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How Far Do Animals Go? Determinants of Day Range in Mammals

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abstract: Day range (daily distance traveled) is an important measure for understanding relationships between animal distributions and food resources. However, our understanding of variation in day range across species is limited. Here we present a day range model and compare predictions against a comprehensive analysis of mammalian day range. As found in previous studies, day range scales near the 1/4 power of body mass. Also, consistent with model predictions, taxonomic groups differ in the way day range scales with mass, associated with the most common diet types and foraging habitats. Faunivores have the longest day ranges and steepest body mass scaling. Frugivores and herbivores show intermediate and low scaling exponents, respectively. Day range in primates did not scale with mass, which may be consistent with the prediction that three-dimensional foraging habitats lead to lower exponents. Day ranges increase with group size in carnivores but not in other taxonomic groups.

Keywords: day range, diet, body size, comparative methods, allometry.

Understanding the relationship between the distribution of animals and that of food resources is fundamental to ecology (Brown 1995; Gaston and Blackburn 2000). Two widely studied measures of animal distributions are population density (Damuth 1981, 1987, 1993; Carbone and Gittleman 2002) and home range (Gittleman and Harvey 1982; Mace et al. 1983; Kelt and Van Vuren 1999; Nunn and Barton 2000; Haskell et al. 2002). These measures show divergent scaling patterns (Damuth 1987), and fur-

ther research is needed to understand the relationships between them (Nunn and Barton 2000; Carbone and Gittleman 2002; Haskell et al. 2002). A third measure of space use, day range, or daily distance traveled, is very poorly studied (Garland 1983; Gittleman 1985; Wrangham et al. 1993). Day range represents a short-term measure of space requirements that at least in part reflects food resource needs (Garland 1983) and, as such, may help us to understand longer-term measures of space use such as home range and population density (Jetz et al. 2004).

Garland (1983) developed a simple model to predict variation in day range in relation to body size and tested this model using estimates of mammalian day ranges obtained from the literature. The predicted relationship between day range and body mass matched the average observed relationship remarkably well, but there was wide variation due to differences among taxonomic groups and dietary categories. Garland's article represents an important step in our understanding of patterns in day range; however, his model is based on the scaling of home range with mass, and this relationship itself is still poorly understood (Kelt and Van Vuren 1999, 2001; Nunn and Barton 2000; Haskell et al. 2002). A more parsimonious approach would be to develop a day range model based on the consumers' resource requirements and distributions. Here we develop a simple energetic model to predict patterns in day range, taking into account recent literature on scaling patterns in mammals. We then conduct an analysis of an extensive data set on day range, exploring the effects of phylogenetic and ecological factors, in order to test the model predictions.

Model of Day Range

Garland (1983) used a simple theoretical approach based on observed relationships among home range, gut capacity, and food intake to predict patterns in day range. Garland assumed that day range scales to the square root of an animal's area requirements. This assumption is used to compare relationships between one- and two-dimensional space. Home range typically scales to approximately 1.0 of body mass, or higher (Kelt and Van Vuren 2001; Haskell et al. 2002), and so day ranges derived from home range

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should scale to 0.5 of body mass. Garland also believed that large animals have relatively higher food processing rates, leading to a further reduction in the scaling of day range. He assumed this because gut capacity scales more steeply than does food intake (Davis and Golley 1963; Bourliere 1964; Calder 1974; Demment 1982; Garland 1983); however, the steeper scaling of gut capacity, rather than leading to a foraging advantage, may simply be linked with foraging constraints. For example, the quality of forage consumed by herbivores declines with increasing body size, leading to lower food passage rates (Demment 1982; Demment and Van Soest 1985; Illius and Gordon 1992). The combination of the higher scaling of gut capacity and lower scaling of passage rate results in an intake volume that scales to 0.75 of mass (Garland 1983; Gordon et al. 1996).

Here we develop a model based on the geometric relationship between an individual consumer's day range and its resource needs and resource distribution that can be adapted to predict average day ranges in predatory and herbivorous consumers. First, we define the number of items consumed per day, I, as a function of food item mass, M_i, and the consumer's food requirements, Q_c:

$$I_c = \frac{Q_c}{M_i}. \tag{1}$$

We then define the area that must be searched in order to supply the consumer's daily food requirements, A_c, in relation to intake and the density of food items, D_i:

$$A_c = \frac{I_c}{D_i}. \tag{2}$$

Prey items are qualitatively different entities for predators and herbivores, and the densities of items are accordingly defined differently for these two groups. For predators, we assume that a prey item is an individual animal and that for cases where prey live in groups, only one individual is taken per group attacked. The effective density of prey items is thus given by

$$D_i = \frac{D_i'}{G_i}, \tag{3}$$

where D_i' is the density of individuals and G_i is the average group size of the prey.

For herbivores, we define a food item as a bite, and the density of items is therefore calculated as the quotient of total available plant biomass, B_i, and bite size, M_i:

$$D_i = \frac{B_i}{M_i}. \tag{4}$$

Substituting equation (1) and either equations (3) or (4) into equation (2) gives for predators and herbivores, respectively,

$$A_c = \frac{Q_c G_i}{M_i D_i'}, \tag{5a}$$

$$A_c = \frac{Q_c M_i}{M_i B_i} = \frac{Q_c}{B_i}. \tag{5b}$$

Note that in equation (5a), the term $G_i/(M_i D_i')$ represents the inverse of available resource biomass and is therefore directly equivalent to equation (5b).

Finally, using the geometric argument set out by Garland (1983), day range, R, scales with area according to the dimensionality of the foraging habitat:

$$R_c \propto A_c^{1/f}, \tag{6}$$

where $f = 2$ for two-dimensional habitat or $f = 3$ for three-dimensional habitat. Substituting these scaling relationships into the simpler form of equations (5) gives

$$R_c \propto \left(\frac{Q_c}{B_i}\right)^{1/f}. \tag{7}$$

Given these fundamental relationships (eqq. [5]), we can use known scaling rules to derive a predicted scaling relationship for day range with body mass, assuming the
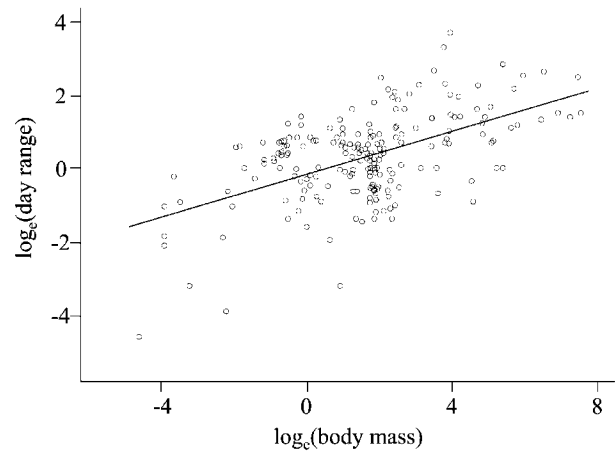

Figure 1: The $\log_e$(day range) against the $\log_e$(body mass). Each point represents a single species average. The fitted line illustrates the least squares linear regression.

Table 1: Summary of the minimum adequate ANCOVA model for $\log_e$(day range)

Variable	χ^2	df	P		Estimate	SE
					Parameter estimates	
$\log_e$(group size)	8.75	1	<.005		.197	.06
Diet	6.62	2	<.05	Faunivores	.238	.18
				Frugivores	−.321	.196
				Herbivores	−.741	.211
Order	86.8	3	<.0001	Artiodactyla	.734	…
				Carnivora	−.162	.153
				Primates	−.187	.053
				Rodentia	−.385	.06
Order × $\log_e$(body mass)	48.7	3	<.0001	Artiodactyla	.133	.128
				Carnivora	.438	.066
				Primates	.028	.063
				Rodentia	.345	.088

Note: Overall $r^2 = 59.8$. Group size and body mass are continuous variables, and their parameter estimates are therefore slopes (order-specific in the case of body mass), while diet and order are categorical variables, and their parameter estimates are therefore intercepts.

distance traveled is sufficient to provide the consumer's daily energy requirements. First, food requirements scale with consumer body mass according to

$$Q_c \propto M_c^r. \tag{8}$$

Prey item mass scales with body mass according to

$$M_i \propto M_c^p. \tag{9}$$

For predators, individual prey density scales with prey mass according to

$$D_i \propto M_i^d, \tag{10}$$

and prey group size scales with prey mass according to

$$G_i \propto M_i^g. \tag{11}$$

For herbivores, we expect the biomass of food plants to scale with consumer mass according to

$$B_i \propto M_c^b. \tag{12}$$

Substituting these scaling relationships into equations (5) and using the derivation for day range given in equation (6) gives for predators and herbivores, respectively,

$$R_c \propto \left(\frac{M_c^r M_c^{pg}}{M_c^p M_c^{pd}} \right)^{1/f} \propto M_c^{[r+p(g-d-1)]/f}, \tag{13a}$$

$$R_c \propto \left(\frac{M_c^r}{M_c^b} \right)^{1/f} \propto M_c^{(r-b)/f}. \tag{13b}$$

Note that for herbivores, the bite size scaling exponent p has no influence on the scaling of day range. This is because both food requirements, Q, and density of bites, D, are inversely related to bite size (eqq. [1], [4]), and since these terms appear on opposite sides of the area requirement quotient (eq. [5b]), the influence of bite size is cancelled out.

We base our food requirement exponent r on estimates of metabolic rate scaling exponents (Kleiber 1932; but see White and Seymour 2003); thus, we set $r = 0.75$. For the predator model, we assume that prey mass is directly proportional to predator mass ($p = 1$), as has commonly been described (Vezina 1985; Carbone et al. 1999; Cohen et al. 2003), and that prey density scales with prey mass according to $d = -0.75$ (Damuth 1981; Enquist et al. 1998). We were unable to find studies estimating the scaling of prey group size with body mass except in African bovids, where $g = 0.66$ (Brashares et al. 2000). Since some prey types may not show a grouping effect with mass (e.g., invertebrate prey), we show a range of predictions with and without this prey grouping effect (g varies from 0 to 0.66).

For the herbivore model, we expect herbage biomass to scale positively with body mass ($b > 0$; Demment and Van Soest 1985). There is little published information on the scaling of available plant biomass with herbivore mass (taking into account selectivity and digestibility); however, two studies estimate a positive scaling in North American herbivores (Belovsky 1997) and grazers in Tanzania (Wilmshurst et al. 2000) of 0.21–0.22, respectively. Thus, we used $b = 0.21$.

We use our basic model to make predictions about the effects of group size and resource density. Equation (7) predicts that day range will be inversely proportional to
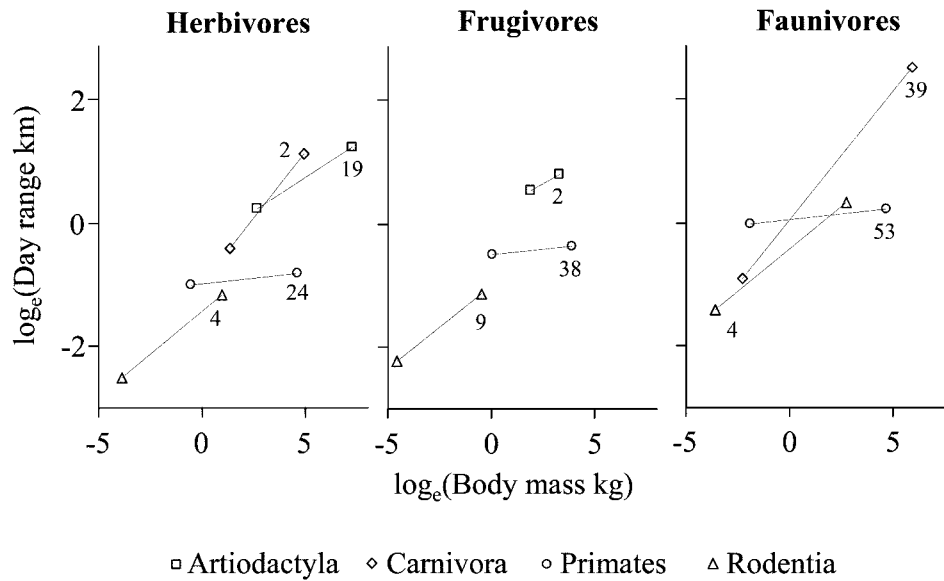
Figure 2: Slopes of day range in relation to body mass separated by diet and order, derived from ANCOVA. Numbers refer to the numbers of species in each group. Line coverage illustrates the extreme body mass values in each group.

the resource biomass density. Assuming a relationship between herbivore biomass (predator food) and plant biomass (herbivore food) of 1 : 10 (Ricklefs 1996), we might expect that day range of predators would be $10^{0.5} = 3.16$ times that of herbivores of comparable body mass and foraging habitat.

Our basic model could also be developed to look at the effect of consumers' group size (Wrangham et al. 1993), although the full development of this is beyond the scope of this article. However, assuming that grouping does not enhance feeding efficiency (Wrangham et al. 1993; Creel 1997; Packer and Caro 1997; Krause et al. 1998; Brashares et al. 2000), we would expect the day ranges of groups to increase linearly with the group size because each individual adds directly to a group's resource requirements.

Our allometric day range model (eqq. [13]) is used to make predictions of day range scaling exponents in relation to body mass and dietary strategy. For predators, including prey mass and prey density scaling relationships cited above, we predict day range to scale with body mass to 0.25–0.58 for two-dimensional habitat, without and with a prey grouping effect (e.g., most mammalian carnivores) and, correspondingly, 0.17–0.39 for a three-dimensional habitat (e.g., insectivorous bats). For herbivores, including resource distribution exponent estimates for b, we predict a day range exponent in two-dimensional habitats of 0.27 (e.g., ungulates) or in three-dimensional habitats of 0.18 (e.g., most primates).

Methods

Data for day range and other biological traits were obtained from primary and secondary sources in the literature for 200 species of mammals (see appendix in the online edition of the *American Naturalist*). We initially classified diet type into eight categories, following Robinson and Redford (1986) and Fa and Purvis (1997). Preliminary regression analysis indicated that some of the categories had very similar day ranges, whereas others were clearly different. Inspecting diet-factor-level parameter values, there were three apparent groupings (see appendix): herbivores, frugivores, and faunivore-omnivores (henceforth faunivores). Collapsing diet types into these three groups did not significantly reduce the variance explained ($F = 0.38$, df $= 5, 187$, $P > .8$), and we therefore used this grouping in all subsequent analyses. Relating these categories to the predictions of the model, we would expect patterns for herbivores and faunivores to correspond to model predictions for herbivores and predators, respectively. Frugivores do not correspond to a specific model prediction, but on the basis of resource distributions, we would expect them to be intermediate between the two other foraging modes.

For those species with more than one estimate of day range (due to differences between sexes or between study sites), the mean value was used. Continuous variables (day range, body mass, and foraging group size) were $\log_e$ transformed prior to analysis.

Table 2: Results of phylogenetic correlations between each predictor variable and day range

Trait	No. positive	No. negative	Slope[a]	t^a	Slope[b]	t^b
ln body mass	112	67	.341	7.05***	.352	7.24***
ln group size	94	63	.235	3.07**	.132	1.95
Diet	44	33	.351	3.02**	.455	4.39***
Substrate use	26	33	−.380	−2.61**	NS	NS

Note: No. positive is the number of comparisons in which the clade with the larger value of the trait also possessed the larger day range, and no. negative is the converse. *P* values for continuous variables are estimated using regression through the origin. NS indicates that a term was excluded from the model due to a lack of significance.

[a] Bivariate regression with contrasts in ln (day range).

[b] Multiple regression.

** $P < .01$.

*** $P < .0001$.

Our analyses progressed as follows. We first used non-phylogenetic linear regression (least squares and structural relations) and phylogenetically independent contrasts (Felsenstein 1985) to measure the allometric relationship between body size and day range across the whole data set. For the structural relations model, we estimated the ratio of error variance in day range to error variance in body size as 4.81, following the method of Harvey and Pagel (1991) and using additional body mass data provided by the Pantheria Project, version 1 (K. E. Jones, personal communication). We then used ANCOVA to study the correlates of day range in a multivariate context and to obtain coefficients against which to test the model's predictions. A starting model was fitted with order, diet, substrate use, group size, and body mass, as well as two-way interactions between body mass and the other four variables. Nonsignificant terms were sequentially dropped to find the minimum adequate model. Finally, we confirmed the significance of these results using independent contrasts.

Controlling for phylogeny is important because mammals with large day ranges tend to be related; the maximum likelihood estimate of Pagel's λ (Pagel 1999) for this dataset is 1.0, indicating that species' day ranges co-vary in direct proportion to their shared evolutionary history. A composite phylogeny was constructed using a variety of sources (see appendix). We treated diet (herbivore = 0, frugivore = 1, faunivore = 2) and substrate use (terrestrial = 0, intermediate = 1, arboreal = 2) as continuous variables, following Purvis et al. (2000). We used CAIC 2.6.9 (Purvis and Rambaut 1995) to calculate independent contrasts in day range and in each of the predictor variables. We found that the assumptions of Brownian motion and constancy of variance (Garland et al. 1992) are better fit using equal branch lengths, so these are used throughout. Correlations with day range contrasts were sought using regression through the origin (bivariate and multivariate).

Results and Discussion

Day range provides an important indicator of an animal's use of its environment, and we would expect it to be associated strongly with energetic requirements and to reflect the distribution of food resources and foraging strategy. Our simple model, based on assumptions about resource distributions, animal food requirements, and foraging substrate (terrestrial and arboreal), was used to make broad-scale predictions of patterns in day range.

Overall, we find that day range increases with body mass with a similar scaling exponent to that found by Garland (1983; fig. 1). Least squares regression yielded a slope of 0.29, while the structural relations model gave 0.31. The similarity of these results strongly suggests that slopes obtained using ANCOVA are not seriously underestimated (Harvey and Pagel 1991). The phylogenetic analysis yielded a slope of 0.23–0.35. These slopes are all within the range of values predicted by our model.

In the minimum adequate ANCOVA model (table 1), day range is positively related to both body mass and consumer group size, with additional effects of order and diet (fig. 2). Diet has a significant affect on the intercepts of the day range–body mass relationship. Herbivores have the lowest day ranges, frugivores are intermediate, and faunivores are most mobile for a given body mass and group size. Faunivores travel 2.66 times farther than herbivores ($e^{0.238}/e^{-0.741}$), compared with our model prediction of 3.16 times. Diet type and body mass did not interact significantly, contrary to our model prediction. However, some of the orders are composed largely of a single diet category, allowing us to test this prediction indirectly. Thus, Carnivora show the steepest increase in day range

with body mass (0.44; 95% confidence intervals 0.30–0.57; cf. model prediction of 0.25–0.58 for terrestrial carnivores without and with prey grouping), whereas primates have the shallowest slope (0.03; −0.1–0.15; cf. 0.18 for arboreal herbivores). Artiodactyla have an intermediate slope (0.13; −0.13–0.4; cf. 0.27 for terrestrial herbivores).

In our phylogenetic analysis, all four traits were associated with day range. Longer day range is correlated with large body mass, large groups, and a tendency to be faunivorous rather than herbivorous and terrestrial rather than arboreal (table 2). These findings are all consistent with our model. The relationship between day range and body mass is greatly influenced by the comparison between *Elephas* and *Dendrohyrax*. The relationship remains significant after this point is removed ($t = 4.72$, df $= 177$, $P < .0001$), but the slope is much shallower ($b = 0.23$). In a multiple regression, body mass and diet are both significantly correlated with large day range, but the effect of group size is marginal ($P = .053$), and substrate use is entirely nonsignificant ($P > .8$; table 2). Moreover, the error distribution in this model is significantly nonnormal (Shapiro-Wilks test, $P < .001$). We therefore removed three comparisons with t-deleted residuals in excess of ± 3, following Jones and Purvis (1997). Body mass and diet remain highly significant predictors of day range ($P < .0001$ in both cases), but the effect of group size disappears entirely ($b = 0.085$, $t = 1.48$, df $= 173$, $P = .14$). This model provides a better fit to the assumptions of the regression (Shapiro-Wilks test, $P = .05$). These patterns are not consistent among taxonomic groups. Within the Primates, diet, the only significant predictor of day range, explains nearly 26% of the variance in $\log_e$ day range contrasts ($b = 0.509$, $t = 5.32$, df $= 98$, $P < .0001$). Of 24 clear changes in diet within the Primates, in 20 cases the clade with a higher diet score has a larger day range (one sample sign test, $P = .002$). The situation is very different in the Carnivora, where there is little variation in diet. The multiple model for this order contains two terms: body size ($b = 0.241$, $t = 2.19$, df $= 33$, $P = .036$) and group size ($b = 0.483$, $t = 2.57$, df $= 33$, $P = .015$). Day range does not show significant scaling in the Artiodactyla.

Our phylogenetic and nonphylogenetic results are broadly consistent, which suggests that our quantitative tests of the model predictions are robust to biases due to phylogenetic history. More sophisticated comparisons among the different methods could be made using computer simulations (Garland et al. 1993).

In general, the qualitative predictions of our model match the patterns in day range scaling in relation to body mass and diet types remarkably well. Quantitatively, the slopes predicted by the model tended to be higher than the slopes observed for equivalent taxonomic groups. Heterogeneity within orders may have reduced the observed

slope. Alternatively, biological and methodological factors may have led to these differences. Mammals may adopt strategies to minimize day range. Social predators, for example, sometimes take more than one prey individual per group (Creel and Creel 2002). In addition, wide-ranging species may be harder to monitor or detect, leading to potential biases in the database.

Strictly speaking, the model was designed to predict patterns in day range in relation to diet, not taxonomic group. The main taxonomic groups used in the analysis were dominated by one particular dietary type (Carnivora being almost entirely faunivorous and Artiodactyla almost entirely herbivorous), and variation in scaling between taxonomic groups was consistent with the patterns predicted for the dietary groups most strongly associated with each taxon. However, we did not observe an independent effect of diet itself on the scaling of day range with mass. This may be because other factors that may affect day range, such as habitat type, morphology, and modes of foraging, are more consistent within taxonomic groupings than within dietary groupings.

The model predicts a relatively low scaling of day range in primates because of the three-dimensional nature of their foraging habitat in most cases. Primates were the only well-represented group not to show a significant day range scaling relationship with mass, and this result may have been confounded by the occurrence of pronounced shifts in diet and covariation of group size with body size that would affect foraging strategies and patterns of movement.

Overall, we find only limited evidence for an effect of group size on mammalian day range (except in the Carnivora). Group size is significant using a conventional statistical analysis, but the relationship is weak relative to the correlation with body mass and diet. Using independent contrasts, the effect of group size is dependent on just a few outlying comparisons. We expected that day range would increase with group size if groups effectively act as superorganisms with greater resource requirements. However, given that grouping behavior is likely to provide foraging advantages, it is perhaps not surprising that these findings are inconclusive.

Given the diverse ecologies of species included in our analysis, we might not expect the predictions of our simple day range model to match closely with all of the observed patterns in day range. However, we feel our model, which is based on a few fundamental allometric relationships, represents a useful predictive framework to understand patterns in day range scaling and could easily be adapted to explore specific factors affecting animal ranging behavior.

Acknowledgments

We thank R. Barton for statistical advice, I. Gordon for helpful comments on the model development, K. Jones for providing unpublished data from the Pantheria Project, and J. Long for help with data entry. We also thank two anonymous reviewers for helpful comments on earlier drafts of the manuscript.

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Associate Editor: Raymond B. Huey