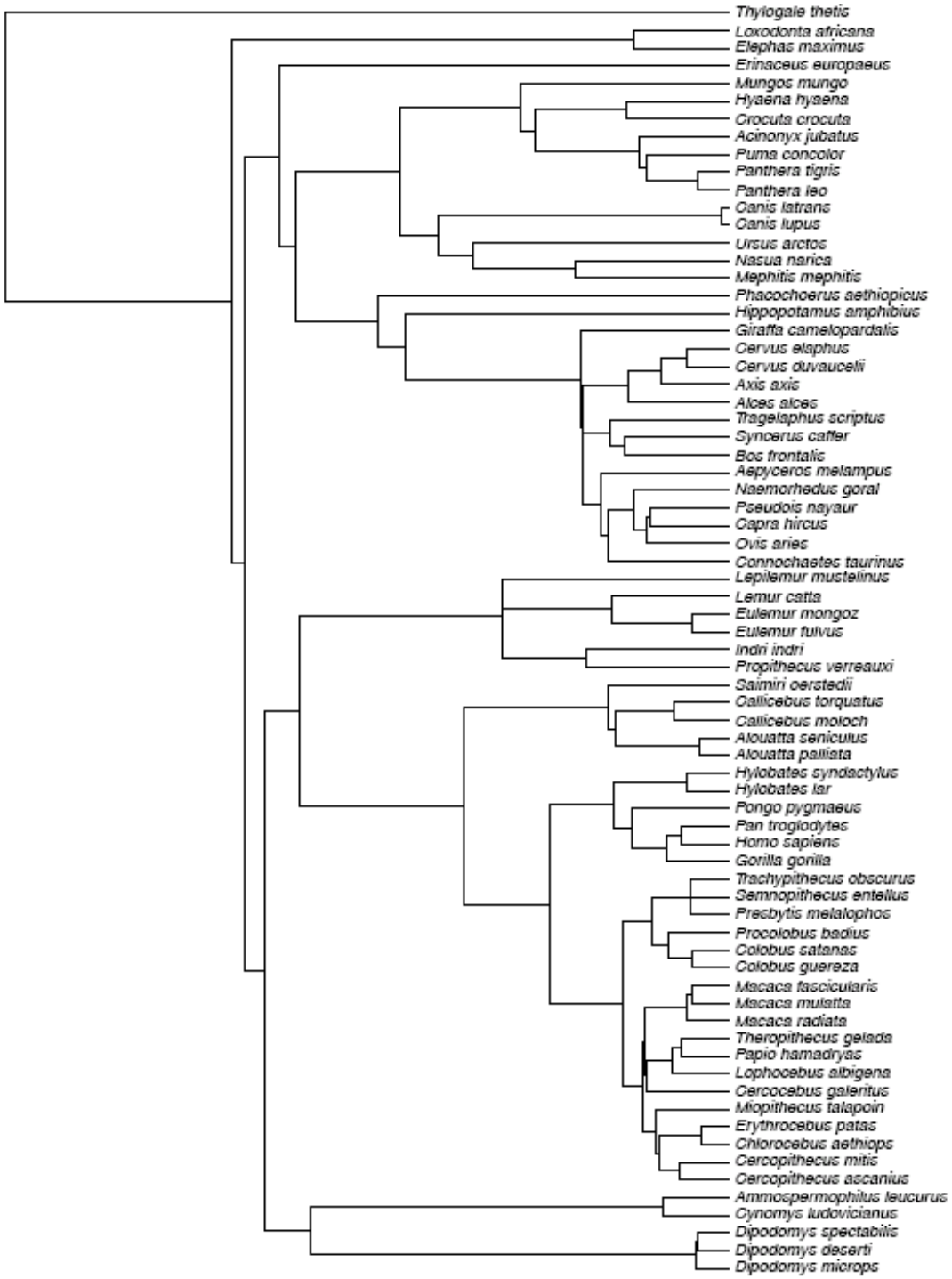

(c)
Ecological cost of transport (%)
0
5
10
15
20
25
-2
-1
0
1
2
PC3

Figure S1. Phylogeny of 72 mammal species used for analysis. Reduced from Bineneda-Emonds et al. (2007).



Name	ECT (%)	Mass (g)	BMR (ml O_2/hour)	Gestation length (days)	Maximum lifespan (years)	Weaning age (days)	Female reproductive maturity (days)	Litter size	Order
Hippopotamus amphibius	10.5	3800000	3488155.77*	235.37	54.5	319.01	1750.87	1	Artiodactyla
Giraffa camelopardalis	1.54	1000000	1281616.74*	455.25	39.5	272.08*	1532.23*	1	Artiodactyla
Syncerus caffer	8.33	750000	1032890.1*	337.49	29.5	319.37	1460	1	Artiodactyla
Bos frontalis	4.46	680000	959709.64*	273.75	26.2	198.17	534.77	1	Artiodactyla
Alces alces	1.7	450000	704153.85*	235	27	98.85	547.49	1.25	Artiodactyla
Cervus elaphus	2.87	275000	486695.91*	255	32	145	852	1.09	Artiodactyla
Connochaetes taurinus	1.17	180000	354170.64*	251.49	21.5	256.32	730	1	Artiodactyla
Cervus duvaucelii	1. 17	160000	324226.24*	245	33.94*	217.79*	732.49	1	Artiodactyla
Tragelaphus scriptus	2.02	100000	227907.2*	182.49	13	193.73*	380.77	1	Artiodactyla
Phacochoerus aethiopicus	8.13	85000	201754.1*	165.4	18.8	111.44	541.97	3.39	Artiodactyla
Axis axis	4.83	65000	164984.52*	227.49	20.8	121.66	462.75	1	Artiodactyla
Pseudois nayaur	2.42	60000	155371.6*	159.74	24	170.58*	364.99	1	Artiodactyla
Aepyceros melampus	3.65	50000	135514.47*	196.74	17.75	150	394.41	1	Artiodactyla
Ovis aries	1.22	50000	135514.47*	152.08	19.17	182.5	699.45	1.19	Artiodactyla
Capra hircus	5.55	34000	101476.94*	156	20.8	158.04	419.67	1.5	Artiodactyla
Naemorhedus goral	2.47	32000	96966.27*	212.91	17.6	55.72	873.99	1	Artiodactyla
Ursus arctos	1.71	350000	583188.84*	224	50	182.5	1150.39	2	Carnivora
Panthera tigris	2.78	230000	425651.38*	105.19	26.25	145.97	1318.92	2.51	Carnivora
Panthera leo	7.03	160000	324226.24*	108.74	30	228.12	873.24	2.67	Carnivora
Puma concolor	2.42	60000	155371.6*	92.29	20	48.31	871.04	0.98	Carnivora
Acinonyx jubatus	2.43	55000	145556.03*	92.24	19	88.63	636.19	2.99	Carnivora
Crocuta crocuta	12.18	50000	135514.47*	112.47	41	385.27	712.95	2	Carnivora
Hyaena hyaena	24.45	45000	125218.23*	90.5	24	124.49	807.96	2.49	Carnivora
Canis lupus	18.41	40000	114631.29*	63.24	29.5	42.13	565.58	4.97	Carnivora
Canis latrans	20.26	16000	57656.48*	61.74	23.79*	43.71	319.38	5.69	Carnivora

Nasua narica	3.95	5000	24098.26*	76.92	17.6	131.77	875	3.99	Carnivora
Mephitis mephitis	5.36	3000	16428.55*	63.29	12.92	55.15	308	5.69	Carnivora
Mungos mungo	4.12	1500	9768.47*	60.91	12	20.74	306.47	2.39	Carnivora
Thylogale thetis	2.6	7500	32662.85*	105.25*	9	209.99	532.45	1	Diprotodontia
Erinaceus europaeus	3.5	800	6096.43*	37	14	40	247.05	1	Eulipotyphla
Gorilla gorilla	0.59	127000	272653.43*	256.99	54	929.63	2828.74	1	Primates
Pongo pygmaeus	0. 61	53000	1415678*	260.05	60	1081.72	2792.57	1	Primates
Pan troglodytes	4.77	45000	125218.23*	231.49	60	1670.46	3309.15	1.07	Primates
Homo sapiens	12.24	44000	123125.41*	274.78	122	721.15	4842.27	1	Primates
Papio hamadryas	11.94	20000	68160.17*	178.05	45	450.71	1411.75	1.25	Primates
Theropithecus gelada	0.8	14000	52162*	178.86	28	493.34	1642.5	1	Primates
Semnopithecus entellus	2.04	13000	49341.88*	197.7	25	400.79	1298.21	1	Primates
Indri indri	0.45	13000	49341.88*	136.5	23.04*	330.26	1559.07	1	Primates
Hylobates syndactylus	1.28	11000	43531.41*	230.04	12	631.25	3285	1	Primates
Colobus satanas	0. 58	11000	43531.41*	192.89	22.46*	111.79*	535.27*	0.99*	Primates
Colobus guereza	0. 68	11000	43531.41*	169.07	24.5	385.27	1672.91	1	Primates
Procolobus badius	0. 84	8200	34923.56*	151.46	21.46*	778.84	1277.49	1	Primates
Lophocebus albigena	1.69	8000	34282.76*	182.93	17.53*	2190	496.96*	1	Primates
Cercocebus galeritus	1.69	7900	33960.85*	174.49	21	102.94*	2372.5	1.01	Primates
Macaca mulatta	1.82	7900	33960.85*	166.18	36	310.57	1089.04	1	Primates
Erythrocebus patas	2.99	7800	33637.92*	167.2	23.9	210.41	1054.36	1	Primates
Alouatta seniculus	0.75	7300	32007.4*	189.96	30.64	1475.2	486.46*	1.01	Primates
Trachypithecus obscurus	1.24	7100	31347.43*	145.88	30.05	100.24*	483.32*	1.02	Primates
Presbytis melalophos	1.57	6700	30013.34*	102.62*	20.8*	98.8*	476.83*	1.02	Primates
Alouatta palliata	0.57	6600	29676.74*	185.48	41	492.32	1368.74	1.01	Primates
Hylobates lar	2.23	5500	25883.93*	212.91	40	721.15	3341.27	1	Primates
Macaca radiata	1.04	5500	25883.93*	161.61	27.59	331.17	1551.25	1	Primates
Macaca fascicularis	0. 922	5000	24098.26*	164.69	38	282.61	1143.07	1	Primates

Cercopithecus mitis	1.72	4500	22267.3*	138.48	27.1	683.61	1779.37	1	Primates
Chlorocebus aethiops	1.86	4100	20765.68*	163.19	31.6	199.3	1465.47	1	Primates
Propithecus verreauxi	1	3600	18835.84*	147.49	20.6	178.8	912.49	1	Primates
Cercopithecus ascanius	1.86	3600	18835.84*	148.5	28.3	141.24	1490.41	1	Primates
Lemur catta	1.28	2700	15180.32*	134.17	30	126.1	754.46	1.17	Primates
Eulemur mongoz	0.83	2100	12572.53*	128.99	30	150.15	919.79	1	Primates
Eulemur fulvus	0.19	2100	12572.53*	120.83	37	134.2	686.8	1.01	Primates
Miopithecus talapoin	3.17	1300	8774.36*	164.49	30.9	177.81	1484.15	1	Primates
Callicebus torquatus	1.14	1100	7741.1*	68.44*	15.74*	121.66	1460	1.02	Primates
Callicebus moloch	0.9	680	5396.84*	163.99	25.3	58.47	1095	1.02	Primates
Saimiri oerstedii	4.8	670	5337.21*	160.99	14.58*	360.57	278.72*	1.01	Primates
Lepilemur mustelinus	0.38	600	4913.28*	133.54	12	75.72	585.48	1	Primates
Loxodonta africana	12.42	6000000	4913281.1*	660	80	1081.72	5475	1	Proboscidae
Elephas maximus	1.78	4000000	3624959.56*	644	65.5	548	3287	1	Proboscidae
Cynomys ludovicianus	2.38	820	6210.39*	33.51	8.5	45.3	588.28	4.45	Rodentia
Dipodomys spectabilis	0.52	120	1469.41*	23.49	3	23.47	270.4	2.67	Rodentia
Dipodomys deserti	1.05	110	1376.58*	30.5	11.03*	23.44	48.37	3.33	Rodentia
Ammospermophilus leucurus	1.51	85	1134.55*	29.46	5.8	63.75	329.04	8.24	Rodentia
Dipodomys microps	0.89	56	829.66*	30.99	9.94*	20.99	128.89	2.39	Rodentia

Dataset S1. Life-history variables and calculated ECT (expressed as %). Data are from the PanThERIA (Jones et al. 2009) and AnAge (de Magalhaes 2009) databases; Ernest (2003); Promislow and Harvey (1991); Western (1979); Wooton (1987). Datapoints marked with an * are interpolated based on body size (see main text for sources). [Note that all BMR data are interpolated.]

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