



Why do population density and inverse home range scale differently with body size? Implications for ecosystem stability

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Abstract

Population density and home range are the two major ecological characteristics pertaining to the ecosystem-level energy use by the species. Home range usually grows more rapidly with body size than does individual metabolic rate. Neither this phenomenon nor the observed absence of isometry between inverse home range and population density (the latter often scaling as the reciprocal of metabolic rate in the inter-ecosystem comparisons) have received a general explanation. Here, we account in theory for the observed scaling exponents in the relationships of population density and inverse home range on body mass and verify our predictions by the available data on birds and mammals. In stable ecosystems, inverse population density and home range represent one and the same measure of animal space use and scale isometrically. Being tightly linked to many genetically encoded morphological and behavioral properties of the species, animal home range, unlike population density, does not change readily with the degree of ecosystem disturbance, thus representing a biological footprint of the undisturbed state of the ecosystem and the animal status within it. The difference between scaling exponents in the mass dependence of home range and inverse population density can reflect the degree of ecosystem disturbance.

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1. Introduction

Home range is defined as the area accommodating all regular activities of the animal, including consump-

tion of energy from the environment (feeding). Already early research in mammals revealed that home range grows significantly more rapidly with body mass than does individual metabolic rate (see, e.g., Harestad and Bunnell, 1979). Recent comprehensive works confirmed this pattern (Nunn and Barton, 2000; Kelt and Van Vuren, 2001). Several theoretical studies sought to quantitatively account for the observed mass scaling

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exponents of home range that typically approximate or somewhat exceed unity. Linstedt et al. (1986) suggested that this value appears as the sum of scaling exponents of individual metabolic rate (3/4) and biological time (1/4) but without proposing a detailed mechanism. Haskell et al. (2002) hypothesized that scaling of home range is controlled by spatial distribution of the available resources; the scarcer the resources (also in terms of space dimensionality), the greater the mass scaling exponent of home range. Haskell et al. (2002) based their consideration on the assumption that all resources available to the animal are consumed during the period of resource renewal; however, no empirical evidence supports this assumption—typically animals are far from fully claiming the available food base. For example, forest rodents normally consume around 14% of the available resources (Grodzinski, 1971). Jetz et al. (2004) proposed that home range scaling in mammals is controlled by the scaling of frequency of interactions between neighbors; however, as we demonstrate below (see Section 4), their analysis suffers from conceptual inconsistencies and contains an incorrect numerical parameterization of neighbor detection distance, which is critical for the model conclusions. These considerations suggest that the theoretical problem of home range, and generally, animal space use scaling, has not been resolved and invites for further exploration.

As illustrated by recent studies, the growing body of evidence suggests that in stable ecosystems energy consumption is dominated by the smallest organisms (Li et al., 2004; Makarieva et al., 2004). This fact was explained under the core assumption that natural ecological communities are organized such as to maximize their stability. To suppress fluctuations of plant biomass introduced by large herbivores, the share of consumption of primary productivity in stable ecosystems must decline with growing body size of the consumers.

Using the developed theoretical approach (Makariev et al., 2004), here, we aim to demonstrate in theory and verify by empirical evidence the following statements:

- (1) In stable ecosystems, population density and inverse home range of herbivores scale isometrically, changing with body mass more rapidly than does individual metabolic rate.
- (2) In unstable (disturbed) ecosystems, population density of herbivores may on average scale as the reciprocal of individual metabolic rate (energy equivalence rule), while the scaling of home range remains the same as in stable ecosystems representing a biological “footprint” of the normal undisturbed state of the ecosystem and the animals status within it.
- (3) Home range of carnivores should grow more rapidly with body mass than does home range of herbivores, the difference depending on scaling of prey size with predator size.

2. Theoretical approach

2.1. Primary consumers

Plants, as primary producers, drive the ecosystem's energetics and local cycles of biogens. To synthesize their biomass, plants take up inorganic nutrients from the local environment. If all biomass synthesized by the plant is subsequently decomposed within the same area occupied by the plant, then the local biochemical cycle is closed. The spatial scale where the local cycle of biogens is closed corresponds to the projection area s_1 of the dominant plant species (e.g., trees in a forest ecosystem), which also accommodates undercanopy vegetation sharing energy and matter fluxes with the dominant plants (Lerat et al., 2002). With fall-off of leaves and fruits, the inorganic biogens are returned to where they were taken from by the plant and are ready for re-use.

Herbivorous animals moving across their home range $H \gg s_1$ enter this scheme as disturbing agents. By consuming more plant biomass in one place and less in the other and excreting the biogens in a similarly spatially random manner, herbivores introduce local fluctuations of energy fluxes and biogen turnover. The magnitude of such fluctuations introduced by a herbivore grows rapidly with body size due to two reasons: first, larger animals have higher per capita energetic demands, and second, larger animals exempt plant biomass in larger portions (e.g., bites, grasps). (For example, in mammalian herbivores, maximum bite size (i.e., the amount of plant biomass taken per bite) grows as $M^{0.71}$ (Shipley et al., 1994).) If these body size effects were not compensated, then

inclusion of large herbivores into any ecosystem in the course of evolutionary process would destabilize the process of photosynthesis, the primary energy flux in the ecosystem, hence undermining ecosystem stability both in terms of live biomass and stores and fluxes of biogens. The potential of large herbivores to destabilize ecosystems is well documented (Van de Koppel and Prins, 1998; Cowling and Kerley, 2002).

At the ecosystem level, the per capita growth of plant biomass fluctuations with herbivore body size can be compensated by a proportional reduction of the share of primary productivity allocated to larger herbivores. That is, while each individual large herbivore does introduce large fluctuations of plant biomass, the cumulative magnitude of fluctuations introduced by the population of large herbivores can be nevertheless kept small if the large animals are few and their population-level energy consumption is low. We have shown (Makariev et al., 2004) that the condition that in stable ecosystems plant biomass fluctuations introduced by herbivores do not grow with herbivore body size makes the share of primary productivity $\beta_h(l)$ claimed by herbivores of linear body size l decline inversely proportionally to l (energetic dominance of the smallest animals):

$$\beta_h(l) \propto \frac{1}{l}. \quad (1)$$

Here, $\beta_h(l) \equiv P_h(l)/P_1$, where P_1 is ecosystem's primary productivity (W m^{-2}) and $P_h(l)$ is the cumulative flux of energy consumption by all herbivorous animals of body size l in a logarithmic body size interval.

Photosynthesizing parts of most higher plants consist of a large number of relatively small, weakly correlated units (leaves, needles). This allows plants to stabilize the flux of photosynthesis and to minimize, in accordance with the statistical law of large numbers, fluctuations of biomass synthesized by the plant (Makariev et al., 2004). This ubiquitous feature of plant organization indicates that the principle of stabilization of energy and matter fluxes is profoundly implicated in the observable biological and ecological structures. Similarly, plants possess a great variety of properties allowing them to control the rate of herbivory, and hence, to minimize fluctuations of plant biomass caused by its consumption by herbivores. Variations in toughness, toxicity, nutrition value of the phytomass produced by the plants, shifts in leaf

phenology, production of attractants for the natural enemies of herbivores (Coley and Barone, 1996; Haukioja and Koricheva, 2000) are but a few means from the vast arsenal employed by plants to control the rate at which their biomass will be consumed by one or another herbivorous species. This suggests that the needed control of energy consumption by herbivores in stable ecosystems resulting in Eq. (1) can be achieved via interactions between plants and herbivores in the natural ecosystems.

The absolute population-level energy consumption P_h of herbivores is related to population density N_h as $P_h = N_h Q_h$, where Q_h is individual metabolic rate (W ind^{-1}) and N_h (ind km^{-2}) is the cumulative population density of herbivores of a given body size. Assuming $Q_h \propto M^{m(Q_h)}$ and $l_h \propto M^{1/3}$, where M_h is herbivore body mass and l_h is its linear body size, we, using Eq. (1), obtain for the mass scaling of population density, $N \propto M^{m(N_h)}$, that $m(N_h) = -(m(Q_h) + 1/3)$. For solitary animals home range H equals inverse population density N , if the latter is measured on contiguous areas inhabited by the species, $H = N^{-1}$, so we have:

$$m(H) = -m(N) = m(Q_h) + 1/3 \quad (2)$$

Field metabolic rate of mammals scales as body mass in the power 0.73 (Nagy et al., 1999). Setting $m(Q_h) = 0.73$ in Eq. (2) gives $m(H_h) = 1.06$ for herbivorous mammals.

Eq. (2) also holds for a more general case when one and the same home territory H is shared by a group of g individuals, $N = g/H$, and g is size-independent. Generally, as demonstrated by recent analyses, change of intraspecific group size with body mass, if any, does not change the scaling exponent $m(H)$ of home range in any significant way, at least in mammals. Indeed, the mass scaling exponents for home range corrected for group size in mammals are 1.02 ± 0.09 , 1.12 ± 0.15 and 1.20 ± 0.19 ($\pm 95\%$ CI) for herbivores, omnivores and carnivores, respectively (Jetz et al., 2004), while with no correction for group size the corresponding values are 1.08 ± 0.15 , 1.21 ± 0.22 and 1.23 ± 0.27 ($\pm 95\%$ CI) (Kelt and Van Vuren, 2001), all falling within the 95% confidence interval of the group-size-corrected values. This suggests that Eq. (2) should be of general validity for mammals in stable ecosystems.

2.2. Secondary consumers: carnivores

Assuming that under natural conditions carnivores (denoted as low index c) exempt a size-independent fraction β_c of productivity of their herbivorous prey (low index h), we have $N_c Q_c = \beta_c N_h Q_h$, where N_c and Q_c are population density and metabolic rate of carnivores. This assumption is supported by the available observations. For example, Carbone and Gittleman (2002) found that at mass-independent $N_h Q_h \propto M^0$, the population density of carnivores per unit productivity of their prey scales inversely proportionally to metabolic rate Q_c , which means that β_c is also size-independent, $\beta_c \propto M_c^0 \propto M^0$. From this, we obtain under the assumption that metabolic rate scales similarly in carnivores and herbivores, $m(Q_h) = m(Q_c) \equiv m(Q)$:

$$N_c \propto N_h \left(\frac{M_h^{m(Q)}}{M_c^{m(Q)}} \right). \quad (3)$$

Here, M_c is carnivore body mass and M_h is body mass of its herbivorous prey. The scaling of carnivore population density will, therefore, depend on how prey mass scales with predator mass. We denote the corresponding scaling exponent as m_{pp} (prey–predator), $M_h/M_c \propto M_c^{m_{pp}}$. Remembering that in stable ecosystems Eq. (2) takes place we obtain from Eq. (3):

$$m(H_c) = -m(N_c) = m(Q) + \frac{1}{3} + \left(\frac{1}{3} \right) m_{pp} \quad (4)$$

Home range in carnivores should grow more rapidly with body mass than home range of herbivores, $m(H_c) = m(H_h) + (1/3)m_{pp}$. This effect becomes stronger with growing m_{pp} , that is, the more rapidly prey size grows with predator size, the more rapidly predator home range grows with predator size.

Before proceeding to testing the derived theoretical predictions, Eqs. (2) and (4), by the available empirical evidence it is necessary to note that these predictions pertain to herbivores with home range H_h greatly exceeding the characteristic vegetation space scale s_1 , $H_h \gg s_1$, and for carnivores feeding on such herbivores. Many smaller animals like small non-flying arthropods can spend most or all of their lives on or under one and the same tree, a home area not exceeding s_1 . Plant biomass consumed by such animals (“residents”, see Makarieva et al., 2004),

and organic matter of their excreta are decomposed under one and the same tree not causing spatial fluctuations of nutrient turnover. Scaling of energy consumption by residents can, therefore, differ from Eq. (1).

3. Empirical evidence

3.1. Herbivore population density in stable versus unstable ecosystems

In disturbed ecosystems, where the natural vegetation cover is disturbed or destroyed altogether and species composition changed, the ecological mechanisms controlling energy consumption by herbivores, based on relationships between indigenous species of plants and herbivores, break down. Consumption of plant biomass by herbivores becomes irregular. Any species independent of its body size can claim a major part of the available primary productivity. This is especially vivid for the artificial agricultural systems. Pests destroying a major part of annual yield ($\beta_h \approx 1$) in such systems may feature greatly varying sizes, from locusts to rabbits and large ruminants. This means that disturbed ecosystems can on average (i.e., when comparisons are made across different ecosystems) conform to the so-called energy equivalence rule, when population energy use is independent of body size, $N \propto 1/Q$ and $m(N) = -m(Q)$. For example, for a world-wide compilation of herbivorous mammals $m(N_h) = -0.73 \pm 0.02$ (± 1 S.E.) (368 species, Damuth, 1987), while $m(Q_h) = 0.73$ (Nagy et al., 1999). This result is in agreement with the well-known fact that most part of terrestrial ecosystems are disturbed by anthropogenic activities, which means that most population density estimates come from ecosystems with varying degrees of disturbance (see also Makarieva et al., 2004, for concrete species examples).

The above consideration does not imply any common scaling pattern for particular disturbed ecosystems, within which the energy consumption is expected to be irregular with respect to body size. Accordingly, scaling exponents $m(N)$ calculated for mammalian population density from various dietary groups in particular habitats vary from -1.41 to $+0.42$ (Damuth, 1993).

As soon as ecosystem stability is taken into account, the energy equivalence rule vanishes. Already a crude division of terrestrial ecosystems into open (less stable) and closed (more stable) showed that in the open systems (pastures, grasslands, etc.) population density of herbivorous mammals is characterized by $m(N_h) = 0.5 \pm 0.1$ (± 1 S.E.), while in more stable closed ecosystems $m(N_h) = 0.9 \pm 0.1$ (± 1 S.E.) (Li et al., 2004), approaching the value predicted by Eq. (3). For plant-feeding vertebrates of undisturbed primary boreal forests, $m(N_h) = -1.03 \pm 0.11$ (± 1 S.D.) (Makariev et al., 2004), in close agreement with Eq. (2).

3.2. Home range scaling in herbivores

While population density of herbivores apparently changes reflecting the ecosystem's state, size of home range is tightly linked to the morphological and behavioral properties genetically encoded in the individual. Indeed, speed at which animals patrol their home territory is a function of the genetically encoded body size (see, e.g., Garland, 1983; Alexander and Maloiy, 1989), actions animals undertake to mark their individual territory and to defend it from intruders (by spraying scents, scratching, vocalization, etc.) (Reby et al., 1998; Revilla and Palomares, 2002; Dulac and Torello, 2003) are also ensured by species-specific biological properties. For example, the rate of territory marking in mice was shown to correlate with prostate size (Vom Saal et al., 1998). Perhaps, the most exciting examples of tight linkage between the genetically encoded morphological properties and territorial behavior have been reported for birds. The African male red-shouldered widowbirds (*Euplectes axillaris*) are black except for red patches on their shoulders (epaulets). By experimentally manipulating the epaulet size and color, it was found that during the breeding season males with enlarged epaulets established larger territories than controls, while most birds with reduced or artificially blackened epaulets were unable to establish a territory at all (Pryke and Andersson, 2003). Studies of passerine birds revealed that territory size in many species increases with the increasing levels of plasma testosterone (Wingfield, 1984).

This consideration suggests that even in disturbed ecosystems, animals are expected to conserve, to a

considerable degree, their home range size, similarly to how they conserve other species-specific biological properties like, e.g., body size, feathering patterns, etc. Home range size thus likely represents a biological “footprint” of the undisturbed state of the ecosystem and the animal status within it. Hence, both in stable and in disturbed ecosystems the scaling exponent $m(H_h)$ of herbivores should conform to Eq. (2). Accordingly, for the home range of mammalian herbivores (164 species) $m(H_h) = 1.08 \pm 0.05$ (± 1 S.E.) (Kelt and Van Vuren, 2001), in excellent agreement with the theoretical value of 1.06 predicted for mammals from Eq. (2).

Note that Eq. (1) describes energy consumption by all herbivores of a given body size, that is, the cumulative energy consumption by all equally-sized species in a stable ecosystem. This is because Eq. (1) conceptually derives from limitation on the cumulative fluctuations of plant biomass introduced by all equally-sized herbivores. Population density data that we discussed for herbivores pertain to individual species. There are more smaller than larger species of mammals. If number $S(M)$ of species of a given body mass M scales as $S \propto M^{m(S)}$, $m(S) < 0$, then the cumulative population density $N = N_s S$ of all species of a given size having a mean population density $N_s \propto M^{m(N_s)}$ would scale as $N \propto M^{m(N_s) + m(S)}$, i.e., decrease more rapidly with M than does species-specific population density N_s . However, the decline of species numbers with body size is most pronounced in a global distribution only (i.e., across ecosystems), but flattens and nearly vanishes on a local scale, i.e., within a particular ecosystem $m(S) \rightarrow 0$ (Brown and Nicoletto, 1991) and $N_s \propto N$. Moreover, when there are several similarly-sized herbivores in the ecosystem one or a few most common species usually claims the dominant portion of energy flux, which can serve as an estimate of the cumulative energy consumption within the corresponding body size interval. For example, among rodents weighing around 20 g in a spruce forest of Alaska *Clethrionomys rutilus* claims around 80% of total energy flux (Grodzinski, 1971); *Rattus rattus* accounts for about 90% of cumulative population density of small rodents in Indian forests (Shanker, 2000); three most common species account for 70% of cumulative population density of the nine mammalian species <200 g in a moist Belizean forest (Kelly and Caro, 2003), etc. As far as the existing compilations of

population density data are naturally biased in favor of more common species, the observed scaling of species-specific population density N_s should be, on average, a good representation of the average scaling of total population density N in particular ecosystems.

3.3. Home range scaling in carnivores

To generate numerical predictions for the home range scaling in carnivores, one needs to know the scaling exponent m_{pp} in the scaling relationship between predator mass M_c and prey mass M_h , see Eq. (4). For 157 species of carnivores (vertebrate consumers) from a variety of taxa including birds, mammals and reptiles (body mass range from 20 g to 160 kg), Vézina (1985) found that mean prey mass grows slightly more rapidly than predator mass, $M_h/M_c \propto M_c^{0.18}$, $m_{pp} = 0.18$. Peters (1983) analyzed the same data while unpublished and reported $m_{pp} = 0.45$ for maximum prey size and $m_{pp} = -0.13$ for minimum prey size. Depending on the preferred prey size of the considered carnivores (whether they mostly rely on the smallest, intermediate or largest prey), the range of home range exponents predicted from Eq. (4) for carnivores is from $m(H_c) = 1.02$ (at $m_{pp} = -0.13$) to $m(H_c) = 1.21$ (at $m_{pp} = 0.45$). The observed value of $m(H_c) = 1.23 \pm 0.09$ (± 1 S.E.) (Kelt and Van Vuren, 2001) for $n = 73$ species of mammalian carnivores coincides with the upper predicted value, suggesting the importance of larger prey in the diets of mammalian carnivores.

We have also studied the corresponding patterns in birds extensively relying on vertebrates (and, in a few cases, large insects) in their diets. Schoener (1968) reported territory size data for 16 such species, defining territory as the exclusive area occupied throughout the breeding season by a breeding pair, which obtains most or all food on the territory. Thus defined, territories are equivalent to non-overlapping (exclusive) home ranges measured during the breeding season. Sticking to this energetically appropriate definition (Schoener, 1968), we enlarged Schoener's dataset to a total of 38 species, mostly hawks, eagles, falcons and owls, Table 1. We considered adjacent home-ranges to be exclusive if the degree of overlap did not exceed 10%.

The log–log ordinary least square regression of exclusive home range (ha) on body mass (g) produced

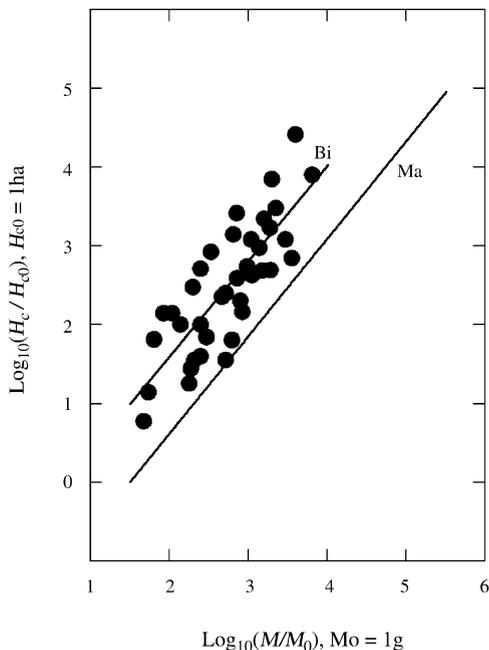


Fig. 1. Dependence of home range H_c (ha) of carnivorous birds (circles, regression line Bi, Table 1) and carnivorous mammals (regression line Ma, Kelt and Van Vuren, 2001) on body mass M (g). Ordinary least square regression parameters: birds $\log(H_c/H_{c0}) = -0.82 + 1.21 \log(M/M_0)$, $R^2 = 0.65$, $p < 0.00001$ (this paper); mammals $\log(H_c/H_{c0}) = -1.84 + 1.23 \log(M/M_0)$, $R^2 = 0.73$, $p = 0.0001$ (Kelt and Van Vuren, 2001).

a slope of 1.21 ± 0.15 (± 1 S.E.), which is nearly identical to that reported for mammalian carnivores, and an intercept of -0.82 ± 0.41 (± 1 S.E.) ($R^2 = 0.65$, $p < 10^{-5}$). Mean territory size of a breeding pair of 1 kg birds of prey is around 650 ha (6.5 km^2). For comparison, mean home range of a 1 kg mammalian carnivore is about 10 times smaller, Fig. 1. This result is consistent with the observation that birds are generally by far less abundant than equally-sized mammals (Greenwood et al., 1996).

4. Alternative explanations of home range versus population density scaling

Recently, Jetz et al. (2004) suggested that the observed scaling of home range is controlled by the frequency f of interactions between neighboring animals. The value of f is equal to the number of

Table 1
Dependence of exclusive home ranges H_c on body mass M in carnivorous birds

Species	M (g)	H_c (ha)	Reference
<i>Accipiter cooperi</i>	470	225	Schoener (1968)
<i>Accipiter striatus</i>	140	100	Schoener (1968)
<i>Aegolius acadicus</i>	85	140	Milling et al. (1997)
<i>Aquila adalberti</i>	3000	1200	Ferrer et al. (2004)
<i>Aquila chrysaetos</i>	1600	2200	Marzluff et al. (1997)
<i>Aquila clanga</i>	1900	1700	Graszynski et al. (2002)
<i>Aquila rapax</i>	2000	7000	Steyn (1982), Tarboton and Allan (1984), Krüger et al. (2002)
<i>Asio flammeus</i>	300	70	Clark (1975), Holt (1992)
<i>Asio otus</i>	250	510	Craig et al. (1988)
<i>Athene noctua</i>	190	28	Schönn et al. (1991)
<i>Bubo virginianus</i>	1510	480	Rohner (1997)
<i>Buteo buteo</i>	850	145	Schoener (1968), Krüger (2004)
<i>Buteo jamaicensis</i>	1130	425	Schoener (1968)
<i>Buteo lineatus</i>	630	64	Schoener (1968)
<i>Buteo regalis</i>	1100	1200	Leary et al. (1998)
<i>Buteo swainsoni</i>	970	545	Schoener (1968), Bechard (1982), Gerstell and Bednarz (1999)
<i>Circus cyaneus</i>	520	250	Schoener (1968)
<i>Corvus corax</i>	1400	940	Schoener (1968)
<i>Elanus caeruleus</i>	250	40	Mace and Harvey (1983), Dunk and Cooper (1994)
<i>Falco femoralis</i>	340	840	Montoya et al. (1997)
<i>Falco mexicanus</i>	720	2600	Schoener (1968)
<i>Falco sparverius</i>	110	140	Schoener (1968)
<i>Falco tinnunculus</i>	200	300	Newton (1979)
<i>Lanius excubitor</i>	65	65	Yosef et al. (1991)
<i>Lanius ludovicianus</i>	48	6	Schoener (1968), Yosef and Grubb (1994), Yosef and Lohrer (1995)
<i>Micrastur gilvicollis</i>	210	36	Klein and Bierregaard (1988)
<i>Ninox natalis</i>	180	18	Hill and Lill (1998)
<i>Ninox novaeseelandiae</i>	250	100	Olsen and Trost (1997)
<i>Nyctea scandiaca</i>	1920	490	Schoener (1968)
<i>Otus flammeolus</i>	55	14	Linkhart et al. (1998)
<i>Parabuteo unicinctus</i>	730	390	Gerstell and Bednarz (1999)
<i>Pithecophaga jefferyi</i>	6500	8000	Collar et al. (1994), Bueser et al. (2003)
<i>Polemaetus bellicosus</i>	4000	26000	Tarboton and Allan (1984), Krüger et al. (2002)
<i>Stephanoaetus coronatus</i>	3600	700	Mitani et al. (2001), Shultz and Noë (2002)
<i>Strix aluco</i>	520	36	Schoener (1968)
<i>Strix occidentalis</i>	650	1400	Solis and Gutiérrez (1990), Call et al. (1992), Zwank et al. (1994)
<i>Strix varia</i>	800	200	Mazur et al. (1998)
<i>Terathopius ecaudatus</i>	2250	3000	Tarboton and Allan (1984), Krüger et al. (2002)

interactions with conspecifics experienced by a given animal per unit time. Jetz et al. introduced proportional home range exclusivity $\alpha \equiv H_0/H$, where $H_0 \equiv 1/N$ is the portion of home range H which is used exclusively by a given animal, while the remaining portion $H - H_0$ is used by its neighbors (intruders) only. Frequency f of interactions between a given animal and its neighbors was set as $f = 4/\pi N D d$, a formula valid for collisions of spherical gas particles in a two-dimensional space, where D is the animal average speed (particle velocity) and d is detection

distance of neighbors (particle radius). Jetz et al. (2004) assumed that average daily speed D scales as $M^{1/4}$, $m(D) = 1/4$, population density N scales as $M^{-3/4}$, $m(N) = -3/4$, and that detection distance d scales as $M^{1/4}$, $m(d) = 1/4$. From these assumptions and postulating that $\alpha = 1/NH$ is proportional to f Jetz et al. (2004) obtained:

$$m(H) = -2m(N) - m(D) - m(d) = 1 \quad (6)$$

This predicted value was shown to fall within the 95% interval of the scaling exponents for home range

corrected for group size in mammalian carnivores, omnivores and herbivores, ranging from 1.04 to 1.20.

The proposed explanation fails on both theoretical and empirical grounds. First, according to the model, while in small animals $H_0 = H$ (the entire home range is exclusively used by its owner), in large animals, a significant or even most part of their home range is lost to neighbors, as far as $H_0 \propto M^{3/4}$, $H \propto M$ and $H_0/H \propto M^{-1/4}$ (Jetz et al., 2004). This result creates the following paradox: why a large animal satisfying all its energetic needs on a small territory H_0 should spend its energy and undertake complex actions to mark, patrol and defend a much larger home range $H \gg H_0$?

Second, the basic model assumption, $\alpha \equiv H_0/H \propto f$, is not given any responsible justification. Jetz et al. (2004) write that “interactions with conspecific neighbors leads to temporary reinforcement of exclusive home range use and hence to reduced resource extraction by home range intruders”, indicating that there must be a positive relationship between H_0 and f . However, this assumption contradicts the other model’s assumptions, like $H_0 \equiv 1/N \propto M^{3/4}$ and $f \propto M^{-1/4}$, which means that among different-sized animals H_0 decreases with increasing f , and not vice versa, as assumed by Jetz et al. (2004). On the other hand, for a fixed body mass, the assumed positive relationship between exclusive home range H_0 and frequency f at fixed body mass strongly contradicts the available evidence. Exactly the opposite, inverse relationship between the exclusive area used by the individual and intrusion pressure was demonstrated in a variety of bird species (see, e.g., Myers et al., 1979; Ewald et al., 1980; Norton et al., 1982). For example, Norton et al. (1982) studied the effect of intrusion pressure on space use by the black-chinned hummingbirds *Archilochus alexandri*. It was found that the exclusive home range H_0 used by the birds decreases inversely proportionally to the intrusion pressure measured as the frequency $F = ND$ of conspecific intrusions per unit time per unit territory border length, which, at fixed detection distance d , is exactly the opposite to the positive relationship between H_0 and $f \propto NDd \propto Fd$ postulated in the model of Jetz et al. (2004). Similarly, dominant males of the red-shouldered widowbird *Euplectes axillaris* occupying larger exclusive territories experience less intrusion pressure than males occupying smaller

territories (Pryke and Andersson, 2003). In other animals no dependence at all between space use and frequency of direct interactions (fights) with conspecifics was found, as, e.g., in mockingbirds (Logan, 1987) or primates (Grant et al., 1992).

Third, by postulating different scaling patterns for H_0 and H the model of Jetz et al. (2004) rejects the existence of territorial animals, that is, those defending exclusive all-purpose territories accommodating all activities of the animal, i.e., animals with $H_0 = H$. In birds, where exclusive territoriality is most widely documented, the scaling of H_0 with body mass M coincides with the scaling of home range H in mammals, see the previous section, Fig. 1 and (Schoener, 1968). The observed $m(H_0) = 1.2$ in birds contradicts the prediction of the model of Jetz et al. (2004), where $H_0 = 1/N$, $m(N) = -3/4$, and hence, $m(H_0) = 3/4$.

Besides these conceptual flaws, the model of Jetz et al. (2004) fails at the more specific level of adopted parameterizations. Scaling of detection distance d , $d \propto M^{1/4}$, $m(d) = 1/4$, Eq. (6), was chosen by Jetz et al. (2004) as the presumable midpoint of the observed range of scaling exponents $0 \leq m(d) \leq 0.5$. This choice was justified by a reference to three literature sources, Garland (1983), Kirschfeld (1976) and Kiltie (2000) and by noting that $1/4$ is an appropriate scaling exponent for “a typical biological distance”. The last argument contradicts the model’s result, as far as if all typical biological distances scaled as $L \propto M^{1/4}$, then all typical biological areas, including home range, should have scaled as $L^2 \propto M^{1/2}$, and not as M^1 as the model predicts for home range.

Among the cited sources, Garland (1983) did not study detection distance at all. Kiltie (2000) analyzed the evidence presented in the earlier work by Kirschfeld (1976), as well as the newly available data, to conclude that detection distance in birds and animals (i.e., the maximal distance at which birds and mammals can notice their conspecifics) scale more rapidly than $M^{1/3}$, i.e., $m(d) > 1/3$ and not $m(d) = 1/4$ as assumed by Jetz et al. (2004). Already at $m(d) = 0.33$, their model predicts $m(H) = 0.92$. This value falls outside the 95% confidence interval of the observed $m(H)$ values for all groups of mammals analyzed by Jetz et al. (2004).

Generally, detection distance d is proportional to the product of linear size of the detected object (which,

in the case of intraspecific detection distance, is simply equal to linear body size l of the considered species) and visual acuity A , which is, in its turn, proportional to the ratio of eye focal length to the linear distance separating the receptors, $d \propto Al$. Kiltie (2000) found that the scaling exponent δ in the dependence of visual acuity A on linear body size l , $A \propto l^\delta$, ranges from 0.76 to 1.10, depending on the animal group studied (nocturnal versus diurnal mammals and birds) and the type of regression applied, $0.76 \leq \delta \leq 1.10$. This means that the mass scaling exponent of detection distance $m(d) = (\delta + 1)/3$ satisfies $0.59 \leq m(d) \leq 0.70$. At the lowest value of $m(d) = 0.59$, $m(d) \propto M^{0.59}$, the model of Jetz et al. (2004) predicts $m(H) = 0.66$, Eq. (6), which is sharp disagreement with the observed $m(H) \geq 1$ in mammals and birds.

It is interesting that the estimated range of the mass scaling exponent for detection distance, $0.59 \leq m(d) \leq 0.70$, rather accurately corresponds to the range of halved scaling exponents $m(H)$ for the home range theoretically obtained for herbivores and carnivores in the present paper, $1.06 \leq m(H) \leq 1.21$ and $0.53 \leq m(H)/2 \leq 0.60$. This means that detection distance d can scale as the square root of home range H , $d \propto H^{1/2}$. This would have a profound biological meaning: species can discern conspecifics at a distance d proportional to the linear dimension of the occupied home range area H . Or, putting it differently, species occupy such home range areas which they normally are able to control and defend from intruders at all times. (Apparently, there are also species where territory control occurs via audible information or by spraying scents or leaving other territory markings, these should be separately studied.)

The idea that animals are biologically designed to occupy exclusive home ranges that are fully controlled by the owners and where no intruders are normally tolerated is further supported by the following consideration. If the population density of animals is N and their movement speed is D , then there are:

$$f_{\text{in}} = NDH^{1/2} \quad (7)$$

intrusions into a home range H having border of length $H^{1/2}$ per unit time. Assuming (to the accuracy of a geometric coefficient) that the home range owner experiences $f = NDd$ interactions with intruders per unit time (Jetz et al., 2004) let us equate f and f_{in} ,

which would mean that the owner responds to all intrusions occurring per unit time:

$$NDd = NDH^{1/2}, \quad d \propto \sqrt{H} \quad (8)$$

In other words, the condition that the owner meets and expels all intruders from its home range independently yields the result which we have previously obtained from the observed scaling exponents for H and d : detection distance should be proportional to the linear size of animal's home range. Remarkably, this result is independent of either N or D or their mass scaling, as far as both N and D terms cancel from Eq. (8).

Detection distance correlates with such species encoded properties as, e.g., eye size (Kiltie, 2000). The obtained theoretical result, Eq. (8), and its agreement with the available evidence confirm our proposition that territorial requirements of the animal represent an inherent species-specific characteristic.

5. Discussion

We have proposed that home range size is an inherent species property, while population density is a more flexible parameter reflecting ecosystem state. It follows from this statement that with the onset of ecosystem disturbance (cutting, burning, invasions, habitat fragmentation, etc.) animal population density is the first spatial variable to distort from its ecologically stable value. Animals should be able to tolerate changes in population density more easily than those of home range. For example, animals can survive overcrowding on areas equal to or exceeding their natural home range, but should rapidly become extinct if concentrated on areas significantly smaller than their natural home range. One can expect, for example, that large carnivores, featuring the largest home territories among vertebrates, will be the first victims of habitat loss and habitat fragmentation. This prediction is consistently supported by observations (Primm and Clark, 1996; Woodroffe and Ginsberg, 1998).

The pervasive importance of natural home range area for normal biological performance can also explain why it is often impossible to obtain viable progeny of large animals in captivity (e.g., in zoos), where animals are forced to occupy tiny areas

incomparable with their natural territory requirements. For example, analyses of zoo environments undertaken to investigate causes of high mortality and suboptimal, unsustainable reproduction in captive populations of black rhinoceros (*Diceros bicornis*) revealed that breeding success of the captive animals was positively correlated with enclosure area (Carlstead et al., 1999). Perhaps, even more vivid is the fact that rhinoceros kept in open areas (where they could see, albeit not move across, a large territory) reproduced better than those enclosed by high walls. This means that the territorial requirements of the species are encoded on the physiological level: a visual signal that a large territory is potentially available is essential for facilitating reproduction process.

We suggested that the fact that in stable (*s*) ecosystems population density N_h and inverse home range H_h of herbivores decline with growing body size more rapidly than the reciprocal of individual metabolic rate Q , $m_s(H_h) = -m_s(H_h) = m(Q) + 1/3 > m(Q)$, can be explained under the assumption that natural ecological communities are organized such as to stabilize local energy and matter fluxes. In this sense, the species encoded territorial requirements and their tight coupling with reproduction (i.e., when individuals failing to establish a territory of sufficient size and quality do not reproduce) serve to keep species population numbers within safe limits not threatening normal functioning of the ecosystem supporting the species' existence. Long-term sustainable existence of species where such genetically encoded intraspecific control of population numbers is absent or weakened (like, for example, is apparently the case in *Homo sapiens*) is more problematic. Uncontrolled exponential increase of population numbers in such species leads to overexploitation of natural vegetation and break down of ecosystem functioning and ultimately brings the species on the verge of extinction. An alternative to intraspecific control of population numbers of a given herbivorous species can be performed by other species of the ecological community. For example, insect–plant interactions in the natural ecological communities are responsible for the fact that in stable forest ecosystems the rate of insect herbivory does not exceed about 10–20% of net primary productivity, i.e., is about ten times lower than the available 100%

(Coley and Barone, 1996) (the remaining 90–80% is consumed in dead form by bacteria, fungi and other small-sized detritivores (Makarieva et al., 2004)). Similarly, studying abundance-size spectra in forest and meadow *Hymenoptera* Ulrich (1999) concluded that there are ecological factors that “force the species to range inside an “allowed” area of density”, which marks the range of population stability. Ulrich (1999) found that in any species exceeding the stability boundaries was followed by a decline or even a collapse of the population in the next generation.

These examples confirm our point that in disturbed (*d*) ecosystems with distorted species composition the ecological mechanisms of population control fail, and some species can claim a major part of primary productivity or even fully destroy vegetation, like, e.g., locusts and other insect pests in agricultural ecosystems (Showler and Potter, 1991). Where ecological limitations on fluctuations of local fluxes of matter and energy are absent or weakened, energy consumption can be on average independent of body size, $m_d(N_h) = m(Q)$, and herbivore population density N_h is not proportional to inverse home range H_h . Scaling of home range area, representing a species-specific property rather than an indicator of ecosystem state, does not depend on the degree of ecosystem disturbance, $m_d(H_h) = -m_s(H_h) = m(Q) + 1/3 > m(Q)$.

This means that in disturbed ecosystems the degree of home range overlap and the number g of herbivores sharing one and the same home range (forming a correlated group or competing for the territory) should grow with body size (Damuth, 1981). This can be manifested as the increased number of non-territorial floaters, enhancement of migration processes, growing social tension and intensification of aggression in larger animals. For example, several groups of gazelles *Gazella gazella* forced to share a small territory surrounded by human settlements and agricultural fields try to maximally avoid contacts, which, if do happen, end in clearly manifested antagonistic behavior (Geffen et al., 1999). For correlated groups, the relationship $m_d(H_h) > -m_d(N_h)$ predicts that in unstable ecosystems group size in large animals should increase as compared to the natural undisturbed ecosystem. This pattern is indeed observed: in seven species of large herbivores group

size is on average 2.9 (from 1.6 to 5.8) times larger in open (less stable) ecosystems (pastures, grasslands) than in closed (more stable) ecosystems (forests) (Gerard et al., 2002).

We conclude that the difference between the absolute values of the scaling exponents $m(H_h)$ and $m(N_h)$ describing scaling of herbivore population density and home range with body mass observed in a particular ecosystem can serve as an indicator of ecosystem state, with $m(H_h) = -m(N_h)$ corresponding to stable and $m(H_h) > -m(N_h)$ to unstable (disturbed) ecosystems.

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