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HOME RANGE, TIME, AND BODY SIZE IN MAMMALS[1]

STAN L. LINDSTEDT, BRIAN J. MILLER, AND STEVEN W. BUSKIRK
Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA

Abstract. The relationship between home range area and body size of terrestrial mammals is reconsidered in light of the concept of biological time. Biological time is an internal, body-mass-dependent, time scale to which the durations (or rates) of biological events are entrained. These events range from purely physiological (e.g., muscle contraction time) to purely ecological (e.g., time to traverse home range).

Evidence is presented that home range size scales linearly to body mass, for carnivores as it does for herbivores. This scaling supports the hypothesis that animals select their home range areas to meet metabolic demands integrated over biologically critical periods. Confounding variables in the home range–body mass regression include habitat productivity and methods of location. Data on home ranges derived from telemetry studies of terrestrial carnivores are presented and used to derive allometric equations for home range area. The exponents of these equations are shown to approximate 1.0, although intercept values vary with latitude and, presumably, habitat productivity. Social organization and behavior may also influence the relationship of home range area to metabolic needs for different sex and age categories within a species.

Key words: allometry; biological time; carnivores; home range; latitude; productivity.

a ~ M.
see Blackburn 96

INTRODUCTION

An animal's body size affects virtually all aspects of its morphology, physiology, and ecology. Over a quarter century ago Haldane (1956) referred to it as the most obvious distinguishing feature among animals, yet one of the least studied. Only recently have ecologists and comparative physiologists begun to investigate seriously the consequences of body size. Usually these investigations are expressed in the form of interspecific allometric (power-law) equations relating some variable (Y) to body mass (X):

$$Y = aX^b \qquad (1)$$

Often, the resultant exponents (b) are quantitatively grouped. Hence, these equations have suggested several design constraints, at least among birds and mammals. For instance, virtually all volumes or capacities of the body scale linearly with body mass. The volume of the heart or lungs, total blood volume, and tidal volume, are all a constant percentage of body size within each vertebrate class. Likewise, body mass (M) exponents describing the lengths of biological times or periods are clumped, but near ¼. (Exponents expressed as fractions are theoretical; those expressed as decimals are empirically derived.) Thus, each order of magnitude increase in body mass is accompanied by an 18% increase in the lengths of identical physiological and ecological events. The fact that there is a body mass synchrony of these biological times means that the duration of each is a constant multiple of the others. From fast cycles such as muscle contraction time or cardiac cycle time to the time of food passage through the gut, growth times, or even life-span itself, virtually all biological periods scale near $M^{¼}$ (Lindstedt and Calder

1981, Lindstedt 1985). Hence, in spite of the chronologic time over which they transpire, all mammals live a nearly constant multiple of, for example, breath time, blood circulation time, time to reach sexual maturity, or time for each gram of tissue to "burn" one joule of energy. From this constancy of volumes and synchrony of times (Stahl 1962), volume-rates such as metabolic rate or cardiac output can be derived as volume (M^1) divided by time ($M^{¼}$); these therefore scale in proportion to $M^{¾}$.

Among ecologically relevant time-scale variables, the intrinsic rate of natural increase (r) has the units of time^{-1}, and therefore scales as the inverse of biological time, $1/M^{¼} = M^{-¼}$ (Fenchel 1974). Consequently, assuming a logistic growth model, population growth times (e.g., time to population doubling) must also vary as $M^{¼}$ (Lindstedt and Calder 1981). Population cycles of growth and decline also occur with periods near $M^{¼}$ (Calder 1983). These are examples of a large number of parameters of life history and ecology which are body-size dependent (see Blueweiss et al. 1978, Western 1979, Peters 1983, Calder 1984).

The area of an animal's home range (A_{hr}) is likewise body-size dependent. In a now classic paper, McNab (1963) reported that:

$$A_{hr} = 2.70 \, M^{0.63} \qquad (2)$$

(To standardize equations from different sources, we have expressed all equations in the following units: A_{hr} in hectares and M in kilograms.) As home range is a measure of available energy, this suggested to McNab that the area over which an animal is foraging or hunting should be linearly proportional to its metabolic rate. Inasmuch as basal metabolism scales as $M^{¾}$, he examined Eq. 2 and found that the 95% confidence interval of the slope included 0.75. Thus, he accepted

0.63 ± at least 0.12 Oh dear

the hypothesis that metabolic rate determines, and is linearly proportional to, home range in mammals. In the past two decades many more data have become available, permitting this relationship to be re-examined. Buskirk (cited in Calder [1974]) examined the home range of "primary consumers" and found:

$$A_{hr} = 4.7M^{1.02} \quad r^2 = 0.87, \, N = 32 \quad (3)$$

Subsequently Harestad and Bunnell (1979) separated the data by trophic status and likewise reported higher exponents. They noted that the 95% confidence intervals of the slopes for both herbivores and carnivores *wow!* → did *not* include 0.75. If not metabolic rate, then what are the criteria that determine home range size? In this paper we argue that home range is a linear function of body size because the timing of physiological and ecological processes is scaled to body mass as $M^{1/4}$.

ANALYSIS AND RESULTS

An animal's net energy intake is a complex function of nutritional adaptations and availability of food. Nevertheless, a home range contains a finite potential energy resource which is proportional to its area. Assuming no difference in habitat patches, doubling of home range will result in a doubling of an animal's potential energy base, although its net energy intake may not double. Home range is therefore a measure of energy availability, and it can be expressed in units of energy (E), inasmuch as an animal has access to the average standing crop of food in its home range. The conclusion is unaltered if we consider the renewal rate of food inasmuch as "the higher the productivity of a community, the greater the amount that is likely to accumulate as biomass," (Lieth 1975:206).

Metabolic rate is a measure of energy use (or power) and has units of energy divided by time. The quotient of home range divided by metabolic rate is not dimensionless, but has units of time. Thus it is not physically possible to equate metabolic rate ($\dot{E}$) with home range area (A_{hr}), without first considering their dimensional incompatibility. To convert both to units of energy, metabolic rate must be multiplied by some measure of time (t).

$$A_{hr} \propto E = \dot{E} \cdot t \quad (4)$$

There are two potential time scales important in determining home range; the most obvious is chronologic time (t_c). If an animal selected the size of its home range in proportion to its daily or yearly energy demands, then home range should scale in proportion to metabolic rate multiplied by chronologic time. Because chronologic time is obviously body-size independent ($t_c \propto M^0$), we would predict home ranges to scale as:

$$M^{3/4}(\dot{E}) \times M^0(t_c) = M^{3/4}(A_{hr}) \quad (5)$$

Another possibility is that animals may measure time by *biologically* meaningful units. As mentioned above, physiological and ecological time is body-size depen-

dent, scaling near $M^{1/4}$. Among the periods that could be critical in determining an animal's energy demands, and therefore its home range, may be: gestation period (days) = $66.2 \, M^{0.26}$, growth to 50% adult size (months) = $4.29 \, M^{0.25}$ (Calder 1982a), or time for each gram of animal tissue to exhaust a finite energy source. These are only some examples of size-dependent biological time, which apparently sets the pace of biological function at all the levels of organization from single tissues to populations of organisms (Lindstedt and Calder 1981, Calder 1984, Lindstedt 1985). Thus, if biological time (t_b) is incorporated in place of chronologic time, then home range should scale as:

$$M^{3/4}(\dot{E}) \times M^{1/4}(t_b) = M^1(A_{hr}) \quad (6)$$

Harestad and Bunnell (1979) reported the following results relating home range to body mass in mammals:

$$\text{Herbivores: } A_{hr} = 2.71M^{1.02} \quad (7)$$
$$r^2 = 0.75, \quad N = 28$$
$$\text{Omnivores: } A_{hr} = 3.4M^{0.92} \quad (8)$$
$$r^2 = 0.90, \quad N = 7$$
$$\text{Carnivores: } A_{hr} = 137M^{1.37} \quad (9)$$
$$r^2 = 0.81, \quad N = 20$$

(Harestad and Bunnell made an arithmetic error in their calculation of carnivore home range size. We have recalculated the equation, using their data, and found a decimal point error in the intercept [a] and an insignificant error in the exponent [b]. The correct equation appears above. Thus their results, and the discussion of those results, are based on 10-fold overestimates of carnivore home range sizes.)

The disproportionate increase in home range, relative to metabolic rate, suggested to Harestad and Bunnell a body-size-dependent decrease in food density. Thus, they hypothesized that the "relative productivity of the habitat" must decrease as body size increases. However, the magnitude of this postulated productivity scaling seems very large to us. According to their model, the relative productivity of the habitat of a vole (in kilograms per square kilometre per year) would have to be >10 times greater than that of a sympatric bison, though both may feed on the same grass species. Likewise, according to their prediction, a marten's habitat must be about five times more productive than that of a bobcat. However, the habitats of large and small carnivores appear to be about equally productive, for two reasons. First, large carnivores can utilize a broader range of potential prey sizes than do the smallest carnivores (Peters 1983), which are restricted to preying on the smallest mammal herbivores extant. Second, the productivity of those smallest herbivores is likely no greater than that of large herbivores. Eisenberg et al. (1979) reported productivity values of 10 species of mammals spanning three orders of magnitude in body mass. In analyzing their data, we found little correlation ($r^2 = 0.06$) between body mass and

TABLE 1. Home range areas (A_{hr}), body masses, and geographic latitudes of study sites for terrestrial carnivores.

Species	Sex	Body mass (kg)	A_{hr} (ha)	Method*	Latitude (°N)	Reference
Felis concolor	M	71	32 000	T	44.2	Logan 1983
	F	41	6730	T	44.2	Logan 1983
Canis lupus	B	45	5700	T	60.8	Peterson et al. 1984
	B	33	6800	T	48.0	Fritts and Mech 1981
Canis latrans	M	12.5	2820	T	40.9	Andelt and Gipson 1979
	F	11.5	2420	T	40.9	Andelt and Gipson 1979
	M	12.5	6800	T	48.0	Berg and Chesness 1978
	F	11.5	1600	T	48.0	Berg and Chesness 1978
Gulo gulo	M	14	42 200	T	48.8	Hornocker and Hash 1981
	F	10	38 800	T	48.8	Hornocker and Hash 1981
Lynx rufus	M	12.0	494	T	30.5	Hall and Newsom 1976
	M	12.0	4210	T	48.0	Bailey 1974
	F	9.0	1930	T	48.0	Bailey 1974
Taxidea taxus	M	7.6	583	T	42.0	Lindzey 1978
	F	6.3	237	T	42.0	Lindzey 1978
Procyon lotor	B	6.4	49	T	41.6	Urban 1970
Vulpes vulpes	M	5.6	395	T	37.3	Storm 1965
	M	5.6	1967	T	59.8	Jones and Theberge 1982
	F	4.5	1137	T	59.8	Jones and Theberge 1982
Martes pennanti	M	3.7	1402	T	41.2	Buck et al. 1979
	F	1.9	522	T	41.2	Buck et al. 1979
	M	4.6	2000	T	44.7	Kelly 1977
	F	2.1	1500	T	44.7	Kelly 1977
Alopex lagopus	B	3.6	2080	T	70.3	Eberhardt et al. 1982
Urocyon cinereoargenteus	M	3.7	137	T	37.3	Follmann 1973
	F	3.5	107	T	37.3	Follmann 1973
	M	3.7	102	T	37.5	Trapp 1978
	F	3.5	113	T	37.5	Trapp 1978
Martes americana	M	1.3	682	T	63.0	Buskirk 1983
	F	0.93	371	T	63.0	Buskirk 1983
	M	0.99	369	T	39.2	Simon 1980
	F	0.63	308	T	39.2	Simon 1980
Bassariscus astutus	M	1.0	43	T	30.0	Toweill and Teer 1980
	F	0.9	20	T	30.0	Toweill and Teer 1980
Mustela nivalis	M	0.11	11	C	51.7	King 1975
	F	0.06	2.5	C	51.7	King 1975
Mustela erminea	M	0.08	16.3	C	43.8	Simms 1979
	F	0.06	11.7	C	43.8	Simms 1979

* T = telemetry, C = capture-recapture.

productivity (expressed as kilograms of animal biomass per square kilometre per year). While habitat productivity certainly varies geographically and among species, we question if indeed it scales systematically to herbivore or carnivore body size. Instead, we view Eqs. 3, 7, and 8 as supporting the importance of biological time in determining home range dimensions.

We believe the carnivore data (Eq. 9) contain two complicating variables compared to those for herbivores. First, the methodologies used in studies of carnivore movements affect resultant home range sizes and are body size dependent. Radiotelemetry produces larger calculated home range areas than does trapping (Trevor-Deutsch and Hackett 1980) and has been used more extensively on large-bodied carnivores than on small ones. Second, because human beings have worked diligently to exterminate large carnivores at temperate latitudes, a high proportion of data for large

carnivores comes from areas with low human population densities, such as high latitudes, where productivity is low (Bray and Gorham 1964). The negative correlation between net productivity and home range size is well documented (King 1975, Eisenberg 1981). These uncorrected variables may explain the apparently steeper slope of carnivore home range size. Both variables tend to produce high values for home range areas of large carnivores and "rotate" the least squares line above a slope of 1.0.

To eliminate the effects of these confounding variables, we have recalculated the relationship between home range area and body mass, using, wherever possible, values for adults from North American telemetry studies and dividing them into two groups based upon geographic latitude, both containing the same range of body sizes (Table 1). We deleted bears from the data set because of the high proportion of plant material in

their diets. Capture-recapture values for weasels were included because they extended the size range of the sample and would, if anything, tend to increase the regression coefficient, making our hypothesis less easily defended. Home range areas of social species were divided by mean group size. Body masses, when not available from home range references, were taken from Chapman and Feldhamer (1982) or Eisenberg (1981).

Carnivores (all): $A_{hr} = 170M^{1.03}$ (10)

$N^* = 38$ $r^2 = 0.66$

Carnivores ($\leq 45°$ latitude): $A_{hr} = 115M^{0.94}$ (11)

$N^* = 23$ $r^2 = 0.61$

Carnivores ($> 45°$ latitude): $A_{hr} = 339M^{1.08}$ (12)

$N^* = 15$ $r^2 = 0.79$

*N = number of mean home range determinations.

Carnivore home range areas scale linearly to body mass (Fig. 1). The 90% confidence interval around the slope of the regression line for all carnivores (0.82–1.24) includes neither 0.75 nor 1.33. When grouped by geographic latitude the groups also scale near 1.0, but carnivores from high latitudes have much larger home ranges than those from temperate latitudes (Fig. 2; cf. Eisenberg 1981: Fig. 47).

Recently Gittleman and Harvey (1982) re-examined the size of home ranges, restricting their investigation to species in the order Carnivora. Like Harestad and Bunnell (1979), they predicted a linear relationship between home range and metabolic rate (calculated as $M^{3/4}$) and thus compared the two directly rather than expressing each as a function of body size. (Therefore their analysis also contains either a dimensional error or an inherent, unexpressed dimension of chronologic
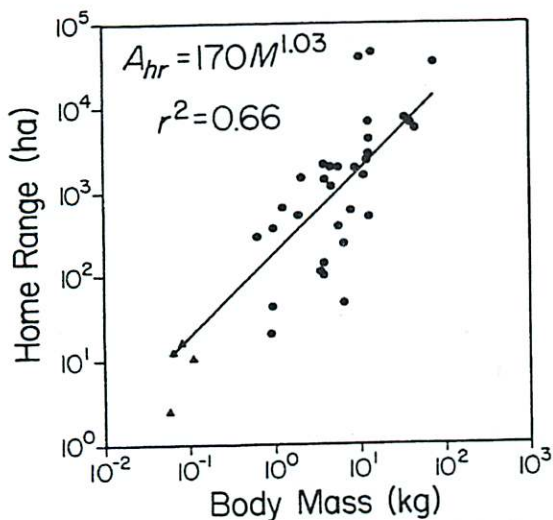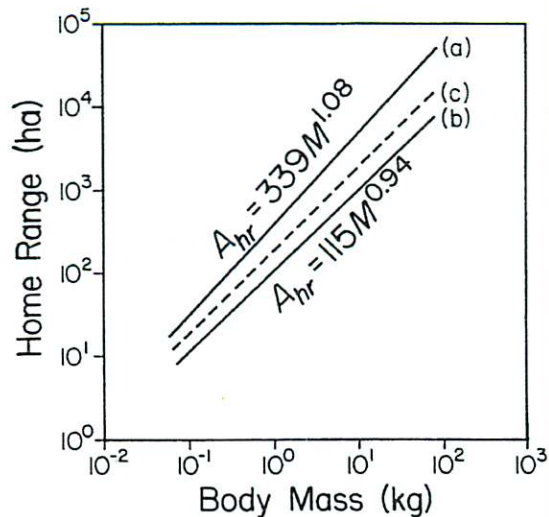

FIG. 2. Regressions of home range areas on body mass for (a) terrestrial carnivores studied at latitudes >45° and (b) terrestrial carnivores studied at latitudes ≤45°. The regression line for terrestrial carnivores studied at all latitudes (c) is shown for comparison.

time.) To correct for group size, they calculated "standardized metabolic needs" as group size times $M^{3/4}$ (although they could also have divided the group home range by group size), which produced a new measure of metabolic rate ($\dot{E}$). In addition they used median rather than mean home range areas whenever possible, which effectively buffered the effects of including outlying values from very low-productivity environments (e.g., extreme northern latitudes). Although they cautioned that the highly variable behavior among carnivores may confound interspecific comparisons, they were still able to demonstrate a highly significant ($P < .001$) correlation between group home range area and standardized metabolic requirements.

$$A_{hr} \propto \dot{E}^{1.33}   r^2 = 0.44, N = 43   (13)$$

Like McNab, they reasoned that because the 95% confidence interval of the slope included the predicted 1.0, home range could be explained as a linear function of metabolic rate. However, if biological rather than chronologic time is the critical time element, how should group home range vary as a function of standardized metabolic rate? As $\dot{E} \propto M^{3/4}$ and $t_b \propto M^{1/4}$, then $M \propto \dot{E}^{4/3}$ and $t_b \propto (\dot{E}^{4/3})^{1/4} = \dot{E}^{1/3}$, so:

$$A_{hr} \propto \dot{E} \cdot t_b = \dot{E} \cdot \dot{E}^{1/3} = \dot{E}^{4/3},   (14)$$

precisely the relation reported by Gittleman and Harvey.

Home ranges of carnivores are much larger than those of similar-sized herbivores, but within each trophic level home range areas scale linearly with body size. This implies to us that an animal sets the size of its home range to ensure adequate energy to last for the duration of critical biological time periods, rather than chronologic times of days or years.

FIG. 1. Regression of home range area (A_{hr}) on body mass (M) for terrestrial carnivores. ● home range areas determined from radiotelemetry. ▲ home range areas determined from capture-recapture techniques.

DISCUSSION

Allometric equations describe patterns, but they are not precise predictive laws. Additional data could modify the above equations. For instance, as the time to harvest available energy increases (e.g., in large animals), so does the time for replacement of the energy resource within the home range. Further, while both basal and maximal metabolism scale near $M^{3/4}$, "existence" energy may scale with a lower exponent (King 1974). Finally, social interaction and behavior (Gittleman and Harvey 1982), habitat productivity, and investigative methods (Laundré and Keller 1984) are complicating factors in determining home range size. For instance, observed sexual differences in home range size often exceed that predicted by size dimorphism alone. Indeed, a male carnivore's (territorial) home range may include those of several females. Yet since the young are frequently dependent on the mother during and after lactation, the female has higher energy requirements. Ackerman (1982) reported that female mountain lions with two or three yearlings must consume 12 kg of food per day, whereas a single male needs only 4 kg. Although a female's home range must meet her higher energy requirements, males range farther, presumably to increase their likelihood of breeding successfully. Considering only energetics, females and accompanying offspring should have larger home ranges than males.

Home range area may also vary as a function of age class within a species. Subadults may disperse and be forced to live as transients until they can establish themselves socially. They may be forced to live in suboptimal habitat because more dominant individuals exclude them from preferred areas. In addition, subadults may need more nutrients for growth, yet lack food-gathering skills. These factors appear to favor larger home ranges. Thus, behavior and social organization play an important role in determining home range area within a species.

Inasmuch as home range area is a measure of energy available to an animal, it is also to be expected that productivity and biomass density of food will strongly influence the size of the area that an animal will regularly cover. Productivity, in turn, is a function of latitude, elevation, and other geographic variables. Only by controlling the more influential of these is it possible to place confidence in a home range–body size regression coefficient. Confounding methodological variables include techniques (e.g., capture) used to gather spatial data and the various means by which these data are interpreted (and reported) as home ranges. We believe that it is these variables that produced the regression coefficient > 1.0 reported by Harestad and Bunnell (1979).

In spite of the above caveats, repeated patterns (including simplifying assumptions) still provide the strongest evidence on which models should be built

and modified. The current model (suggested previously, Lindstedt and Calder 1981, Calder 1982b) is a simple explanation that seems to describe observed allometric patterns of home range area in mammals. With additional data, the inclusion of social and behavioral interactions could refine the model.

The relations between home range, metabolic requirements, and biological time are so consistent that all mammals appear to select the size of their home ranges to ensure survival through critical biological periods. Physiological and ecological times, such as gestation or lactation periods, time to reach independence or adult size, or even life-span itself appear to outweigh chronological times of days or years in determining the size of the energy base needed by an animal.

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