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Review Article

Testing Relationships between Energy and Vertebrate Abundance

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Understanding what drives variation in the abundance of organisms is fundamental to evolutionary ecology and wildlife management. Yet despite its importance, there is still great uncertainty about the main factors influencing variation in vertebrate abundance across taxa. We believe valuable knowledge and increased predictive power could be gained by taking into account both the intrinsic factors of species and the extrinsic factors related to environmental surroundings in the commonly cited *RQ* model, which provides a simple conceptual framework valid at both the interspecific and the intraspecific scales. Approaches comparing studies undertaken at different spatial and taxonomic scales could be key to our ability to better predict abundance, and thanks to the increased availability of population size data, global geographic datasets, and improved comparative methods, there might be unprecedented opportunities to (1) gain a greater understanding of vertebrate abundance patterns and (2) test existing theories on free-ranging animals.

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1. Introduction

Understanding the factors driving patterns in abundance of living organisms is a central challenge in ecology [1, 2], being of both theoretical and practical importance in wildlife management and conservation biology [3]. Such challenge has been defined at different spatiotemporal scales, ranging from understanding temporal variation in abundance at a population scale, a major aim of population dynamics studies [4], to understanding spatial variation in abundance at global scales, one of the major aims of macroecology [1, 2].

At global scales, resource use and supply are often assumed to be major factors driving variation in vertebrate abundance [5–11] and species richness (More Individuals Hypothesis (MIH) [12, 13]). Yet because factors linked with energy are not specifically measured, these assumptions remain highly controversial [13–19]. In addition, studies have been criticized for failing to consider confounding factors [20] and the ecological context in which estimates have been made [21] and overall this situation has led to a lack of generality and precision in previous work as well as poor statistical fits to expected patterns. Here we provide a short perspective on how one might gain a greater understanding of abundance patterns in vertebrates,

at a range of spatial scales through the use of improved analyses taking into account intrinsic factors (e.g., biological traits) and extrinsic factors (e.g., environmental factors) determining energy use and availability (Table 1).

2. Resource Availability and Vertebrate Abundance: A Simple Framework

In order to illustrate our perspective on the importance of defining factors related to energy use and supply, we use a commonly cited simple ecological model [5, 22–24]. The model assumes abundance varies as a function of resource supply and resource use, that is, $N \propto R/Q$ where N is consumer abundance, Q the consumer resource requirements, and R the resource supply rate.

Damuth [5] originally defined Q as the consumer resource requirements, which is linked to metabolic rate [5, 6, 25]. By far the most common measure to approximate Q is Basal Metabolic Rate (BMR [26–28]). Yet basal metabolic rate is measured in captivity under fasting and resting conditions and often represents only a fraction of normal resource requirements in the wild, which are better represented by Field Metabolic Rate (FMR [29]). In addition,

TABLE 1: Possible factors affecting the strength of the energy/abundance relationship at both the intraspecific and interspecific levels. Q refers to the consumer resource requirements, R refers to the resource supply rate, I refers to intrinsic factors (e.g., biological traits), while E stands for extrinsic factors (e.g., environmental factors).

Variable	Intrinsic/Extrinsic	Possible factors (intraspecific level)	Possible factors (interspecific level)
Q	I	Age/Size structure of the populations considered	Body temperature, Phylogeny
	E	Average climatic conditions	Average climatic conditions
R	E	Competition intensity, predation level	Diet (when considering indirect measures of resource abundance such as satellite-based indices of primary productivity)
	I	Spatial location of the studied population within the distribution range of the species	Competitive skills, trophic position, social system

BMR can scale differently from FMR with respect to mass for different taxonomic groups and this can profoundly influence our estimates of metabolic rate for species varying widely in size [30]. Unfortunately, measuring FMR is difficult and costly and there are only a limited number of species for which FMR has been obtained [29]. FMR estimates are especially rare for larger species (20 kg+) and this forces us to speculate on field requirements for these species, either through the use of surrogate measures (e.g., BMR [31]), intake rates or activity budgets [32], or theoretical arguments [33].

Typically, approximations of Q are thus based on body mass, since this parameter has been shown to be closely linked to basal metabolic rate [34]. Across taxonomically similar species, Q can be represented as a simple function of body mass (M) as the power equation $Q \propto M^q$, where q is the resource requirement scaling exponent. Earlier work [5, 25] also found evidence that the density scaling in animals from a range of taxonomic groups falls near the inverse of the expected metabolic rate scaling, $N \propto M^{-q}$. Damuth concluded then, as an approximation, that total population energy use $NQ (= R)$ does not vary systematically across species, or $NQ \propto M^0$. This empirical result, described as “energy equivalence” [22, 35], implies that resource supply rate R is independent of body mass, $R \propto M^0$. This view is, for example, supported in terrestrial mammals where good fit between animal abundance and animal body mass has been reported [5, 23, 25] (Figure 1(a)).

Energy equivalence is however difficult to justify on theoretical grounds especially at global scales [15, 18] and has not been well supported within other taxonomic groups (e.g., birds (see Figure 1(b))) [15, 16] or on smaller spatial scales [15, 18]. Despite these conflicting views, there is a lot of evidence that food resources are limiting in many systems, especially in intraspecific studies where positive relationships between food abundance and population density are commonly reported (e.g., [37–43]).

3. Moving Forward

Having established the view that energy supply and energy use are critical factors driving patterns in animal abundance, we believe a framework defining how abundance studies

vary across taxonomic and spatial scales can help us to develop and focus future research. We present a range of potential complementary approaches, based on the belief that working at different spatial and taxonomic scales is needed to get a complete and integrated understanding of the factors influencing abundance patterns.

3.1. Quantifying Factors Related to Resource Supply, R . Intra-specific studies of abundance patterns on vertebrates have been most successful at incorporating resource information and the same success could be expected by making use of the recent availability of global, detailed spatial datasets regarding primary productivity and climate as well as the large range of intraspecific studies which quantify prey availability (e.g., [37–44]) in interspecific comparisons in abundance. Resource supply rate could indeed be indexed using (i) indirect measures such as rainfall [37] or energy availability derived from satellite data [45, 46] or (ii) direct measures such as prey abundance, biomass, or productivity of resources per unit area [47].

Even though the consideration of such information represents an important step forward, one should keep in mind that indirect measures might not be linearly correlated to resource supply, and the strength of the correlation with resource supply might be dependent on the location and the species considered. For example, herbivore food plants vary greatly in their digestibility so that a satellite-based index (such as the Normalized Difference Vegetation Index (NDVI) [46]) or food volume may not have much meaning to species which select less dominant plant species [48–51]. In addition to resource availability, other factors may have an important influence on abundance, such as the importance of intraspecific and interspecific competition and predation, as these may affect the proportion of available resources that can be allocated to the species considered [52–57]. Across ecologically similar species, there is, for example, sometimes considerable dietary overlap between species [58, 59], so that studies of abundance may be improved by considering local richness of competing species [18, 21]. Another factor potentially affecting resource supply is the spatial location of the population under study within the species range [60]. Densities have often been assumed to be lower at the edge of a geographic range [61, 62], although there is limited empirical evidence for such systematic patterns [63]. Finally,

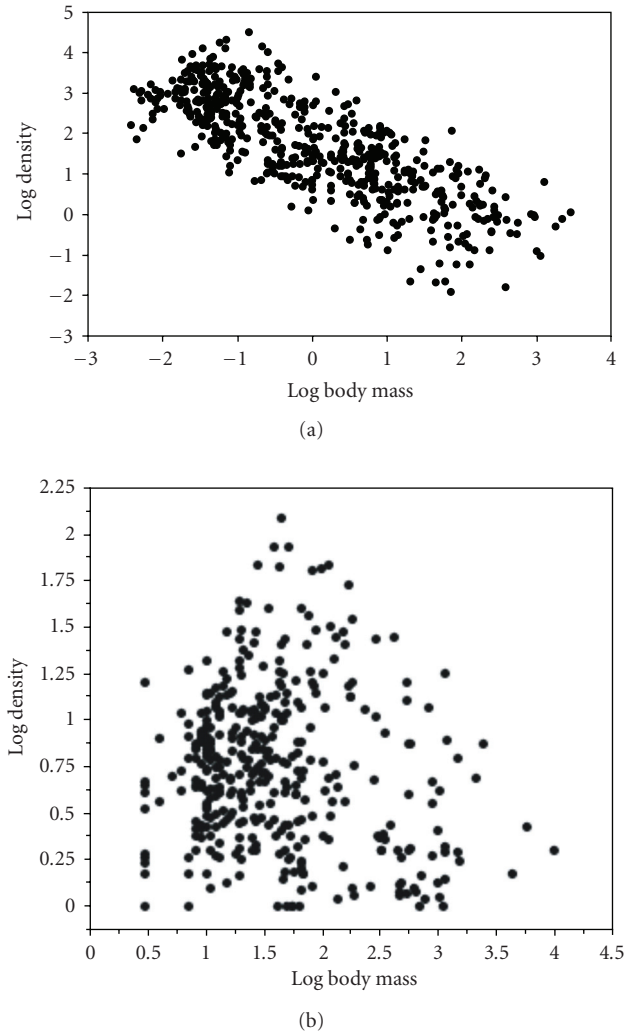


FIGURE 1: Relationship between the \log_{10} of body mass and \log_{10} of density for (a) all mammals (figure based on the original data from Damuth [25]) and (b) birds in North America (figure extracted from Gaston and Blackburn [2]). For mammals, body mass is expressed in kg while density is measured as the number of individuals per km^2 . For birds, body mass is expressed in g while density is measured as the number of individuals per Breeding Bird Survey (BBS) route (see Brown and Maurer [36] for the original dataset description). As it can be seen, body mass is tightly linked to density for mammals (slope = -0.78 , $r = -0.80$, $N = 467$; from Damuth [25]), while the linear relationship between body mass and density is far less tight for birds (slope = -0.08 , $r = -0.13$, $N = 368$; these estimates are based on data reconstruction and subsequent analysis from the original data presented in Brown and Maurer [36, Figure 2]).

when considering scaling relationships, the productivity of resources (measured as biomass/time), rather than biomass alone, provides a more appropriate measure of resource supply [21, 23, 64].

3.2. Quantifying Factors Related to Resource Use, Q . Studies which have focused on traits associated with variation in resource use, Q , have largely been based on interspecific

studies at global [5, 6, 65] and local [7, 11, 66, 67] scales. This is due to the ease with which one can associate differences in size with metabolic rate and resource use [6]. There is, however, the potential to use natural variation in body size within species, to test for the effects of variation in resource requirements. In some species, adult body mass varies several fold across populations (e.g., marine iguana *Amblyrhynchus cristatus*; [68]). Such species provide a great opportunity to explore how abundance varies with mass without added confounding species effects. Size during ontogeny can also vary greatly for some species (e.g., reticulated python *Python reticulatus*; [69, 70]) and there may be the potential in some of these species to examine variation in abundance with growth.

Species do not then represent independent entities, and several studies have suggested that phylogeny might influence the energy/abundance relationship [71]. Across taxonomic groups, species however vary greatly in the physiology and ecology. Endothermic mammals and birds have, for example, been previously reported to have field metabolic rate about 12 and 20 times higher, respectively, than field metabolic rates of equivalent-sized, ectothermic, species (e.g., reptiles; [30]). Likewise, island species of lizards were shown to display consistently higher apparent digestive efficiency than their mainland sibs [72]. Such results highlight the multiple ways in which phylogeny might affect energy-abundance relationships, depending on the phylogenetic scale considered (e.g., endothermic versus ectothermic species; carnivorous mammals versus herbivorous mammals; island versus mainland species). Average climatic conditions (e.g., temperature) experienced by individuals might then influence their metabolic rates, especially in ectothermic species [73]. A key factor that might finally influence the use of resources, space use, and abundance patterns might be the mode of transport [6, 34]. Birds are indeed capable of travelling large distances between food patches compared to mammals and this allows the potential for small species to range widely and occur at low population densities [2]. This might explain the striking differences between birds and mammals in body mass-abundance relationships (Figure 1).

3.3. Building Up a Broad Conceptual Model of Density Variation Based on Detailed Case Studies. Testing separate components of the RQ model using smaller subsets of data which are designed to control for other factors could constitute a complementary approach to developing an integrated understanding of the factors affecting R , Q , and ultimately N . The idea would be, for example, to consider several single species systems from different taxonomic groups to gather knowledge on the factors determining R and Q at this lower scale, in order ultimately to build a broad conceptual model of abundance variation. In indeterminate growing organisms, one could also look at a combination of factors related to R and Q where both body mass and resources may vary across sites and stages of development: this could, for example, be done in reptiles [69], where different age classes live independently and may have different abundance size scaling relationships.

Such knowledge could be gathered using both experimentation and comparative observational studies on focal species. For example, species metabolism (sometimes used to index Q) is expected to vary with environmental conditions such as temperature, and this is especially for ectotherms. Experimentation could help quantifying this relationship for many species, while information on temperature conditions could be integrated in models exploring the relationships between consumer resource requirements, resource supply rate, and the abundance of the focal species.

4. Conclusions

Understanding the relationship between energy and abundance is a fundamental question in ecology, being posed at all spatial scales and for all organisms. When it comes to macroecology, the next challenge is to gain greater predictive understanding of abundance patterns, taking into account both the intrinsic factors of species and the extrinsic factors related to environmental surroundings. In that respect, the RQ model provides a simple conceptual framework to understand abundance patterns in vertebrates, valid at both the interspecific and the intraspecific scales to face such challenge. This simple model allows identifying current gaps in our general understanding of the factors structuring abundance variation, highlighting the need to consider both resource supply and resource use. The challenge lies in correctly indexing R and Q , and we believe gaining a deeper understanding of the factors influencing resource accessibility and energy requirements at different scales and for different species will help identify better proxies of these crucial parameters. Previous analogous conceptual approaches, such as the ideal free distribution model [52], have demonstrated their usefulness in developing an understanding of animal distributions [74], and the RQ model could be as successful in developing an understanding of spatiotemporal variation in animal abundance.

Acknowledgments

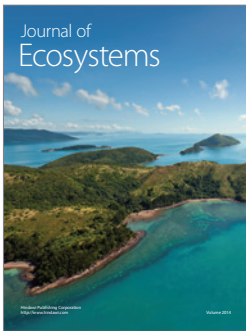
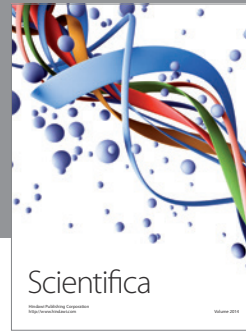
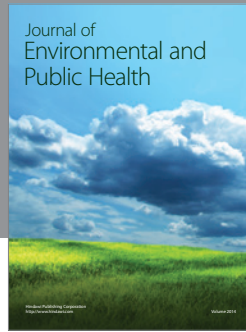
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