

Spatial and temporal scaling of population density and animal movement: A power law approach¹

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Abstract: Many ecological patterns are sensitive to spatial and temporal scale, but no general protocol has emerged for dealing with scale-dependence. We suggest that power laws, regularly used in the study of body size, can be applied to many such features. We used these techniques to describe two scale-sensitive aspects of caribou (*Rangifer tarandus*): population densities of North American herds when measured at varying spatial extents, and speeds of radiotracked individuals when observed at varying temporal resolutions. Log-log regression was applied, based on the power formula, $Y = cX^z$. Non-isometric relationships existed for abundance versus area of the population range, but the pattern differed between groups. For sedentary caribou, animal numbers increased more slowly than spatial extent ($z = 0.503$). For migratory populations, this relationship was hyper-allometric ($z > 1$), and densities were generally lower for continental herds compared to insular Newfoundland herds living without wolves (*Canis lupus*). We surmise that defining population bounds may be more subjective for sedentary herds; migratory herd densities may increase with increasing population size. Distance moved versus the interval between radiolocations was also non-isometric ($z = 0.551$). We standardized these movements to eliminate the confounding effects of scale, enabling comparisons across seasons and populations. The power formula helps to clarify the debate over the use of ratios, where variables may change non-isometrically. Power laws may enable the synthesis of ecological patterns sensitive to scales of space and time.

Keywords: density, movements, *Rangifer tarandus*, spatial scale, temporal scale.

Résumé : Plusieurs des patrons écologiques observés dans la nature sont sensibles aux échelles spatio-temporelles. Il n'existe toutefois pas de protocole de recherche prenant en considération une telle sensibilité. Nous suggérons que les fonctions de puissance, qui sont fréquemment utilisées dans les études de taille corporelle, soient applicables dans de telles circonstances. Nous avons donc choisi ces techniques pour décrire deux aspects de la vie du caribou (*Rangifer tarandus*) sensibles aux échelles spatio-temporelles : la densité de population des hardes nord-américaines lorsqu'elle est mesurée à des échelles spatiales variées et la vitesse des individus suivis par télémétrie lorsqu'elle est mesurée à différentes résolutions temporelles. Nous avons utilisé une régression log-log basée sur la formule de puissance $Y = cX^z$. Des relations non isométriques existent entre l'abondance des individus et la superficie de l'aire de répartition d'une population, toutefois ces relations diffèrent entre les groupes. Chez les caribous sédentaires, le nombre d'individus augmente à un rythme moins rapide que celui de l'aire de répartition ($z = 0,503$). Chez les populations migratrices, cette relation est hyperallométrique ($z > 1$) et les densités des hardes continentales sont généralement inférieures à celles de Terre-Neuve où le loup (*Canis lupus*) est absent. Nous émettons l'hypothèse qu'il serait plus subjectif de définir les limites des populations sédentaires que celles des hardes migratrices. En effet, chez ces dernières, la densité des individus peut augmenter avec la taille de la population. La relation qui existe entre les distances parcourues et l'intervalle entre les localisations télémétriques est également non isométrique ($z = 0,551$). Nous avons procédé à une uniformisation de ces déplacements afin d'éliminer les effets confondants de l'échelle, ce qui permet de comparer entre elles les saisons et les populations. La formule de puissance aide à clarifier la discussion concernant l'utilisation de rapports lorsque les variables peuvent changer de façon non isométrique. En somme, les fonctions de puissance peuvent aider à synthétiser les patrons écologiques sensibles aux échelles spatio-temporelles.

Mots-clés : densité, déplacements, échelle spatiale, échelle temporelle, *Rangifer tarandus*.

Nomenclature: Mitchell-Jones *et al.*, 1999.

Introduction

Spatial and temporal scaling have advanced swiftly to the forefront of ecological thought. Now a central concept in ecology (Withers & Meentemeyer, 1999; Schneider, 2001), scale has been championed as possible framework for unification of the discipline (Wiens, 1989; Allen & Hoekstra, 1992; Levin, 1992). Despite the explosion of interest in scale, ecologists remain immersed in data (Peters, 1983; Allen & Hoekstra, 1992) but equipped

with an incomplete theory of scaling (Wiens, 1999). One obstacle to broader synthesis, in our view, has been methodological. There are myriad techniques for handling scale. As yet, no general strategy has emerged that is applicable to the wide assortment of patterns that are sensitive to the extent or resolution of observations in space and time.

The need for a comprehensive methodology is growing. Scaling is implicit in some of the most elementary attributes in ecology, such as rate of movement and population density. For instance, the apparent speed along a

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fractal path will increase if an individual is observed at a finer temporal resolution (Wiens *et al.*, 1995; Bascompte & Vilà, 1997; Ferguson, Rettie & Messier, 1998); the abundance of animals per unit area often declines with increasing bounds of the study area (Smallwood & Schonewald, 1996; Gaston, Blackburn & Gregory, 1999; Gaston & Matter, 2002). Marshalling together such scale-dependent observations is a central challenge to ecology.

Space and time are but two dimensions of scale. Allometry, “devoted to understanding [body] size and its consequences” (Gould, 1979), has garnered a long tradition, large literature, and well-developed methodology (Peters, 1983; Schmidt-Nielsen, 1984; Brown & West, 2000). At its foundation is the power equation, $Y = cX^z$, an empirical approach where Y represents some scale-dependent feature or function, X is body size, and c and z are empirically-fitted coefficients. The origins of this equation date to the 19th century, and its interpretation has been debated intensely since the 1930s (Gould, 1979). Despite its clear capacity to synthesize patterns (Schneider, 2001; 2002), applications of the formula to issues of temporal and spatial scaling, apart from the species-area relationship (Lomolino, 2000), remain surprisingly scant. We believe that power laws represent a methodology with great leverage and scope, a potential still largely untapped.

Here, we illustrate the value of power laws in analyzing two fundamental and scale-sensitive ecological features of caribou (*Rangifer tarandus*) across space and time. Using the power equation, we analyzed the population densities of caribou across North America when framed at varying spatial bounds; we also examined individual speeds of caribou when radiotracked at varying time intervals. In the latter case, we extended conventional procedures for allometric treatments of body size (Reist, 1985; Smith, 1993) to produce scale-adjusted estimates. This strategy, we believe, can lead to conclusions with greater generality.

Methods

DATA COLLECTION

We assembled information on the abundance and occupancy of 59 caribou populations in North America (Messier *et al.*, 1988; Bergerud, 1992; Farnell *et al.*, 1996; Seip & Cichowski, 1996; Valkenburg *et al.*, 1996; Schaefer *et al.*, 2001; Newfoundland & Labrador Wildlife Science & Research Division, unpubl. data). For each observation, abundance was expressed as the estimated total number of animals, and occupancy as the maximum area in which the population ranged during the annual cycle, usually based on radiotelemetry studies. For some populations that experienced large changes in abundance (*i.e.*, Avalon, George River, and Red Wine Mountains herds), more than one density observation was included. We classified each population according to the common ecotypic designations for *Rangifer* (Bergerud, 1996): the sedentary ecotype, generally forest-dwelling caribou that disperse at calving time in spring, and the migratory ecotype, animals that undertake longer movements and aggregate at calving. Because of the strong limiting effects of predation by wolves (*Canis lupus*; Bergerud, 1996), we

further categorized the migratory populations, *i.e.*, continental herds *versus* insular herds from Newfoundland, where wolves have been absent since about 1922.

Our observations of movements were from the Buchans Plateau caribou herd, a migratory population that occupied 12,000 km² in west-central Newfoundland (Mahoney & Schaefer, 2002). Adult caribou were tracked using VHF radio transmitters (Lotek Engineering, Newmarket, Ontario, Canada), September 1994 to June 2000. Radio-locations were determined with a STOL (short take-off or landing)-equipped Cessna 185 aircraft with an onboard Global Positioning System. The median interval between consecutive relocations of individuals was 6 d, with the actual interval varying between 3 and 14 d. Radiolocations had an accuracy of ≤ 500 m based upon repeated blind test positioning of dummy transmitters. Data from 54 individuals (14 males, 40 females), each tracked for ≥ 360 d and ≥ 30 locations, were used.

DATA ANALYSIS

We used log-log regression of the power formula, $Y = cX^z$, to quantify scaling relationships: the estimated population size (Y) *versus* area of the population range (X); and the distance travelled by radiocollared individuals (Y) *versus* the time between relocations (X). The 95% confidence interval (CI) was computed for each slope, z . To provide wider variation in the temporal grain of movements, Y was determined for each X in all instances with intervals of 3-14 d and of one to three surveys.

For the analysis of speed, log-log regression was applied, then allometric formulae (Thorpe, 1975; Reist, 1985; Leonart, Salat & Torres, 2000) were used to remove the effect of time, adjusting each observation to a standard time scale (X_0). An adjusted value of distance (Y_{ADJ}), scaling each observation to X_0 (Thorpe, 1975), was determined as

$$Y_{ADJ} = 10^k \quad [1]$$

where

$$K = \log Y - z(\log X - \log X_0) \quad [2]$$

A standard time scale of 4 d (*i.e.*, $X_0 = 4$) was selected. This value, within the range of our data collection, avoided the dangers of extrapolation (Gould, 1979; Schmidt-Nielsen, 1984) and allowed comparison to other studies where the data were collected at that scale (Schaefer & Luttich, 1998; Bergman, Schaefer & Luttich, 2000; Rettie & Messier, 2001). In addition, detransformation using antilogs results in negative bias because logarithmic regressions generate the geometric, rather than the arithmetic mean (Smith, 1993). As a correction, the ratio estimator, *i.e.*, the mean of the dependent variable on the original measurement scale divided by the mean of the detransformed predicted values (Snowdon, 1991; Smith, 1993), was adopted. Corrected estimates of distance travelled were computed by multiplying the detransformed predictions by the correction factor.

Non-migrants were classified as those that spent ≥ 12 consecutive months on the herd's summer and calving grounds (Mahoney & Schaefer, 2002). Log Y_{ADJ} was

used to describe and test the influence of migrant status, sex, and time of year on movement rates using ANOVA. The individual was retained as experimental unit for these tests.

Results

The population densities and rates of movement of caribou were scale-dependent. Most log-log regressions generated slopes substantially different from unity, indicating non-isometric relationships of abundance *versus* spatial extent and of movement *versus* temporal grain.

Abundance-occupancy relationships differed between ecotypes and between continental *versus* insular herds (Figure 1). Abundance of sedentary populations tended to increase more slowly than extent of their population range ($z = 0.503$, CI = 0.281 - 0.725, $n = 28$), whereas the converse was exhibited by migratory herds from continental North America ($z = 1.338$, CI = 1.124 - 1.462, $n = 27$) and from insular Newfoundland ($z = 1.178$, CI = 0.498 - 1.858, $n = 10$). Hence the densities of sedentary caribou tended to decline, and migratory caribou increase, with increasing extent. For migratory caribou, insular Newfoundland populations attained higher densities than continental herds, as indicated by their higher y-intercept, although the slopes in the abundance-area relationships were comparable (Figure 1).

In the case of movements, the relationship of apparent distance moved (Y) to time between relocations (X) was also non-isometric ($z = 0.551$, CI = 0.503 - 0.601; Figure 2). Movements were fractal; apparent speeds of caribou increased with shortened time intervals. Adjusted distances (Y_{ADJ}), standardized to 4-d intervals, were weakly and negatively related to time between relocations ($r = -0.0841$; $n = 5,830$). This appeared to be an artifact of more frequent radiotelemetry surveys during spring and autumn, when caribou movements were expected to be greater. In such a circumstance, there is perhaps no complete remedy for temporal scale-dependence. The ratio estimator correction factor was $13.74/7.46 = 1.84$,

signifying that detransformation from the allometric prediction substantially underestimated caribou movements. Distances were strongly positively skewed.

Expressed in 4-d intervals, Buchans caribou displayed a distinct annual rhythm of movement, denoted largely by the twice-yearly migrations (Figure 3). A crescendo of activity was associated with each migration, peaking at $11.1 \text{ km}\cdot\text{d}^{-1}$ in late spring and $11.3 \text{ km}\cdot\text{d}^{-1}$ in mid-fall. In spring, the onset of calving was coincident with a drop in activity, which ebbed, to as low as $2.4 \text{ km}\cdot\text{d}^{-1}$, at 4 weeks post-calving. Overall, caribou moved an average of $7.8 \text{ km}\cdot\text{d}^{-1}$ or a total of $712 \text{ km}\cdot\text{y}^{-1}$, when measured at this grain.

Rates of movement (Table I) were not significantly different between sexes ($F_{1,350} = 0.02$; $P = 0.895$), nor were there significant interactions between sex and season ($F_{6,350} = 0.471$; $P = 0.829$), sex and migrant status ($F_{1,350} = 0.129$; $P = 0.720$), or among these three factors

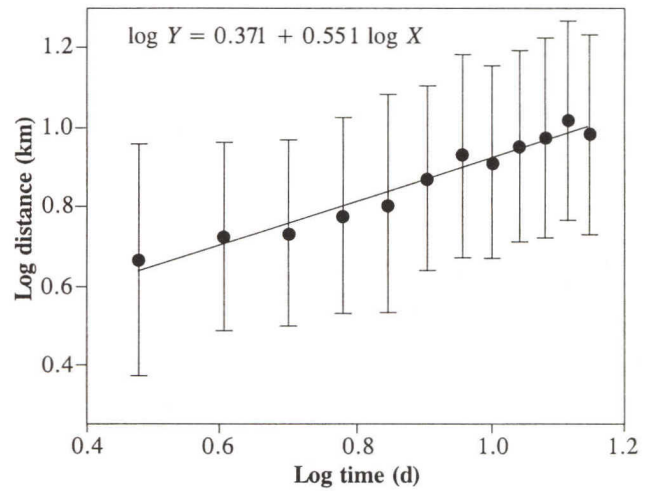


FIGURE 2. Log-log plot of the average distance moved by radio-tracked Buchans caribou (± 0.5 SD) as a function of time between telemetry relocations.

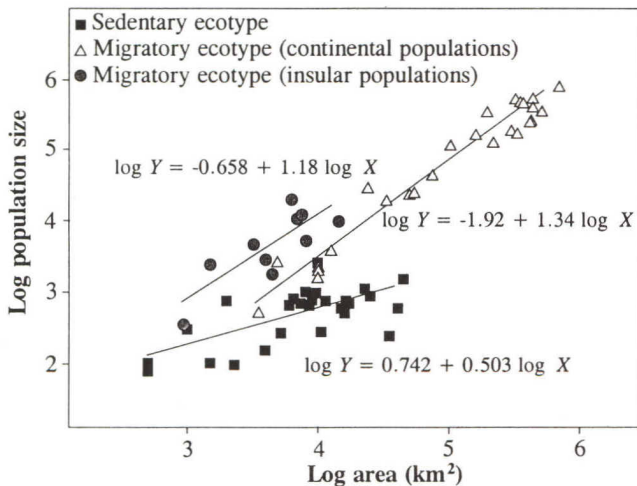


FIGURE 1. Log-log plot of population size as a function of area of the population range for North American caribou herds. Sources of these data are given in the Methods section.

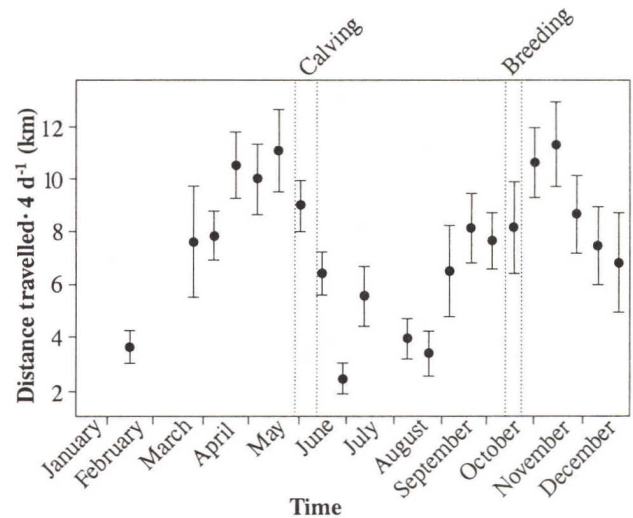


FIGURE 3. Annual profile of the mean rate of movement of radio-tracked Buchans caribou, standardized as the distance travelled $\cdot 4 \text{ d}^{-1}$. Error bars represent 90% confidence limits.

TABLE I. Average distance moved $\cdot 4 \text{ d}^{-1}$ (SE in parentheses) by season for migratory ($n = 42$) and non-migratory ($n = 12$) Buchans caribou. Dates in parentheses refer to the first day of each season.

Status	Spring migration (1 April)	Calving (24 May)	Post-calving (15 June)	Pre-breeding (2 September)	Breeding (9 October)	Fall migration (20 October)	Winter migration (27 December)
Migrant	11.4 (0.49)	7.5 (0.47)	4.6 (0.32)	8.3 (0.56)	8.9 (1.27)	11.3 (0.64)	7.3 (0.44)
Non-migrant	5.4 (0.62)	5.7 (0.79)	4.2 (0.40)	5.3 (0.51)	5.3 (0.51)	6.6 (0.81)	4.4 (0.59)

($F_{6,350} = 0.843$; $P = 0.537$). The speeds of migrants and non-migrants tended to be differentially affected by the seasons ($F_{6,350} = 1.93$; $P = 0.075$). Migrants were consistently more mobile than non-migrants, but the discrepancy was accentuated during spring and fall migrations (Table I).

Discussion

Synthesis is one of the grand goals of ecology. Yet, as Ehrlich (2002: 34) has observed, ecologists are increasingly awash in data, the journals "clogged with dribs and drabs of information on a vast variety of organisms and communities – increasingly sophisticated studies of more and more trivial problems." While test systems (Ehrlich, 2002) may represent one means to generalization, power laws offer another. Indeed, one of their demonstrated powers is to uncover sweeping patterns by synthesizing large volumes of information (Peters, 1983). Other than the scaling of species richness with area, a pattern that approaches the status of an ecological "rule" (Lomolino, 2000), remarkably few temporal and spatial patterns have been examined through the lens of power laws (Bell *et al.*, 1993; Smallwood & Schonewald, 1996; Kunin, 1998; Johnson, 1999; Ritchie & Olf, 1999). Size may denote the grain and extent of observations in time and space (Wiens, 1989; Withers & Meentemeyer, 1999; Schneider, 2001) and allometric techniques may lend themselves to a much broader array of scaling problems.

Many ecological patterns are sensitive to scale. This may impede generalization because observations collected at one scale may not reliably be scaled-up or scaled-down (Wiens, 1989; Schneider, 2002). Although other approaches are available, including fractal geometry, we concur with others that log-log regression based on the power formula, $Y = cX^z$, may represent the most straightforward (Bell *et al.*, 1993) and well-understood (Gould, 1979) scaling procedure. In power laws, interest often lies in comparing scaling functions in their slope or intercept (Gould, 1979; Figure 1) or examining deviations of individuals from a common standard (Reist, 1985; Figure 2). By standardizing to a common interval or area (Smallwood, Jones & Schonewald, 1996; Kunin, 1998; Gaston, Blackburn & Gregory, 1999), one purposefully corrects for the confounding effects of scale. Each original observation can be re-scaled and represented by a transformed variate; this is equivalent to what the observation would be made at some common scale (Reist, 1985). An interest in scale, therefore, may reside in removing its effects.

Nevertheless, assumptions of the approach must be carefully considered. For example, log-log regressions of pooled data to compute coefficients, although most straightforward, are valid only if the coefficients are similar to the between-group slopes and intercepts (Reist, 1986). For example, because animal pathways may vary seasonally in displacement and tortuosity (Ferguson, Rettie & Messier, 1998; Bergman, Schaefer & Luttich, 2000), separate regressions for each period in our investigation might have been warranted. This difficulty is not unique to our study: how to treat multiple groups is a frequent conundrum in allometry (Schmidt-Nielsen, 1984).

Organism density, the number of individuals per unit area, is a cornerstone of population ecology. As noted by Gaston, Blackburn, and Gregory (1999), estimating the numerator of this ratio has received appreciable attention; surprisingly less has been devoted to the denominator. There is increasing evidence that intraspecific density and census area may not be independent (Haila, 1988; Blackburn & Gaston, 1996; Smallwood, Jones & Schonewald, 1996; Smallwood & Schonewald, 1996; Bowers & Matter, 1997; Gaston, Blackburn & Gregory, 1999; Gaston & Blackburn, 2000); densities often decline when considered over larger spatial extents. For North American caribou, we found strongly diverging patterns for migratory and sedentary ecotypes (Figure 1), a difference may stem from the way in which populations are defined in space. For migratory caribou, aggregation on distinct calving grounds (Bergerud, 1996; Schaefer, Bergman & Luttich, 2000) promotes greater discreteness of population units. Increases in migratory herd occupancy appear to accompany even larger increases in abundance (Figure 1). Herds in wolf-free environments, such as Newfoundland, exhibit a similar abundance-area relationship but may attain higher densities (Bergerud *et al.*, 1983; Figure 1). For sedentary caribou, populations tend to be more sparsely and continuously distributed, dispersed across regions of favourable calving sites (Bergerud, 1996; Schaefer *et al.*, 2001). Hence, delineating populations may be prone to greater subjectivity. This pattern for sedentary herds follows the general within-species tendency for apparent declines in density as an artefact of increased extent. Study areas are commonly selected *a priori* for high densities; larger areas may encompass higher proportions of less favourable conditions (Smallwood, Jones & Schonewald, 1996; Smallwood & Schonewald, 1996; Gaston, Blackburn & Gregory, 1999).

In most studies, density (Y/X), rather than abundance (Y), has been regressed against size of the study area (X). However, as noted by Gaston, Blackburn, and Gregory

(1999), a potential bias exists: if only non-zero observations are used, density has a lower bound of $1/X$, perhaps leading to exaggerated likelihood of Type 1 errors. For this reason, we suggest plotting abundance (Figure 1) instead of density. Impossibly low densities ($< 1/X$) are eliminated, thus lowering this risk of bias.

Speed is another fundamental feature of mobile animals. Because animals commonly assume convoluted travel paths (Wiens *et al.*, 1995; Bascompte & Vilà, 1997; Ferguson, Rettie & Messier, 1998), expressions of speed are not detached from the temporal scale at which they are measured. Conventionally, a ratio of distance per unit time has been computed. Ratios do not, however, alleviate scale-dependence when the numerator and denominator vary non-isometrically (Reist, 1985; Leonart, Salat & Torres, 2000; Schneider, 2002; Figure 2). Conventional speeds ($\text{km} \cdot \text{d}^{-1}$) thus may not be comparable under varying time intervals, circumstances which are common in radiotelemetry. We generated allometrically-adjusted estimates of distance travelled, standardizing our observations to 4-d intervals to allow comparisons across studies and seasons. At a mean of $7.8 \text{ km} \cdot 4 \text{ d}^{-1}$, Buchans caribou displayed movements that were intermediate compared to other herds where raw observations were made at 4-d intervals (Torgat Mountains herd, $8.3 \text{ km} \cdot 4 \text{ d}^{-1}$: Schaefer & Luttich, 1998; Red Wine Mountains herd, $8.4 \text{ km} \cdot 4 \text{ d}^{-1}$, and George River caribou herd, $33.6 \text{ km} \cdot 4 \text{ d}^{-1}$: Bergman, Schaefer & Luttich, 2000; central Saskatchewan, $\approx 4 \text{ km} \cdot 4 \text{ d}^{-1}$: Rettie & Messier, 2001).

Our approach also allowed us to make comparisons within our study population. Buchans caribou displayed the annual rhythms typical of *Rangifer*, but their more conservative summer movements (Figure 3) were unlike migratory caribou elsewhere. Peak activity of caribou usually coincides with the emergence of biting and parasitic insects, after calving (Bergerud, 1974; Fancy *et al.*, 1989; Schaefer & Luttich, 1998; Bergman, Schaefer & Luttich, 2000). We surmise that the more sedentary habit of the Buchan herd may be afforded by the topography of their summer range, a high barrens with numerous ephemeral streams and ridges, offering exceptional visibility of potential predators and relief from insects.

The use of ratios in ecology is both common and controversial (Atchley, Gaskins, & Anderson, 1976; Prairie & Bird, 1989; Jasienski & Bazzaz, 1999). Computing ratios is an act of scaling (Schneider, 1994). As is clear from the power formula, for two quantities that vary non-isometrically, taking the ratio of one to another does not remedy scale-dependence. Hence ratios, valuable in a descriptive sense, present statistical deficiencies when attempting to correct for scale (Reist, 1985; Jasienski & Bazzaz, 1999; Leonart, Salat & Torres, 2000). Power laws may provide an alternative to the apparent simplicity of ratios.

Uniting approaches across sub-disciplines may be the first step in the unification of ecology. Power laws, "the rules by which scaling is achieved" (Peters, 1983: 11), may provide for this common conceptual framework. We believe that power laws represent a means to synthesis, not only of scaling of body size where they have predom-

inated, but of space and time, the primary dimensions of animal ecology.

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