Great ranging associated with greater reproductive investment in mammals

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Most animals must travel to find food, incurring an unavoidable energy and time cost. Economic theory predicts, and experimental work confirms, that within species, increasing the distance traveled each day to find food has negative fitness consequences, decreasing the amount of energy invested in maintenance, repair, and reproduction. Here, we show that this relationship between daily distance traveled and reproductive success is fundamentally different between species and over evolutionary time in many lineages. Phylogenetically controlled analyses of 161 eutherian mammals indicate that, after controlling for body mass, evolutionary increases in the daily distance traveled are associated with corresponding increases in both total fertility (number of offspring per lifetime) and total offspring mass (grams of offspring per lifetime). This suggests that over evolutionary time, increasing travel distance is often part of a strategy for procuring more food energy and not necessarily a response to decreased food availability. These results have important implications for ecological comparisons among species, including assessments of habitat quality based on locomotor behavior.

ecology | energetics | reproduction | life history | foraging economics

How far will an animal travel each day? A broad range of ecological pressures influence ranging decisions (1–7), making this seemingly straightforward question exceedingly difficult to answer definitively. In the simplest case, in which an animal requiring a net energy intake of E_{net}(J/day) acquires food energy at a constant rate B (J/m) and spends energy on travel at some rate C (J/m), it must travel sufficient distance, D (m/day), so that $D\ (B\text{–}C) = E_{net}$.

Perhaps surprisingly, despite considerable variation and complexity in foraging and ranging behaviors, this simple relationship between daily movement distance, food availability, and energy requirements is generally supported by behavioral observation in a broad range of species. While ecological constraints cannot always be linked to foraging behavior (7) and physiological constraints may limit ranging ability (8), large interspecific comparisons of foraging behavior indicate that daily movement distance, D, is primarily determined by the need to acquire sufficient food energy (2, 3, 6). For example, daily movement distance increases with body size and diet quality, reflecting both size-related increases energy requirements and the relative scarcity of high-quality, energy-dense foods on the landscape (2, 6). Further, decreases in an individual's rate of food acquisition, B, whether through experimental manipulation in the laboratory (9–14), increased foraging group size (1, 4, 6, 15) or through seasonal changes in food availability in the wild (16–19) typically leads to increases in the daily distance traveled.

In principle, one might expect longer daily movement distances to be energetically beneficial, since greater D will lead to greater E_{net} as long as $B > C$ (10, 20). In practice, however, while some species may increase foraging effort to maximize energy gain during food-rich periods (21, 22), intake and E_{net} are limited by an animal's maximum sustained (i.e., over several days) metabolic rate, typically 3–4× its resting metabolic rate (RMR) (maximum 6–7×; ref. 23). Since normal daily energy expenditure approaches this limit in wild populations, with field metabolic rates of 2–4× resting metabolism (24–26), a zero-sum system apparently prevails, in which increasing the energy spent on travel decreases the energy available for maintenance and reproduction (2) (Fig. 1*A*). Thus, rodents and birds challenged with decreased food per meter in experimental settings increase their ranging but lose weight and spend less energy on maintenance and reproduction (9–14), even when $B > C$ and feeding is ad libitum. Similarly, daily movement distance increases (16–19) and body mass and condition decrease (27–30) during periods of food shortage for mammals in the wild, even though the average estimated food energy gained per meter for most free ranging mammals is over an order of magnitude greater than the travel cost per meter (Fig. 2).

While increased ranging and decreased E_{net} have been repeatedly demonstrated within numerous species, we propose that this relationship may be fundamentally different among species and over evolutionary time (Fig. 1*B*), at least in some lineages. Maximum daily metabolic rate may be constrained within a species (12) but is variable among species (23), indicating that this physiological constraint is evolutionarily labile. If so, longer daily movement distances and greater daily travel costs may be part of a strategy for expanding the daily energy budget and increasing net energy intake, thereby increasing the energy available for maintenance and reproduction, and not solely a strategy for compensating for decreased food availability (Fig. 1*B*). Under favorable ecological conditions, perhaps where food is predictably available and not easily depleted, species may be selected to increase ranging and daily intake to increase the energy available for maintenance and reproduction. Conversely, decreased daily travel may reflect an evolutionary shift toward smaller energy budgets and less net energy intake.

This model suggests that the reliability of food resources (e.g., lack of seasonality, resistance to depletion) may be more important than the ratio of B:C in encouraging evolutionary expansion or contraction of ranging and the daily energy budget. Energy budgets may expand when B:C increases and contract when B:C decreases, or vice versa (Fig. 1*B*), but changes (or stasis) in B:C do not dictate changes in the energy budget in our model, provided $B > C$. Instead, our model predicts expansion of ranging and the energy budget when increased ranging is profitable (e.g., food does not become depleted), and contraction when large energy budgets are a liability, perhaps in seasonal or stochastic environments prone to periods of extreme food shortage. In addition, factors unrelated to food availability, such as time constraints (31), limits to endurance (8), thermoregulatory constraints (32), or predation pressures (4), may limit ranging and consequently constrain the daily energy budget.

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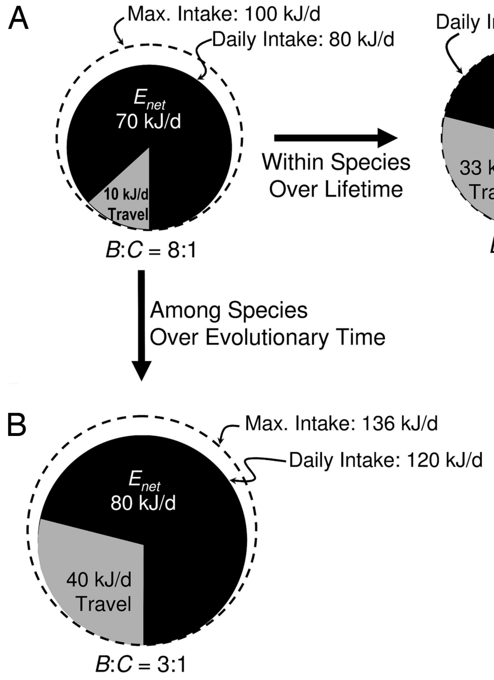

Fig. 1. Hypothetical energy budgets for a 100 g mammal (see ref. 24), showing proposed differences in travel costs versus net intake, E_{net}, over different time scales. (*A*) Within species, decreasing the ratio of food gained per meter, *B*, to travel cost per meter, *C*, from 8:1 to 3:1 increases daily travel distance and cost by 3.3× (right arrow), but limited maximum intake results in decreased E_{net}. (*B*) In contrast, with an evolutionary increase in maximum intake (down arrow) increasing daily travel 4× results in greater E_{net} even with the lower ratio *B*:*C*. Note that changes *B*:*C* do not dictate evolutionary changes in ranging and maximum intake in this model; see text for discussion.

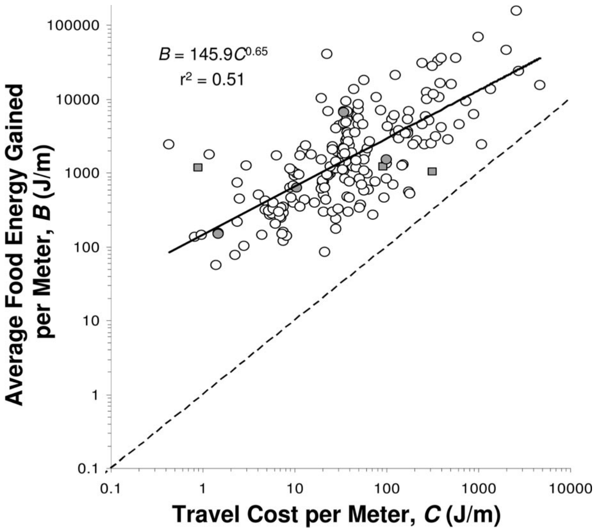

Fig. 2. Estimated food energy acquired per meter, *B* (J/m), versus the energy cost of travel per meter, *C* (J/m), for 161 mammal species. *B* is calculated by dividing estimated daily energy expenditure (kJ/day, equation 1 in ref. 24) by daily movement distance, *D* (km/day, Appendix 1). *C* was estimated from body mass using published allometric equations (156 terrestrial species, ref. 50; 5 aquatic species, ref. 51). Filled symbols: species for which direct measures of daily energy expenditure (circles) or both daily energy expenditure and cost of travel (squares) are available. As *C* increases with body size (42), the ratio of *B*:*C* changes with body size, from a mean of 65:1 for a 1 kg animal to 13:1 for a 800 kg animal. Dashed line indicates $B = C$. Note that *C* in this figure, also termed the ''incremental cost of locomotion'' (2) does not include the ''postural cost'' of travel (52).

The implication that increased ranging may be an energy-maximizing response to favorable ecological conditions is consistent with recent work showing that both basal metabolic rate and activity level are positively correlated with food availability for rodents across different habitats (33) and seasons (34), as well as data suggesting that foraging effort and net intake may increase during food-rich periods in some species (21, 22). A positive interspecific relationship between ranging, food availability, and daily energy budget would also be consistent with the longstanding (26, 35), but contentious (36), hypothesis that RMR is positively correlated with food availability, since RMR is both a large component and strong correlate of field metabolic rate (24, 26; but see ref. 25). Again, while these examples suggest increased ranging is favored in habitats with increased food availability, our model suggests an increase in ranging and net energy intake can also occur with a decrease in the ratio of *B*:*C* (Fig. 1*B*), provided that maximum daily intake increases.

Here, we test the hypothesis that longer daily movement distances are often part of a strategy for maximizing net energy intake, using a large comparative dataset of 161 mammals to investigate whether evolutionary changes in daily movement distance are positively associated with reproductive investment. Given the diversity of ranging and reproductive strategies (31, 37), we do not expect increased ranging to be associated with greater reproductive investment in every case; larger ranging costs may well be associated with decreased reproductive investment in some cases, as suggested by intraspecific studies (9–13). Rather, we seek to compare ranging and reproduction to determine whether increased ranging is associated with increased reproduction in a significant proportion of lineages. Such results would shed new light on the diversity of foraging strategies seen in mammals, suggesting that evolutionary changes in ranging behavior may be correlated with expansion or contraction of daily energy budgets.

Results

Phylogenetically controlled multiple regression revealed a positive relationship between daily movement distance and both total fertility (offspring per lifetime; $\beta = 0.265$, $P = 0.007$, $n = 109$) and total offspring mass (grams offspring per lifetime, $\beta = 0.155$, $P = 0.024$, $n = 108$), once outliers were removed (Table 1). Other measures of reproductive and somatic investment, including litter mass (g/litter), litter mass per year (g/year), and lifespan (years), were not significantly related to travel distance (Table 1). Reducing the degrees of freedom due to polytomies in the phylogeny did not alter the results, nor did removing aquatic species (Table 1). Similarly, retaining outliers had negligible effects on results (Table 1).

Conventional multiple regression analyses, using phylogenetic Order and species values of body mass and daily movement distance as independent variables and reproductive investment or maintenance measures as dependent variables, revealed significant positive relationships between daily movement distance and investment in maintenance and reproduction (Table 2). While effect sizes were generally small (partial η^2 less than 0.1), daily movement distance was significantly positively correlated with litter mass ($\beta = 0.113$, $P = 0.020$, $n = 150$), offspring mass per year ($\beta = 0.202$, $P = 0.002$, $n = 113$), total fertility ($\beta = 0.138$, $P = 0.016$, $n = 113$), and total offspring mass ($\beta = 0.213$, $P = 0.007$, $n = 111$) (Table 2). As in the phylogenetic contrasts analysis, lifespan was not significantly associated with daily movement distance. Removing aquatic species did not significantly affect results.

Discussion

Three conclusions can be drawn from these results. First, the positive relationship between daily movement distance and

Table 1. Results of the phylogenetically controlled analysis

Dependent Variable	Independent Variables	Degrees of Freedom	F	p	β
log Litter Mass	log Body Mass	1	578.19	<0.001	0.91
	log Daily Movement Distance	1	0.30	0.588	−0.02
	Error	143			
log Offspring Mass per Year	log Body Mass	1	155.05	<0.001	0.75
	log Daily Movement Distance	1	0.49	0.487	0.04
	Error	126			
log Total Fertility	log Body Mass	1	9.19	0.003	−0.29
	log Daily Movement Distance	1	7.69	0.007†	0.27
	Error	107			
log Total Offspring Mass	log Body Mass	1	102.25	<0.001	0.69
	log Daily Movement Distance	1	5.25	0.024‡	0.16
	Error	106			
log Maximum Lifespan	log Body Mass	1	48.50	<0.001	0.57
	log Daily Movement Distance	1	0.29	0.591	−0.04
	Error	124			

†, $P = 0.006$ excluding aquatic spp., $P = 0.012$ including outliers. ‡, $P = 0.057$ excluding aquatic spp., $P = 0.059$ including outliers.

lifetime reproductive output in both phylogenetically controlled and conventional multiple regression (Table 1 and 2) indicates that evolutionary increases in ranging are commonly associated with increased energy investment in reproduction. This supports our hypothesis that evolutionary increases in daily movement distance are often part of a strategy for increasing net energy intake, thereby making more energy available for maintenance and reproduction (Fig. 1*B*). Conversely, decreases in daily movement distance are often associated with decreased investment in maintenance and reproduction. Data on daily metabolic rates for these species in the wild (24) are necessary to determine whether these evolutionary changes in ranging are in fact associated with corresponding changes in the size of the daily energy budget, as suggested by our model.

Second, the small effect size of daily movement distance, and the lack of a relationship between travel distance and reproductive output in some comparisons, demonstrates the considerable variability in the relationship between ranging and reproduction. Given the diversity of sources used to compile the ranging and life-history data (6, 38), a large portion of this apparent variability is likely due to differences in data quality and collection. Still, when the studentized residual contrasts, controlled for body mass, of ranging and reproductive output are plotted against each other (Fig. 3), it is apparent that evolutionary changes in daily movement distance are associated with a range of responses in reproductive output. For example, relatively large changes in daily movement distance (studentized residual > ±0.5) were negatively correlated with correspondingly large changes in total fertility and total offspring mass (studentized residual > ±0.5) in 34/90 and 33/85 cases, respectively (Fig. 3). This is similar to what is seen in most laboratory investigations of decreased food availability (9–13) and is consistent with the view of ranging as a cost that decreases the energy available for other activities (2). In contrast, in many cases, changes in daily movement distance have no significant effect on reproduction; relatively large changes in daily movement distance (studentized residual > ±0.5) were associated with little or no change in total fertility or total offspring mass (studentized residuals < ±0.5) in 14/90 and 11/85 cases, respectively (Fig. 3). This suggests that travel may be responding to food availability, with increased travel used to maintain net energy intake at some constant level in the face of decreased food availability. This is occasionally reported in laboratory experiments (14) and is commonly cited as the mechanism underlying increased ranging in food-poor seasons in wild populations (16–19). Finally, as suggested by our model, evolutionary increases in daily movement distance are often associated with increased investment in reproduction and maintenance. In the plurality of cases, relatively large changes in daily movement distance (studentized residuals > ±0.5) were positively correlated with large changes (studentized residuals > ±0.5) in total fertility (42/90 cases) and total offspring mass (41/85 cases) (Fig. 3).

Table 2. Results of conventional species data multiple regression

Dependent Variable	Independent Variables	Degrees of Freedom	F	p	η^2	β
log Litter Mass	log Body Mass	1	515.27	<0.001	0.788	0.681
model adjusted $r^2 = 0.95$	log Daily Movement Distance	1	5.58	0.020	0.039	0.113
	Phylogenetic Order	8	9.55	<0.001	0.355	-
log Offspring Mass per Year	log Body Mass	1	126.81	<0.001	0.514	0.451
model adjusted $r^2 = 0.90$	log Daily Movement Distance	1	10.46	0.002	0.080	0.202
	Phylogenetic Order	8	14.00	<0.001	0.483	-
log Total Fertility	log Body Mass	1	19.94	<0.001	0.164	−0.153
model adjusted $r^2 = 0.44$	log Daily Movement Distance	1	5.98	0.016	0.055	0.138
	Phylogenetic Order	8	6.09	<0.001	0.323	-
log Total Offspring Mass	log Body Mass	1	148.06	<0.001	0.597	0.580
model adjusted $r^2 = 0.91$	log Daily Movement Distance	1	7.55	0.007	0.070	0.213
	Phylogenetic Order	8	8.58	<0.001	0.407	-
log Maximum Lifespan	log Body Mass	1	63.70	<0.001	0.349	0.155
model adjusted $r^2 = 0.71$	log Daily Movement Distance	1	0.27	0.606	0.002	0.016
	Phylogenetic Order	9	14.49	<0.001	0.523	-

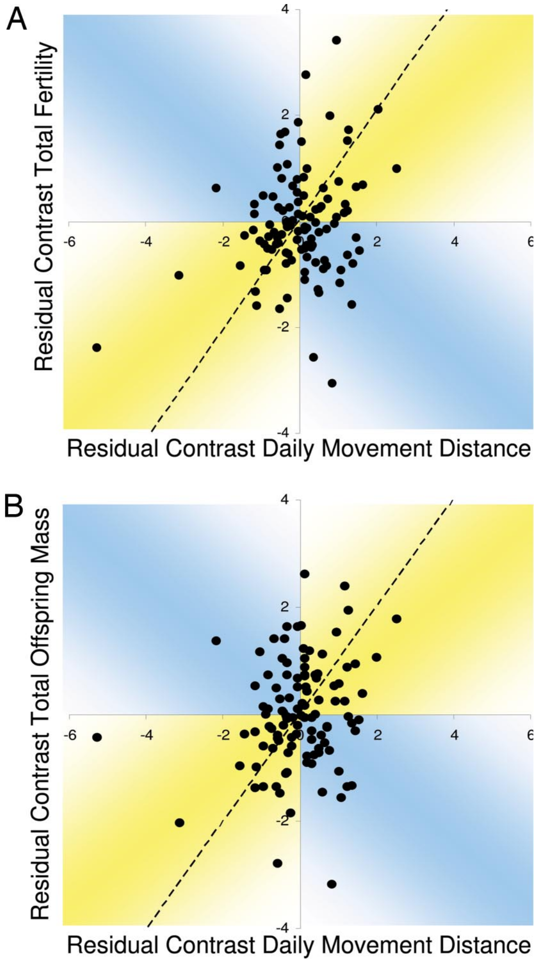

Fig. 3. Studentized residual phylogenetic contrasts, corrected for body mass, of daily movement distances versus (*A*) total fertility and (*B*) total offspring mass for 113 and 111 mammalian species, respectively. Dashed line indicates the Reduced Major Axis trendline. While some evolutionary changes in daily movement distance are negatively correlated with changes in reproduction (blue quadrants), in most instances, daily movement distance is positively associated with reproductive output (yellow quadrants). In contrast, within species, daily movement distance is negatively correlated with reproductive and somatic investment (see text).

Third, our data strongly support the hypothesis that the relationship between ranging and reproductive effort is fundamentally different over different timescales. Within species, over a lifetime, increased ranging is consistently associated with decreased net energy intake, reproductive effort, and maintenance, both in the wild (27–29) and in the lab (9–12). In contrast, among species, over evolutionary time, increased ranging is commonly associated with increased reproductive output (Tables 1 and 2; Fig. 3). We propose that this difference is due to the constraint of maximum daily metabolic rate (Fig. 1), which is relatively inflexible for an individual but may be labile over evolutionary time. This hypothesis could be tested with data on daily energy budgets for wild populations (24, 25, 33) or laboratory comparisons of maximum daily metabolic rate (12, 23).

The positive relationship between daily movement distance and investment in reproduction and maintenance may help explain some of the interspecific variation observed in daily movement distance. While the scaling of daily movement distance generally correspond to predicted energy requirements (3, 5, 6), considerable variation in ranging remains unexplained by body size, diet, and foraging group size (7). Our results suggest that species may increase daily movement distances as part of a strategy of increasing daily energy budgets: two species with similar body size, diet, and foraging group size may differ in daily movement distance if one adopts a larger daily energy budget. Including some measure of net energy intake, apart from body mass, may therefore improve predictive ranging models.

Our results suggest a new approach for interpreting interspecific differences in daily movement distance. Short daily movement distances are often viewed as a reflection of low diet quality (i.e., a diet focused on low energy-density foods) and/or relatively high food abundance (6) but results here suggest that short daily movement distances may also reflect the adoption of a smaller daily energy budget, with less energy invested in reproduction and maintenance. Conversely, while long daily movement distances are often viewed as diminishing the energy available for maintenance and reproduction (2), results here indicate that, in interspecific comparisons, longer daily movement distances may reflect an expansion of the energy budget, with greater investment in maintenance and reproduction. As suggested by previous work in ectotherms (39), contraction of the energy budget may be advantageous in seasonal or stochastic environments in which animals with large energy requirements are prone to starvation during food-poor periods, while expansion of the energy budget may be advantageous in more stable environments. Alternatively, decreased ranging and smaller energy budgets may be part of a risk-averse strategy focused on low-variance foods, while increased ranging and larger energy budgets are part of a risk-prone strategy of focusing on high-variance foods (40, 41). In linking expansion and contraction of the energy budget to daily movement distance, our model suggests that constraints on ranging, such as predation (4), endurance (8), or thermoregulation (32) may also constrain the energy budget.

These findings highlight the need for more direct measurements of energy budgets in wild populations. Laboratory and field studies have provided critical insight into foraging energetics and ecology within various species. Comparative efforts, using doubly labeled water (24, 25, 33) or similar techniques to measure foraging costs and benefits in a common currency of metabolic energy are necessary to understand how these species-specific strategies evolve.

Methods

We examined the relationship between mean daily movement distance with several life-history and reproduction traits for 161 mammalian species representing 7 Orders to determine whether, after controlling for phylogenetic relatedness and body mass, increased daily movement distance is associated with greater energy investment in reproduction and maintenance between species. Species means for body mass, daily movement distance, and several life-history variables were taken from the literature (ref. 6, 38,; see Table S1). Some life history traits were not available for all species (Table S1), and so sample sizes varied for each statistical test. Energy invested in reproduction was operationalized as litter mass (n = 150 species, Table S1; ref. 42) and as the mass of offspring produced per year calculated as the product of litter mass and litters per year (n = 113). Energy investment in maintenance was operationalized as expected maximum lifespan (n = 131). Combined investment in maintenance and reproduction was operationalized as total fertility (number of offspring per lifetime, n = 113) and total offspring mass (grams of offspring per lifetime, n = 111). For these lifetime investment variables we multiplied reproductive lifespan (i.e., maximum life span–age at first reproduction), by offspring per year to give total fertility or by mass of offspring per year to give total offspring mass.

Data were analyzed using phylogenetic independent contrasts (43). We used the tree topology and estimated divergence times from a recent mammal phylogeny (44) (Fig. S1). For these analyses, we transformed all variables using $\log_{10}$. This data transformation best met an important assumption of the test, the lack of relationship between the branch length and the absolute value of the standardized contrast (45, 46). We accounted for polytomies by calculating contrasts using zero branch lengths for all lineages originating from multifurcating nodes (47) and reduced the degrees of freedom accordingly. Body mass was entered as a second predictor variable in all multiple regressions to control for its effect on ranging, life-history, and reproduction. We considered outliers as data points with studentized residuals greater than ±3.0 and/or a Cook's distance greater than 1.0. If outliers were present, we reanalyzed the dataset with outliers removed. Independent contrasts were calculated using the PDAP module for Mesquite (48, 49). We used Statistica 6.0 to run the multiple regressions using independent contrasts, as well as to determine the possible presence of outliers.

Additionally, following previous workers (e.g., 6, 24, 26, 35), we analyzed the relationship between body mass, daily movement distance, and investment in reproduction and maintenance using conventional multiple regression of log10 transformed species means. Phylogenetic Order (Table S1) was entered as a fixed factor in a general linear model (SPSS 15.0) with body mass and daily movement distance entered as covariates. As in the phylogenetic contrasts analyses, we predicted that interspecific differences in daily movement distance would be positively correlated with reproductive output and maintenance (Fig. 1*B*), after controlling for the effects of body mass and phylogeny.

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