

despite the high level of extinction. Only the end-Permian event matches the model of a “mass extinction regime” (5), arguing for a catastrophic cause consisting of a brief but major event, independent of earlier variations in diversity, with a worldwide effect and, for the most part, the nonselective demise of taxa.

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The Scaling of Animal Space Use

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Space used by animals increases with increasing body size. Energy requirements alone can explain how population density decreases, but not the steep rate at which home range area increases. We present a general mechanistic model that predicts the frequency of interaction, spatial overlap, and loss of resources to neighbors. Extensive empirical evidence supports the model, demonstrating that spatial constraints on defense cause exclusivity of home range use to decrease with increasing body size. In large mammals, over 90% of available resources may be lost to neighbors. Our model offers a general framework to understand animal space use and sociality.

Space use in animals is strongly tied to body size and has been a focal point of ecological research (1–7). This research has led to the formulation of scaling rules—power law relations between body size and animal area use—in two separate lines of research: population density and home range size. Here we develop a simple model for the use of space by animals that incorporates energy requirements and interactions with neighbors to unify these approaches.

We assume that energy and material resource requirements are determined by the whole-organism field metabolic rate *B* (in units of kJ/day or watts), which has been shown to scale as

$$B = B_0 M^{3/4} \quad (1)$$

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*B*₀ is a normalization constant that also incorporates the diet-specific assimilation efficiency, which determines the proportion of ingested energy available for activity. Let *H* be the home range area in km² and *R* the species-specific rate of supply of usable resources available in *H*, in units of W/km². However, intrusions from foraging conspecific neighbors into a portion of the home range may decrease the proportion of *R* available to the home range owner (8). This resource depletion can be put into a spatial context by thinking in terms of a portion of the home range that is used exclusively only by the owner, *H*_o, and a portion that overlaps with neighbors and whose resources are harvested only by intruders. We use *α* to designate the proportion of the resource supply rate across a home range that is harvested exclusively by the owner: *α* = *H*_o*R*/*H**R*. This can be simplified to

$$\alpha = H_o/H \quad (2)$$

Accordingly, the proportion of resource supply rate taken by the neighbors, or home range overlap, is 1 – *α*.

It follows that if an individual uses an area just sufficient to meet its metabolic

requirements, it requires a home range of area

$$H = B/\alpha R = B_0 R^{-1} \alpha^{-1} M^{3/4} \quad (3)$$

Population density, *N*, can be used to empirically quantify *α*. Its reciprocal, *N*^{–1} indicates the average area per individual and is equivalent to *H*_o, and thus from Eq. 2 it follows that

$$\alpha = N^{-1}/H \quad (4)$$

Finally, the scaling of *N*^{–1} is identical to that of *H*, without the effect of neighbors on scaling and normalization constant

$$N^{-1} = B/R = B_0 R^{-1} M^{3/4} \quad (5)$$

These equations can serve to illustrate three potential scenarios for the scaling of home range size that are dependent on the examination of the two key parameters, *R* and *α*. (i) Both *α* and *R* are body size-invariant (*R* ∝ *M*⁰ and *α* ∝ *M*⁰). This is the hypothesis initially proposed by McNab (1). It predicts that home range size should scale as *M*^{3/4} (*H* ∝ *M*^{3/4}), but it was not supported by subsequent analyses indicating home range scaling close to 1 (9–12). (ii) *R* decreases with body size approximately to the quarter power, whereas *α* is body size-invariant (*R* ∝ *M*^{–1/4} and *α* ∝ *M*⁰). This predicts the observed *H* ∝ *M*¹. This idea was originally proposed by Harestadt and Bunnell (13) and recently refined by Haskell et al. (14), who modeled the potential interaction between the fractal distribution of resources and foraging mode. This scenario predicts that larger species require larger home ranges than the scaling of their energy needs alone would suggest, because of their lower encounter rates with food items. Because *R* affects the scaling of both *N*^{–1} and *H* equally (compare Eqs. 3 and 5), their scaling lines should have no distinct intersection. (iii) Resource supply rate *R* does not scale with body size, but proportional access by the home range owner, *α*, scales approximately to the negative one-

quarter power ($R \propto M^0$ and $\alpha \propto M^{-1/4}$), leading to the observed $H \propto M^1$ and an intersection of the scaling lines. A potential role of home range overlap with neighbors has been pointed out previously (7, 15, 16), but an understanding of the scaling remains little developed. Here we develop a new theory that quantifies the effect of neighbors, α , and provide an empirical test for all core scenarios for the scaling of animal space use.

Larger home ranges are more difficult to defend from intrusion. This idea is supported by field observations (8), but its conceptual basis can be seen by considering the task of defending an increasing area (fig. S1). From Eq. 3, it follows that the minimum area of a home range in the absence of competition scales as $M^{3/4}$. It has been found empirically that the day range, or the average distance traveled in 1 day, scales as $M^{1/4}$ (16–18). Hypothetically, this is equivalent to a mouse traveling 110 m in a 70-m-diameter home range, versus an elephant traveling 2 km in a 6-km-diameter home range. Clearly, the larger animal faces a more formidable task of detecting and minimizing overlap with intruders.

The magnitude of this task can be modeled quantitatively by using the equation from physics for collisions among gas particles to predict the frequency of interactions between owners and intruders (19–21). In two-dimensional space, the frequency of interactions f among individuals is

$$f = \frac{4}{\pi} N D d \quad (6)$$

where N is the population density (in individuals per km^2), D is the average speed (the day range in km traveled per day), and d is the average neighbor interaction distance (in km). We use the above well-established scaling relations to characterize how density and speed of movement vary with body size: $N \propto M^{-3/4}$ (5) and $D \propto M^{1/4}$ (7, 16–18). Less is known about the scaling of interaction distance, which is likely to vary with communication system and habitat structure. Limited sources indicate a scaling of detection distance between M^0 and $M^{1/2}$ (17, 22, 23), and here we attempt a first test of its effect using the midpoint, $d \propto M^{1/4}$, the scaling of a typical biological distance (7, 24, 25).

We assume that interactions with conspecific neighbors lead to temporary reinforcement of exclusive home range use and hence to reduced resource extraction by home range intruders (2). All else being equal, neighbors that encounter each other more frequently should be able to maintain more fixed home range boundaries and thus get by with relatively smaller home ranges, because the resources are used more exclusively. Quantitatively, we assume that the proportion of the total resources or proportional home range area that is exclusive to a home range owner,

α , is proportional to the neighbor interaction frequency, so $\alpha \propto f$. Substituting the assumed allometric scalings of population density, day range, and interaction distance into Eq. 4 gives the predicted scaling of α

$$\alpha \propto f \propto M^{-3/4} M^{1/4} M^{1/4} \propto M^{-1/4} \quad (7)$$

The assumption of random movement in Eq. 6 can be relaxed to allow a wide variety of movement patterns without altering Eq. 7; the critical feature is that the way owner and intruder move with respect to each other is independent of body size. We now modify Eq. 3 to model home range area, incorporating the fraction of the total home range whose resources are used by the neighbor. Following scenario (iii) and assuming body size invariance of resource supply rate R this leads to

$$H = B/\alpha R = B_0 R^{-1} M^{1/4} M^{3/4} = B_0 R^{-1} M^1 \quad (8)$$

The above equations provide a simple general model for how animals use space and interact with neighbors. This model makes a number of predictions that can be tested empirically. We use two extensive compilations on home range size and population density in mammals (11, 26) to test the model predictions. In order to account for the effect of grouping in the context of our model, we perform our analyses with home range size per individual, $H = (\text{observed home range}/\text{social unit size})$, as a response (27).

A log-log plot of H as a function of M has a slope of 1.07, which is not statistically distinguishable from the value of 1 estimated in Eq. 8 (Fig. 1 and Table 1) but is significantly higher than 0.75, which rejects body size invariance of R and α predicted by scenario (i) (1). A log-log plot of N^{-1} , the reciprocal of population density, as a function

of M has a slope of 0.76 (Fig. 1 and Table 1), which is almost identical to the value of 3/4 predicted in Eq. 5, given body size invariance of R [see also (5, 28–30)]. Across trophic groups, the slopes vary from 0.73 to 0.86 but are never significantly different from 0.75 (t tests, $P > 0.1$ in all cases). This supports the assumption of scenario (iii) that resource supply rate R is body size-independent ($R \propto M^{-0.02}$ to $M^{0.11}$ across trophic levels) and rejects the supply rate-based scenario (ii) for the scaling of home range size (13, 14). The intercepts of the relations in Figs. 1 and 2 at $M = 1$ kg indicate the ratio between energy expenditure and energy supply rate (B_0/R) as a function of body size. Given empirical estimates of mammalian field metabolic rates and assimilation efficiencies, we can estimate how the different area needs point to the highly different resource supply rate experienced across trophic levels. We find that the energy supply rate R is approximately 2188 W km^{-2} in herbivores, 408 W km^{-2} in omnivores, and 32 W km^{-2} in carnivores, independent of body size.

Following Eq. 4, the difference in scaling exponents of H and N^{-1} , or their slopes on the log-log plot with body size (Fig. 1), indicates the value of α , proportional home range exclusivity. We find that α is statistically different from zero in all trophic groups and ranges from 0.26 to 0.39, without any consistent effect of diet (Table 1). These values are not different from those predicted by Eqs. 7 and 8 (t tests, $P > 0.1$ in all cases). Together with the body size independence of R , these results support scenario (iii), the proposed scaling of neighbor interaction, as a general mechanism explaining the scaling of animal space use in the presence of neighbors.

We can further estimate the home range exclusivity at a given body size by synthesizing

Fig. 1. The body size dependence of individual area use and overlap in mammals. (A) Individual home range size H , corrected for grouping. (B) Per-individual area use or reciprocal density, N^{-1} . (C) The above scaling relations of H (solid line) and N^{-1} (dashed line) plotted together for comparison. (D) The resulting scaling of α (in percent); that is, the percentage of resources exclusively taken by the home range owner or percent of home range overlap is given as $1-\alpha$ as percentage). Data points are species; thick lines are least-squares fits; dotted lines are their 95% confidence intervals. For detailed regression results, see Table 1.

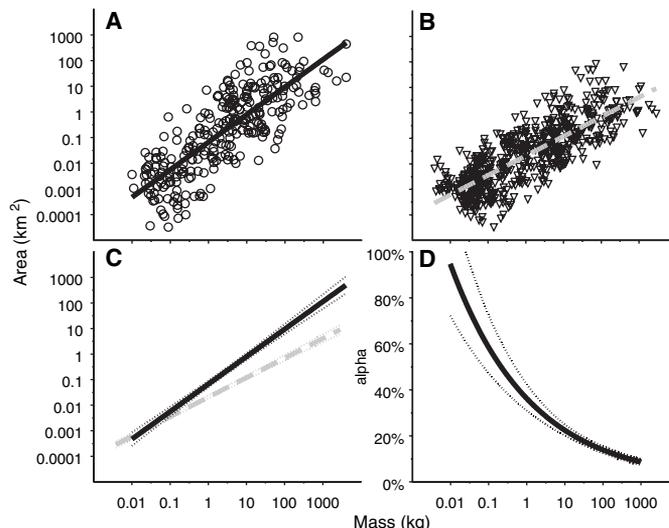


Table 1. Observed scaling relations of per-individual area use in mammals. Data are obtained from two measures: the inverse of population density (N^{-1}) and individual home range size (H , corrected for group size). These data are also analyzed by trophic level, herbivores (Herb), omnivores (Omn), and carnivores (Carn). The slope analysis gives the individual scaling exponents m

and the scaling exponents for α , proportional home range exclusivity, which are given as $\alpha = m(N^{-1}) - m(H)$, where m refers to the calculated scaling exponents. Numbers in brackets are the 95% confidence intervals. The r^2 values are based on log-transformed data. n indicates sample size (number of species).

		n	Cross over		Intercept		Slope		Model	
			M (kg) at $N^{-1} = H$	Area (ha) at $M = 1$	m	$\alpha \propto M^x$	F	r^2		
All	H	274	0.022 (0.215)	6.69 (1.68)	1.07 (0.10)	-0.31 (0.11)	464.3	0.63		
	N^{-1}	563							2.06 (0.28)	0.76 (0.05)
Herb	H	158	0.064 (0.260)	1.01 (0.01)	0.76 (0.05)	-0.26 (0.11)	948.7	0.74		
	N^{-1}	327							2.05 (0.03)	1.02 (0.09)
Omn	H	44	0.022 (0.187)	15.87 (1.30)	1.12 (0.15)	-0.39 (0.18)	208.5	0.83		
	N^{-1}	176							3.62 (0.09)	0.73 (0.09)
Carn	H	70	0.299 (0.596)	52.07 (10.87)	1.20 (0.19)	-0.34 (0.28)	157.8	0.70		
	N^{-1}	38							34.43 (4.03)	0.86 (0.20)

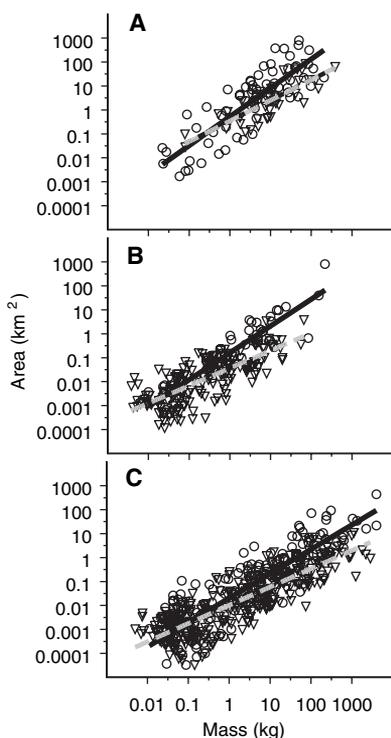


Fig. 2. The scaling across trophic levels of per-individual area (N^{-1} , triangles, dashed line) and individual home range size (H , circles, solid line). (A) Carnivores. (B) Omnivores. (C) Herbivores. Lines are least-squares fits. For detailed regression results, see Table 1.

the data for N and H . In a fully filled landscape, we expect individual home range size to be at least equal to the area per individual, $H \geq N^{-1}$. Because the model predicts increasing overlap in home ranges with increasing size, it follows that log-log plots of H and N^{-1} as function of M should be nearly coincident for the smallest mammals but diverge with increasing body mass. This is exactly what is observed (Figs. 1 and 2). The regression equations for all mammals suggest that although neighbor effects are negligible at the smallest body sizes, already at 1 kg only 31% of home range or resource supply rate is

obtained by the owner, and just 7% at 100 kg (Fig. 1). These surprising results are robust to a more restrictive analysis using only species with data on both H and N^{-1} (table S1), and they highlight the so-far-underappreciated magnitude of neighbor effects.

Our finding of extensive home range overlap at all but the smallest body sizes falsifies key assumptions of hypotheses on the scaling of animal space use that assume exclusive access to resources (12) or, additionally, a body size dependence of resource supply rate (13, 14). Population estimates of large-bodied species are as much as an order of magnitude higher than suggested by home range size. This finding is counter to the idea that increased census areas and the inclusion of unsuitable habitat have led to underestimates of population densities for large-bodied animals [(31), but see (32)]. Indeed, the high degree of home range overlap in large mammals suggests that population density rather than home range size is the better measure to use in quantifying individual area needs for conservation purposes.

Our findings resolve a long-standing conflict resulting from two divergent approaches to studying the use of space in animals, based on home range size and population density. Our approach provides a simple and powerful framework for understanding how animal space use reflects the constraints of both harvesting resources and detecting and responding to intruders. It has important applications in other behavioral ecological phenomena, such as group living, mate finding, disease transmission, and predator-prey encounters. Our results show how mechanistic models based on first principles of physics, ecological energetics, and behavioral ecology can make testable predictions and enhance our understanding of macroecological patterns.

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