Nonlinear scaling of space use in human hunter-gatherers

Marcus J. Hamilton, Bruce T. Milne, Robert S. Walker, and James H. Brown

This information is current as of March 2007.

Notes:

Nonlinear scaling of space use in human hunter–gatherers

Marcus J. Hamilton*†, Bruce T. Milne‡, Robert S. Walker§, and James H. Brown‡¶

Departments of *Anthropology and ‡Biology, University of New Mexico, Albuquerque, NM 87131; §Department of Anthropology, University of Colorado at Denver and Health Sciences Center, Denver, CO 80217; and ¶Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501

Use of space by both humans and other mammals should reflect underlying physiological, ecological, and behavioral processes. In particular, the space used by an individual for its normal activities should reflect the interplay of three constraints: (*i*) metabolic resource demand, (*ii*) environmental resource supply, and (*iii*) social behaviors that determine the extent to which space is used exclusively or shared with other individuals. In wild mammals, there is an allometric scaling relation between the home range of an individual and its body size: Larger mammals require more space per individual, but this relation is additionally modified by productivity of the environment, trophic niche, sociality, and ability to defend a territory [Kelt DA, Van Vuren D (1999) *Ecology* 80: 337–340; Kelt DA, Van Vuren D (2001) *Am Nat* 157:637–645; Haskell JP, Ritchie ME, Olff H (2002) *Nature* 418:527–530; Damuth J (1987) *Biol J Linn Soc* 31:193–246; Damuth J (1981) *Nature* 290:699–700; and other previously published work]. In this paper we show how similar factors affect use of space by human hunter–gatherers, resulting in a nonlinear scaling relation between area used per individual and population size. The scaling exponent is less than one, so the area required by an average individual decreases with increasing population size, because social networks of material and information exchange introduce an economy of scale.

home range | macroecology | scaling theory | social networks

The ecology of all organisms is powerfully constrained by the exchange of energy and matter with the environment to meet metabolic resource demands. The ecology of human hunter–gatherers is particularly interesting, because social organization influences the uptake of energy, materials, and information from the environment and the distribution and transformation of these commodities within societies. Elsewhere we used Horton–Strahler network theory to show how individual hunter–gatherers self-organize into social groups that facilitate the flow of fitness-related commodities among individuals at different hierarchical levels. The result is a complex social structure in which resources flow through social networks, which exhibit self-similar or fractal-like hierarchical scaling (M.J.H., B.T.M., R.S.W., and J.H.B., unpublished work) and are strikingly similar, quantitatively, to the hierarchically branched vascular networks that distribute metabolic resources within the bodies of plants (2, 3) and mammals (4, 5) and water within river drainage basins (6).

Anthropologists have long been interested in the interplay of social structure, environmental conditions, and cultural factors on hunter–gatherer population size and demography (7–10). Here we investigate how the complex social networks of hunter–gatherer societies reflect the spatial and temporal scaling of rates of exchange of energy, matter, and information among individuals and how these interactions result in nonlinearities between human societies and their resource base. Well established macroecological scaling relations based on the first principles of physics, chemistry, and biology can account for much of the variation in the use of space by wild mammals. Here we ask how this framework must be modified to apply to traditional human societies.

Like all biological species, human hunter–gatherers harvest energy and material resources from the environment to meet their metabolic requirements. For all mammals, including humans, energy requirements are set by whole-organism metabolic rate, B (in W), which scales with body size, M (in kg) as given by the following:

$$B = B_0 M^{3/4}, \qquad [1]$$

where B_0 is a normalization constant. The scaling relation described by Eq. **1** holds greater than eight orders of magnitude, from shrews to whales (4, 5, 11). In age-structured populations, whole-organism metabolic demand is age-specific due to variation in body size and changes in the allocation of energy to maintenance, growth, and reproduction over the lifespan (12–15). So individual metabolic demand averaged over all individuals within a population is better approximated by the following expectation:

$$\langle B \rangle = \langle B_0 M^{3/4} \rangle = 1/N \sum_{i=1}^{N} (B_0 M_i^{3/4}). \qquad [2]$$

The metabolic demand of a population of size N is then $N\langle B \rangle = N\langle B_0 M^{3/4} \rangle$.

In this paper, we follow the definition used by animal ecologists and refer to the space used by an individual or social group as its home range. The home range, H_0 (area in km²), required by an individual to meet its metabolic requirements is determined primarily by the rate of resource supply, R (in W/km²). Because humans feed on animal and plant foods, rates of resource supply, like most biological rates, increase exponentially with ecosystem temperature. Ecosystem temperature affects rates of biological production and interaction at multiple levels, including biomass production, ontogenetic and population growth rates, timing of life history events, and interactions with parasites and diseases. Much of this variation is captured by the Boltzmann factor, $e^{-E/kt}$, where E (in eV) is the activation energy for the rate limiting biochemical reactions of metabolism, k (8.62×10^{-5} eV K⁻¹) is Boltzmann's constant, and T (in K) is temperature (16–18). Therefore, to meet metabolic requirements the home range, H_0, must be

$$H_0 \geq \langle B \rangle R^{-1} e^{E/kT}. \qquad [3]$$

Because the average metabolic demand of an individual, $\langle B \rangle$, is a constant, Eq. **3** predicts that home range size should decrease exponentially with temperature, $1/kT$, at a rate E because of the

ANTHROPOLOGY

ANTHROPOLOGY

inverse scaling of resource supply rate with respect to ecosystem temperature.

If home range is determined primarily by resource availability, then the minimum size of the area, A, in km^2, required by a hunter–gatherer population of size N to meet metabolic requirements is then

$$A \geq H_0 N^\beta = \langle B \rangle \, R^{-1} \, N^\beta \, e^{E/kT}, \qquad [4]$$

where β is a scaling exponent: If area of space used by a population, A, simply reflects the linear sum of metabolic demands of N individuals, then $\beta = 1$. Note that when $\beta = 1$, Eq. **4** can be rearranged to show that inverse density, the average area per individual, is equivalent to home range: $D^{-1} = A/N = H_0$. If $\beta > 1$, then the area per individual, D^{-1}, increases with increasing population size, and if $\beta > 1$, D^{-1} decreases with population size. In general, if $\beta \neq 1$, the scaling relation between space use and metabolic demand is nonlinear and density-dependent.

In this paper, we examine macroecological scaling relations between hunter–gatherer space use, population size, and resource supply rate by fitting Eq. **4** to empirical data. We also consider the residual variation due to effects of foraging niche, environmental productivity, cultural phylogeny, and spatial autocorrelation on the area used by each population. We first use least-squares regression to fit a power–law relationship for the overall scaling of the area used by a population, A, with population size, N. Then we analyze effects of trophic foraging niche and ecosystem temperature on space use. Finally, we control for the additional effects of resource supply, cultural phylogeny, and spatial autocorrelation by using a mixed linear model to obtain more accurate estimates of both the scaling exponent, β, and the temperature dependence, E of hunter–gatherer space use.

We make three predictions: (*i*) If the area of space used simply reflects the sum of individual metabolic requirements, then the scaling of area with population size should be linear, $\beta = 1$. (*ii*) Residual variation should be temperature-dependent because of differences in ecological, elevational, and geographic settings. Residual temperature dependence should be reflected in an activation energy E, which for terrestrial ecosystems should be between primary production, ≈ 0.3 eV, and respiration, ≈ 0.7 eV (19). (*iii*) Residual variation in space use should additionally be due to trophic foraging level, measured as the relative contribution of terrestrial and aquatic food items to the diet. In particular, because of energy transfer inefficiencies between trophic levels in ecosystems and differences in resource distributions, we predict that animal hunters require more space per individual and have steeper scaling relations than plant gatherers, similar to differences in home range size between mammalian carnivores and herbivores (20, 21). In addition, we predict that aquatic foragers will require smaller home ranges than terrestrial foragers because of the generally higher predictability and productivity of marine, intertidal, and freshwater invertebrates, fish, and mammals, and to the limited land area required to access these resources.

Data

We used a recently available compilation of hunter–gatherer ethnographic data that contains information on many population, subsistence, ecological, geographic, and environmental parameters (22). This data set is a global sample of 339 hunter–gatherer societies representing diverse geographic, ecological, and cultural conditions. A sample size this large is rare in cross-cultural studies and allows for powerful quantitative statistical analyses. The original data were obtained from published ethnographies (22), which undoubtedly varied in methodology. However, we assume that parameter estimates within each of
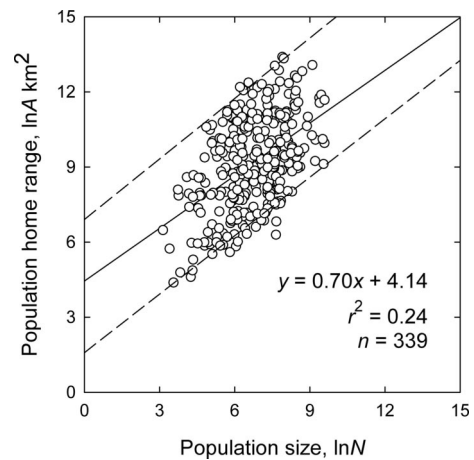
Fig. 1. Log–log plot of area of space used, ln$A$, as a function of population size, ln$N$. The solid line is the least-squares regression fitted to the entire data set. The dashed lines are upper and lower boundaries reflecting constraints on the scaling relation. See *Home Range Size/Population Size Scaling* for details. All three slopes are close to parallel suggesting that (*i*) the least squares regression fits the linear trend of the log-transformed data reasonably well; (*ii*) the scaling is nonlinear, so the slope or scaling exponent is <1; and (*iii*) there are relatively well defined upper and lower constraints on hunter–gatherer space use. However, for any given population size, N, there are ≈ 2 orders of magnitude variation in home range area, ln$A$, suggesting that there is much interesting residual variation likely due to ecological and cultural factors.

these ethnographies are independent and unbiased, because they were obtained by different original investigators. Therefore, errors in these estimates will also be independent and unbiased, allowing underlying statistical trends to be recovered despite variation due to methodology and other uncontrolled and unreported factors.

Results

Home Range Size/Population Size Scaling. Fig. 1 shows that our first prediction is not met, because the area of space used increases allometrically rather than isometrically (linearly) with increasing population size. The scaling exponent, $\beta_N = 0.70$ (0.58–0.83, 95% confidence limits), which is significantly different from 1. Although there is a great deal of residual variation ($r^2 = 0.24$, $F_{1,338} = 105.8$, $P < 0.0001$), the regression model fits the trend of the data reasonably well. This fit is shown by the fact that the upper and lower bounds of the data are approximately parallel to each other and to the overall slope ($\beta_{upper} = 0.81$ and $\beta_{lower} = 0.78$; both significantly <1 but not significantly different from $\beta_N = 0.70$). Upper and lower boundaries were estimated by binning the x axis into widths of $1 \ln N$ and by fitting regressions to maximum and minimum home range sizes for each bin (11, 23). The well defined upper and lower boundaries suggest ecological and physiological constraints on hunter–gatherer spatial scaling relations.

Trophic Foraging Level. Fig. 2 shows the original data decomposed by trophic foraging niche into four plots: hunters, gatherers, aquatic foragers, and terrestrial foragers (hunters and gatherers combined). These groups are determined by their dominant mode of subsistence, defined as >40% contribution from hunting, gathering, or aquatic resources. The results are detailed in Table 1. The slopes for all primary scaling models are <1, although the 95% confidence limits for the hunters and aquatic foragers include 1. As predicted, the slope for the hunters ($\beta_H = 0.90$) is significantly steeper than the gatherers ($\beta_G = 0.64$). The difference between these slopes may be due, in part, to fundamental differences in the distribution of animal and plant resources on landscapes. Because animal resources are, in gen-

Fig. 2. Log–log plots of hunter–gatherer spatial scaling relations by trophic foraging niche. (*Upper Left*) Hunters, *n* = 80. (*Upper Right*) Gatherers, *n* = 142. (*Lower Left*) Aquatic foragers, *n* = 117. (*Lower Right*) Terrestrial foragers, *n* = 222. Solid lines are least-squares regression estimates of the slope of the scaling function, and dashed lines are estimates of the upper and lower constraints to the function. See Table 1 for further details.

Fig. 3. Arrhenius plots of the residuals from Fig. 2 as a function of absolute temperature in units of $1/kT$, by trophic foraging niche. (*Upper*) Terrestrial foragers, *n* = 222. (*Lower*) Aquatic foragers, *n* = 117. Because the *x* axis reflects inverse temperature, the residuals are lower, indicating groups of comparable size use smaller areas in warmer environments.

eral, more localized and occur at lower densities than plant resources, their distributions are quantitatively different. This difference in resource distribution is characterized by a lower fractal dimension for animal resources than for plants, which affects encounter rates, requiring hunters to forage over larger areas than gatherers to meet similar metabolic requirements (21). Also as predicted, aquatic foragers require less space per individual than either the hunters or the gatherers, but the slope ($\beta_A = 0.78$) is not significantly different. Combining the hunters and gatherers into a terrestrial forager category shows that they tend to use absolutely more space than aquatic foragers, al-

though the slope of the relationship is nearly parallel ($\beta_T = 0.79$ and $\beta_A = 0.78$, respectively).

To examine variation in ecosystem resource supply rate due to variation in environmental temperature, we plot the residuals around the regression lines for terrestrial and aquatic foragers as a function of inverse temperature (an Arrhenius plot, Fig. 3). Both relationships are highly significant. As predicted, the activation energy for terrestrial foragers, $E = 0.55$ eV is somewhat less than for aquatic foragers, $E = 0.68$ eV, reflecting the

Table 1. Summary of scaling relations for area of space used as a function of group size

Model	Coefficient	β	SE	95% CL	C_0	SE	95% CL	r^2
All foragers	β_N	0.70	0.07	0.57–0.84	4.44	0.47	3.51–5.37	0.24
	β_{upper}	0.80	—	—	—	—	—	—
	β_{lower}	0.77	—	—	—	—	—	—
Hunters	β_H	0.90	0.10	0.71–1.10	4.46	0.66	3.14–5.78	0.52
	β_{upper}	0.76	—	—	—	—	—	—
	β_{lower}	1.06	—	—	—	—	—	—
Gatherers	β_G	0.64	0.10	0.44–0.84	4.61	0.66	3.30–5.92	0.22
	β_{upper}	0.83	—	—	—	—	—	—
	β_{lower}	0.60	—	—	—	—	—	—
Aquatic foragers	β_A	0.78	0.11	0.56–1.00	3.24	0.79	1.65–4.83	0.31
	β_{upper}	0.32	—	—	—	—	—	—
	β_{lower}	0.91	—	—	—	—	—	—
Terrestrial foragers	β_T	0.79	0.08	0.63–0.96	4.17	0.56	3.05–5.28	0.29
	β_{upper}	0.83	—	—	—	—	—	—
	β_{lower}	1.01	—	—	—	—	—	—
Mixed model	β_{MLM}	0.76	0.04	0.68–0.84	−9.16	4.38	−9.23 to −30.31	0.86

Data is shown for all hunter–gatherer societies in the data set (row 1), for subsets of these data based on foraging niche (rows 2–5), and for the complete mixed model that adjusts for variables that affect rates of resource supply (row 6). CL, confidence limits.

Table 2. Contributions of variables that index potentially important ecological and geographic factors

Factors	df	F	P	Coefficient	SE	P
Intercept	—	—	—	−9.156	4.383	0.038
ln$N$	1	315.40	0.000	0.756	0.043	0.000
E	1	12.65	0.000	0.380	0.107	0.000
AET	1	30.81	0.000	−0.002	<0.001	0.000
AQ	1	88.86	0.000	−0.025	0.003	0.000
CONT	5	1.19	0.317	—	—	—
LOC(CONT)	60	5.71	0.000	—	—	—

Variables contribute to linear models and account for residual variation in the relationship between home range area and group size for human hunter–gatherers. E, activation energy; AET, actual evapotranspiration; AQ, aquatic foods; CONT, continent; LOC(CONT), geographic location within continent. $r^2 = 0.86$, $P < 0.0001$.

combined contribution of plants and animals (and an intermediate activation energy between photosynthesis and respiration) to the diets of terrestrial foragers compared with the primarily animal diet (and the activation energy for respiration) of the aquatic foragers.

Mixed Linear Model. We combine the above information into a mixed linear model that allows us to estimate both the scaling coefficient and temperature dependence, while controlling for trophic effects, other ecological factors, and additional cultural and spatial information. First, we address the issue that, for cross-cultural studies, individual societies rarely meet the statistical assumption of independence due to shared cultural phylogenetic histories (24). This phenomenon is known as Galton's Problem in anthropology. Cross-cultural studies commonly use linguistic phylogenetic trees to control for cultural phylogeny. However, there are no resolved linguistic trees that adequately cover our global sample of hunter–gatherers. A corollary of Galton's Problem is that human societies are often spatially autocorrelated. Therefore, we control for the effects of cultural phylogeny by nesting geographic factors in the model. At the broadest scale, shared cultural phylogenies may be apparent within continents, reflecting prehistoric colonization events. Consequently, for each population we include continent as a fixed effect. Additionally, cultural traits shared among local neighboring populations may result in spatial autocorrelation at a finer regional scale. We include geographic location as a random effect in the model, coding this as the present-day country (within the continents of Africa, Eurasia, and South America) or state (within North America and Australia) where the population occurs. Because geographic locations occur within continents, we maximize the available degrees of freedom by nesting the random effect within the fixed effect.

In addition to population size and absolute temperature as covariates, for each society we also include actual evapotranspiration (AET) as a measure of primary productivity. AET is a measure of energy availability within an ecosystem and should account for aspects of ecosystem productivity not captured by absolute temperature. We also include the relative proportion of aquatic resources to the diet. We include only the effect of aquatic resources, because dietary resources are either terrestrial or aquatic; by using only one measure, we avoid both redundancy and colinearity.

Results of the mixed model are summarized in Table 2. By combining all covariates and factors into a single model, we can explain 86% of the variation in population home range area, A. The scaling coefficient remains significantly different from 1 at $\beta_{MLM} = 0.756 \pm 0.042$. The average activation energy, $E = 0.38 \pm 0.11$ eV, is consistent with the temperature dependence of primary production in terrestrial ecosystems (19). As shown

by comparing the F statistics in Table 2, population size accounts for the vast majority of variation in the model, followed in order by amount of aquatic resources in the diet, actual evapotranspiration, ecosystem temperature, and geographic location. As predicted, area of space used decreases with increasing proportion of aquatic resources in the diet. This is undoubtedly due to the fact that aquatic resources, such as invertebrates, fish, and mammals, are often highly predictable, concentrated, and foraged from areas of shore or water that may not be directly comparable to the foraging areas of terrestrial hunter–gatherers. Also as predicted, home range area decreases significantly with increasing actual evapotranspiration, a measure of ecosystem primary productivity and hence of energy supply.

Of the variables used to index cultural phylogenetic relationships, continent is not significant, but the geographic location term nested within continent is highly significant, suggesting spatial autocorrelation among and within populations. Whether this autocorrelation reflects shared phylogenetic history, horizontal cultural transmission, or simply the spatial autocorrelation of landscapes and ecological factors within continents is unclear.

Of particular interest is the fact that estimates of the two primary parameters of interest, the scaling coefficient, β, and the activation energy, E, do not change significantly from the original least-squares regression model to the subsequent mixed model analysis. In other words, incorporating covariates and mixed effects into the complete model accounts for variation around the regression line due to ecological and cultural factors but only serves to bring out more clearly how area used, A, scales allometrically as a function of population size, N. Furthermore, because individual home range, $H_0 \approx \langle B \rangle / R$, and $\langle B \rangle$ is held constant, the ecological and cultural variables in the mixed model serve to highlight the way that these factors influence use of space by affecting the resource supply rate, R.

Discussion

Our results demonstrate that individual space use in hunter–gatherer societies scales nonlinearly or allometrically with population size. Furthermore, this power–law scaling relation is robust to differences in trophic foraging niche, ecosystem temperature, energy availability, geographic location, and cultural phylogeny. Eq. **4** can be rearranged to express space use per individual as

$$D^{-1} = A/N = \langle B \rangle \, R^{-1} \, N^{\beta-1} \, e^{E/kT}. \qquad [5]$$

By using the estimated scaling exponent from the mixed linear model, $\beta_{MLM} = 0.756 \pm 0.042$, this gives per capita space use, D^{-1}, scaling with population size, N, with an exponent of 0.244. Furthermore, because $\beta < 1$, then $H_0 > D^{-1}$, this implies that home ranges of individuals effectively overlap increasingly with increasing population size. Recalling our definition of the minimum required home range size, $H_0 \geq \langle B \rangle R^{-1} e^{E/kt}$, our results imply that effective resource supply rates increase nonlinearly, as approximately 1/4 power with increasing population size. Larger hunter–gatherer populations are distributed more densely on the landscape, implying that they are more efficient at extracting materials, energy, and information from the environment and redistributing those resources to individuals within societies. This organizational structure represents an important economy of scale: After adjusting for ecological and cultural factors that affect the rate of resource supply, larger populations are able to harvest more resources and to support more people per unit area of home range. It is interesting to note that, recently, both hunting success and day range also have been found to scale nonlinearly with group size in other mammalian carnivore species (25–27).

The exact value of the exponents may hold clues to the mechanistic processes responsible for the formation, structure, and maintenance of these scaling relations. The scaling as a function of group size that we report here have exponents that are uncannily close to simple multiples of 1/4: i.e., 0.756 for area per population and 0.244 for area per individual. Note that none of the scaling models we derive here have exponents significantly different from 3/4 (Table 1), and the scaling exponent from the mixed linear model is extremely close to this value. These apparent 1/4-power scaling relations for human space use and population size may not be coincidental. Biological allometries have long been known to have 1/4-power exponents (28–31). Recent studies, based on both functional models (4, 5, 32) and dimensional arguments (5, 32, 33) suggest that these unusual exponents can be attributed to the fractal properties of three-dimensional resource distribution networks, such as animal and plant vascular systems, which introduce a fourth linear dimension.

At the moment it is not clear exactly how these ideas may apply to the scaling of human ecological relationships and social systems, but it is clear that resources are taken up from the environment and distributed among humans through complex distribution networks. Elsewhere, we show that individuals within hunter–gatherer societies are connected through hierarchical fractal-like distribution networks of interpersonal contacts that serve to exchange energy and material goods, labor services, and culturally and genetically transmitted information (M.J.H., B.T.M., R.S.W., and J.H.B., unpublished work). Individuals move between and interact at different organization levels, termed Horton orders, ω, in response to changing ecological and social conditions (M.J.H., B.T.M., R.S.W., and J.H.B., unpublished work). The effective physical dimension of these social networks is given by the minimum number of coordinates required to describe the location of an individual within two-dimensional space; in hunter–gatherer networks this includes two spatial coordinates and a third social organizational coordinate, ω. It follows from purely dimensional considerations that hunter–gatherer space use might scale as the 3/4 power of population size as the three-dimensional social network has fractal-like properties similar to the vascular networks of organisms. So we hypothesize that when the structural and dynamical properties of these networks are better understood and more precisely quantified, they will be shown to have fundamental features that cause them to scale similarly to resource flows within organisms.

Although the precise mechanisms remain to be elucidated, our results show that hunter–gatherer societies display allometric scaling relations that reflect with the flows of energy, matter, and information within social distribution networks. These results suggest that some aspects of metabolism and the scaling of human social systems may eventually be explained by applying first principles of network and metabolic theories from physics, chemistry, and biology to the complexities of human social systems. We suggest that future research could profitably focus on the following: (*i*) Identifying biological and human currencies and rate processes that could give rise to these nonlinear scaling relations. (*ii*) Quantifying scaling relations and resource distribution networks in other human socioeconomic systems, from horticulturists and subsistence agriculturists to industrialized contemporary human societies. (*iii*) Quantifying within-species population spatial scaling relations for other social species, such as ants, termites, and bees, which may indicate whether these nonlinearities result from general features of social organization or uniquely human attributes, such as cognition and linguistic communication (34, 35). The nonlinear scaling of hunter–gatherer space use offers yet another example of how applications of general principles of macroecology, metabolism, and scaling theory can contribute to understanding important features of human ecology and social organization (1, 36, 37).

1. Brown JH (1995) *Macroecology* (Univ of Chicago Press, Chicago).
2. Enquist BJ, Brown JH, West GB (1998) *Nature* 395:163–165.
3. Enquist BJ, West GB, Brown JH (2000) in *Scaling in Biology*, ed West GB (Oxford Univ Press, Oxford), pp 352.
4. West GB, Brown JH, Enquist BJ (1997) *Science* 276:122–126.
5. West GB, Brown JH, Enquist BJ (1999) *Science* 284:1677–1679.
6. Rodriguez-Iturbe I, Rinaldo A (1997) *Fractal River Basins: Chance and Self-Organization* (Cambridge Univ Press, Cambridge, UK).
7. Stewart JH (1938) *Basin-Plateau Aboriginal Sociopolitical Groups* (Univ of Utah Press, Salt Lake City).
8. Birdsell J (1953) *Am Nat* 87:171–207.
9. Birdsell J (1958) *Evolution (Lawrence, Kans)* 12:189–205.
10. Yengoyan AA (1972) *Oceania* 43:85–95.
11. Savage VM, Gillooly JF, Woodruff WH, West GB, Allen AP, Enquist BJ, Brown JH (2004) *Funct Ecol* 18:257–282.
12. Charnov EC (1993) *Life History Invariants* (Oxford Univ Press, Oxford).
13. Walker RS, Hill K, Burger O, Hurtado AM (2006) *Am J Phys Anthropol* 129:577–583.
14. Gillooly JF, Charnov EC, West GB, Savage VM, Brown JH (2002) *Nature* 417:70–73.
15. West GB, Brown JH, Enquist BJ (2001) *Nature* 413:628–631.
16. Gillooly JF, Brown JH, West GB, Savage VM, Charnov EC (2001) *Science* 293:2248–2252.
17. Allen AP, Brown JH, Gillooly JF (2002) *Science* 297:1545–1548.
18. Brown JH, Gillooly JF, West GB, Savage VM (2003) in *Macroecology: Concepts and Consequences*, ed Gaston KJ (Blackwell Scientific, Oxford).
19. Allen AP, Gillooly JF, Brown JH (2005) *Funct Ecol* 19:202–213.
20. Jetz W, Carbone C, Fulford J, Brown JH (2004) *Science* 306:266–268.
21. Haskell JP, Ritchie ME, Olff H (2002) *Nature* 418:527–530.
22. Binford LR (2001) *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets* (Univ of California Press, Berkeley).
23. Kelt DA, Van Vuren D (2001) *Am Nat* 157:637–645.
24. Mace GM, Pagel M (1994) *Curr Anthropol* 35:549–564.
25. Creel S, Creel NM (2002) *The African Wild Dog: Behavior, Ecology, and Conservation* (Princeton Univ Press, Princeton).
26. Creel S (1997) *Anim Behav* 54:1319–1324.
27. Carbone C, Cowlishaw G, Isaac NJB, Rowcliffe JM (2005) *Am Nat* 165:290–297.
28. Schmidt-Nielson K (1984) *Why Is Animal Size So Important?* (Cambridge Univ Press, Cambridge, UK).
29. Kleiber M (1932) *Hilgardia* 6:315–353.
30. Peters RH (1983) *The Ecological Implications of Body Size* (Cambridge Univ Press, Cambridge, UK).
31. Calder WA (1984) *Size, Function, and Life History* (Harvard Univ Press, Cambridge, MA).
32. West GB, Brown JH (2005) *J Exp Biol* 208:1575–1592.
33. Banavar JR, Damuth J, Maritan A, Rinaldo A (2002) *Proc Natl Acad Sci USA* 99:10506–10509.
34. Kaplan H, Hill K, Lancaster J, Hurtado AM (2000) *Evol Anthropol* 9:156–185.
35. Dunbar RIM (1993) *Behav Brain Sci* 16:681–735.
36. Collard IF, Foley RA (2002) *Evol Ecol Res* 4:371–383.
37. Moses ME, Brown JH (2003) *Ecol Lett* 6:295–300.