Synthesis

Macrophysiology: A Conceptual Reunification

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Submitted February 26, 2009; Accepted June 29, 2009; Electronically published September 29, 2009

ABSTRACT: Widespread recognition of the importance of biological studies at large spatial and temporal scales, particularly in the face of many of the most pressing issues facing humanity, has fueled the argument that there is a need to reinvigorate such studies in physiological ecology through the establishment of a macrophysiology. Following a period when the fields of ecology and physiological ecology had been regarded as largely synonymous, studies of this kind were relatively commonplace in the first half of the twentieth century. However, such large-scale work subsequently became rather scarce as physiological studies concentrated on the biochemical and molecular mechanisms underlying the capacities and tolerances of species. In some sense, macrophysiology is thus an attempt at a conceptual reunification. In this article, we provide a conceptual framework for the continued development of macrophysiology. We subdivide this framework into three major components: the establishment of macrophysiological patterns, determining the form of those patterns (the very general ways in which they are shaped), and understanding the mechanisms that give rise to them. We suggest ways in which each of these components could be developed usefully.

Keywords: biogeography, evolution, geographic range, macroecology, patterns, physiology.

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Am. Nat. 2009. Vol. 174, pp. 595–612.
0003-0147/2009/17405-51109$15.00.
DOI: 10.1086/605982

Introduction

The fundamental importance of documenting and understanding biological patterns at large spatial and temporal scales has come increasingly to the fore in recent decades (Hengeveld 1990; Brown 1995; Maurer 1999; Gaston and Blackburn 2000; Gaston 2003). The principal drivers have arguably been threefold. First, there has been recognition that many local biological, and particularly ecological, phenomena can best be interpreted within a broader regional/global or a longer temporal (including phylogenetic) context (Colwell and Winkler 1984; Ricklefs 1987; Brown and Maurer 1989; Cornell and Lawton 1992; Ricklefs and Schluter 1993; Gaston and Blackburn 2000; Webb et al. 2002). Second, it has become clear that many of the most pressing issues facing humanity are operating on large spatial and temporal scales (e.g., climate change, food security, maintenance of ecosystem services, emergence of new diseases; Rosenzweig and Parry 1994; Barnett et al. 2001; MEA 2005; Wolfe et al. 2007). Third, the availability and analysis of data at large spatial and temporal scales has greatly improved, particularly through growth in the number of local studies and monitoring schemes and better technologies (e.g., satellites), databases, computing power, and statistical tools (Gaston 2003; Kerr and Ostrovsky 2003; Jones et al. 2006; Diniz-Filho et al. 2007; Kozak et al. 2008). This has enabled studies to be conducted in ways that previously were impossible.

Recognition of the importance of studies at large spatial and temporal scales has led to the development of particular bodies of biological research focused on these topics and increasingly explicitly distinguished as coherent fields or subdisciplines of study. Most obviously these include landscape ecology, macroecology, and macroevolution (Stanley 1979; Forman and Godron 1986; Brown 1995; Gaston and Blackburn 2000). Importantly, the more recent work done in such fields has strong historical roots, often building on studies that were conducted many decades ago and resulting in the wider recognition that these subdisciplines are now stimulating new conceptual developments and avenues for research.

In this vein, it has recently been argued that there is a need to reinvigorate large spatial- and temporal-scale studies in physiological ecology through the establishment of a macrophysiology (Chown et al. 2004; Chown and Gaston 2008). Such studies were relatively commonplace in the first half of the twentieth century, following a period when the fields of ecology and physiological ecology had been regarded as largely synonymous (e.g., Shelford 1911; Chapman 1931; Fox 1936, 1938, 1939; Fox and Wingfield 1937; Moore 1939, 1942*b*, 1952; Scholander et al. 1953; Andrewartha and Birch 1954; Scholander 1955; Bartholomew 1958; for reviews, see Vernberg 1962; Garland and Adolph 1991; Huey 1991; Spicer and Gaston 1999). However, compared with the subsequent flourishing of studies of the biochemical and molecular mechanisms underlying the capacities and tolerances of species, large-scale work remained rather marginal. These developments are reflected, for example, in explicit remarks about the absence of ecology in physiological ecology (Kingsolver 1988), the mounting domination of molecular biology in the physiological sciences (Weibel 1997), implicit exclusion of ecology in discussions of new directions in comparative physiology and biochemistry (Mangum and Hochachka 1998), and a detailed treatment of how ecology and physiology drifted apart in the twentieth century (Huey 1991). They are also highlighted by the trend of an increasing subdivision or renaming of journals to deal with the focus on mechanisms at lower levels in the biological hierarchy (e.g., the subdivisions of *Comparative Biochemistry and Physiology*, *Journal of Comparative Physiology*, and *Journal of Experimental Zoology* and the renaming of *Physiological Zoology* to *Physiological and Biochemical Zoology*). In some sense, macrophysiology is thus an attempt at a conceptual reunification that has often been suggested (e.g., Lawton 1991; Spicer and Gaston 1999) and is echoed in its proposed formal definition as "the investigation of variation in physiological traits over large geographical and temporal scales and the ecological implications of this variation" (Chown et al. 2004, p. 160).

Renewed interest in large-scale physiological patterns and processes has been particularly stimulated by recognition that these may provide valuable insights into causes of physiological variation that otherwise are not obvious at local scales (Chown and Gaston 1999; Spicer and Gaston 1999; Hoffmann et al. 2001, 2003; Osovitz and Hofmann 2007; Stillman and Tagmount 2009). Local and short-term studies will, of course, remain important in such an endeavor, but it seems highly likely that the most rapid progress will be made by drawing on the strengths (and acknowledging the weaknesses) of both small- and large-scale, and short- and long-term, investigations. The need for a macrophysiology has also been fueled by the great attention that has been paid to macroecological patterns and processes recently (Brown 1995; Gaston and Blackburn 2000; Blackburn and Gaston 2003) and the physiological assumptions that lie behind many of the explanations that have been proposed for them (Stevens 1989; Gaston et al. 1998; Chown and Gaston 1999; Spicer and Gaston 1999; Clarke and Gaston 2006; Ghalambor et al. 2006; Millien et al. 2006; Kearney and Porter 2009). Moreover, it is increasingly appreciated that prediction of the outcomes of interactions between the major drivers of environmental change will require understanding across a wide range of hierarchical levels (Spicer and Gaston 1999; Pörtner 2002; Ricklefs and Wikelski 2002; Wikelski and Cooke 2006; Chown et al. 2007; Brook 2008; Brook et al. 2008; Cooke and Suski 2008). In general, technological developments have doubtless played a smaller role in stimulating renewed interest in large-scale physiological patterns and processes, although they have been particularly significant in enabling the measurement and investigation of plant physiology, and the consequences of variation therein, over large spatial and temporal scales (e.g., Grace et al. 1995; Running et al. 2000; Buchmann et al. 2002; Baldocchi 2003; Santos et al. 2003; Jones 2004; Wright et al. 2005; Piao et al. 2007; Reich et al. 2007).

In this article, we provide a conceptual framework for the continued development of macrophysiology. We subdivide this framework into three major components: (*a*) the establishment of macrophysiological patterns, (*b*) determining the form of those patterns (the very general ways in which they are shaped), and (*c*) understanding the mechanisms that give rise to them. Although these three components are conceptually helpful, they are clearly interrelated in most investigations (Wiegert 1988; Wilson 1988).

Patterns

MacArthur (1972, p. 1) observed that "to do science is to search for repeated patterns, not simply to accumulate facts" (see also Feder 1987). Both spatially and temporally, three main kinds of macrophysiological patterns may be observed: intraspecific, interspecific, and assemblage (Gaston et al. 2008). These are perhaps most easily construed in terms of a simple species by sites (or, for temporal variation, by times) matrix ($r \times c$), in which species are given in rows (r) and sites/areas or times/periods are in columns (c). Typically the cells of such a matrix would contain the presences/absences of species or their respective abundances at a series of sites or times (e.g., Simberloff and Connor 1979; Gaston 2002; Bell 2003). However, they can equally contain the values of physiological traits or other features (and be subject to matrix algebra in the same way). When we consider spatial patterns, the sites can most usefully be sequenced in terms of the gradient of interest (positional or environmental), and when we consider temporal patterns, they can be thought of as sequenced in some temporal order, although in practice we are often interested in the relative position of sites along a continuum of those gradients (and also in the maps that can be generated by projecting the contents of the $r \times c$ matrix into geographical space).

Intraspecific, Interspecific, and Assemblage Patterns

Intraspecific patterns concern variation in traits along the rows of the matrix. That is, spatial or temporal variation in the physiology of individual organisms or populations with positional (e.g., latitude, longitude, altitude, depth) or temporal variables or environmental variables characterizing those locations or times (e.g., temperature, precipitation, salinity, solar radiation, productivity). Environmental variables, in particular, attract much attention as potential drivers of patterns of spatial or temporal variation in physiological traits. Intraspecific patterns might also concern the frequency distributions of such trait variation and how these change through space and time. In this case, temporal variation tends to be investigated (e.g., invertebrate supercooling points; Cannon and Block 1988; Sinclair et al. 2003), although a few studies have also made comparisons of spatial variation in the form of these distributions (Block 1982; Grant and Dunham 1990; Worland et al. 2006). More typically, spatial or temporal variation among population means and extremes tend to be studied (Garland and Adolph 1991). Those that have been documented include patterns of variation in temperature tolerance (Blem 1974; Smith and Ballinger 1994; Lemos-Espinal and Ballinger 1995; Hoffmann et al. 2001; Klok and Chown 2003; Bernardo and Spotila 2006; Pörtner et al. 2008; Sepulveda et al. 2008; Stillman and Tagmount 2009), desiccation resistance (Arad et al. 1992, 1993), water use efficiency (Hultine and Marshall 2000; Maron et al. 2007), metabolic rate (Kendeigh 1976; Clarke and Johnston 1999; Wikelski et al. 2003; Bernardo and Spotila 2006; Lardies and Bozinovic 2006), development time (Weber and Schmid 1998; Burke et al. 2005; Mitchell et al. 2008), various performance traits such as growth rate and running or swimming speed (Huey et al. 1990; Sinervo and Losos 1991; Bernardo 1994; Miles 1994; Jonsson et al. 2001; Bernardo and Reagan-Wallin 2002; Arnott et al. 2006), gene transcription and translation (Fangue et al. 2006; Whitehead and Crawford 2006; Cheviron et al. 2008; Karl et al. 2008; Stillman and Tagmount 2009), enzyme isoforms (Pierce and Crawford 1996; Rank et al. 2007), and membrane properties (Pernet et al. 2008). Importantly, it should be recognized that patterns at one level (e.g., hydrocarbon properties) may be construed as mechanisms at another (e.g., the mechanistic basis of reduced water loss; see Gibbs 2002). However, such pattern/mechanism relationships among hierarchical levels, within organisms, do not alter the fundamental intraspecific form of the variation. Indeed, they may be vital for understanding the evolution of geographic variation among populations (e.g., Powers 1987; Pörtner 2002; Rank et al. 2007; Saastamoinen et al. 2009). Thus, intraspecific variation also provides a powerful framework for studying adaptive evolution, as the variation among individuals/genotypes in physiological traits within a population represents the variation available for selection to act on, while the variation between populations reflects the competing pressures of divergent selection, gene flow, and drift (see Kawecki and Ebert 2004).

Interspecific patterns principally concern relationships between the traits of different species occurring in different places and the positional or environmental characteristics of the sites or times at which they occur, although they may also concern the frequency distributions of those traits (note that intraspecific and interspecific patterns may be mixed by including separate data points for multiple individuals or populations of multiple species, but this can serve to confound and confuse fundamentally different, albeit often closely related, issues). Most frequently, the traits are expressed at the level of the individual organism and thus concern many of those embodied in intraspecific patterns, with the values typically being derived as means or medians across multiple individuals (e.g., desiccation resistance, immune function, metabolic rate, sprint speed, thermal tolerance, development rate, and regeneration rate; Bosch et al. 1987; Tsuji 1988; van Berkum 1988; Sommer et al. 1997; Andrews 1998; Gaston and Chown 1999; Hoffman and Harshman 1999; Addo-Bediako et al. 2000, 2001; Lovegrove 2000; Gibert and Huey 2001; Van Damme and Vanhooydonck 2001; Stillman 2003; Martin et al. 2004, 2005; Mommer et al. 2006; Bannister 2007; Clark et al. 2007; Clusella-Trullas et al. 2008). A latitudinal midpoint or mean of an abiotic variable is often used as the independent variable against which variation in the trait is assessed. It is important to recognize that using this approach may obscure important intraspecific variation, emphasizing the potential benefits of explicitly exploring both intraspecific and interspecific patterns. Alternatively, the characteristics being investigated may be attributes expressed only at the species level. For example, in macroecological studies, geographic range size or global population size has been examined (Gaston and Blackburn 2000), although to date few macrophysiological studies have investigated equivalent traits.

Assemblage patterns are those in the structure of the assemblages occurring in different places or at different times. They are typically derived from averaging, summing, or otherwise characterizing the columns of an $r \times c$ matrix and, thus, the physiological composition of each site or time across species. The existence of assemblage patterns is implicitly assumed in many statements about the characteristic physiological traits of species inhabiting particular kinds of environments, and they are thus important to much generalization about spatial and temporal variation in physiology. Their documentation has, nonetheless, been surprisingly poor (but see Addo-Bediako et al. 2000).

All three sets of macrophysiological patterns—intraspecific, interspecific, and assemblage—may also include relationships between two or more different physiological traits, across either sites or times. Such patterns essentially concern levels of covariation in these traits as they individually change with position, time, or environmental conditions (e.g., tests of hypotheses of coadaptation often use data on interspecific variation in the mean values of two or more traits; see Huey and Bennett 1987; Angilletta et al. 2006; Clusella-Trullas et al. 2008).

Intraspecific, interspecific, and assemblage macrophysiological patterns all have a phylogenetic context, reflecting the evolutionary relationships between populations and species. The use of formal comparative methodology to account for these relationships is best developed for interspecific patterns, in which it has long been recognized that the failure to do so can lead to misleading interpretations of results (Felsenstein 1985; Martins et al. 2002; Carvalho et al. 2006; for examples of analyses of interspecific macrophysiological patterns, see Ricklefs et al. 1996; Rezende et al. 2004; White et al. 2007*b*; Huey et al. 2009). Although most studies have employed phylogenetic information to control for the nonindependence of the data due to shared ancestry, this information may also provide important clues as to processes underlying the emergence of macrophysiological patterns such as estimations of evolutionary rates and models of character evolution, patterns of dispersion and vicariance of the taxa involved, and reconstruction of ancestral states (for introductory texts, see Pagel 1999; Garland et al. 2005). Evolutionary relationships among populations are only now starting to be employed in the analysis of intraspecific macrophysiological patterns (e.g., Terblanche et al. 2009). The absence thereof may be a particular concern for studies examining numbers of populations over large geographic extents, but appropriate phylogeographic data are often not available. Comparative methods may also be suitable for the study of assemblage patterns, in which nonindependencies between data points result both from particular species being directly shared between assemblages and from different but related species being shared (software such as Phylocom can estimate different metrics of interassemblage phylogenetic dissimilarity; Webb et al. 2008). However, we are not aware of their application as yet in the context of macrophysiological assemblage patterns.

Laws, Rules, Effects, and General Tendencies

Views differ markedly as to how frequently biological patterns have to be documented, and how seldom exceptions have to be found, for them to be regarded as generalities and how firm such generalities have to be before they are more formally termed effects, rules, or even laws (Mayr 1956; Gaston et al. 1998, 2008; Lawton 1999; Lomolino et al. 2006*a*, 2006*b*). Regardless, there are a large number of macrophysiological patterns that have been documented frequently, or otherwise seem likely to have a high degree of generality (table 1). While none of these have formally been termed macrophysiological rules or laws, they seem arguably to be as general as many patterns in other biological fields that have gained such epithets.

The majority of these generalities concern aspects of thermal biology at the intraspecific or interspecific levels (table 1); general patterns at the assemblage level appear to be very scarce. Most have deep historical roots, although they have often been much better documented and are more fully understood in recent work (other generalities with similarly deep roots clearly are closely related but are not treated here as strictly macrophysiological, e.g., Allen's rule, Bergmann's rule, Rensch's rules; Lincoln et al. 1982). However, other macrophysiological patterns that seem likely to stand the test of time at this point have only been revealed much more recently (e.g., Lovegrove 2000; Stillman 2003; Deutsch et al. 2008; Helliker and Richter 2008; Wittmann et al. 2008). This raises the possibility that more such patterns have yet to be discovered.

For each generality, we have attempted to identify the individual researcher with whom it has most closely been associated (table 1). In the past there would have been a general acceptance that the effect, rule, or law became known by the researcher's name. Although such labeling has fallen heavily out of favor, there may be something to be said for reestablishing it, inasmuch as it often makes for a brief and distinct terminology. We note, however, that such labeling risks simplification and overlooking key early work leading to the development of any particular rule. Nonetheless, it may, for example, stimulate investigation to determine the generality (or lack thereof) of key physiological assumptions often made in macroecological investigations (the physiological aspects of the environmental variability hypothesis underlying the Rapoport effect offer an important example; see Stevens 1989; Addo-Bediako et al. 2000). In table 1, one of the named general patterns that is especially contentious is Krogh's "rule," and the contention serves to highlight the need to explore the idea more carefully. Krogh's rule, as expressed here, differs from Krogh's normal curve, which is the positive, intraspecific relationship between metabolic rate and measurement temperature so widely found in ectotherms. Rather, we refer here to among-population and among-species variation in mean metabolic rates. Sometimes also known as metabolic cold adaptation, it appears increasingly that many marine species do not show this pattern and that this may also vary depending on the evolutionary age of a given group in an area (i.e., responses vary among younger vs. older polar species [see, e.g., Clarke 1993, 2003] and may also relate to climate and temperature variability [Pörtner 2006]). Accordingly, the pattern seems to be quite general in terrestrial insects (Addo-Bediako et al. 2000) and in subarctic marine species (e.g., Pörtner et al. 2008). A similar phenomenon is also found in plants, in which annual nighttime CO_2 flux is unrelated to average annual nighttime temperature across a variety of North American and European sites (assemblage level) and mass-corrected tree growth is not influenced by ambient growing-season temperature (Enquist et al. 2007).

A clear preliminary goal of macrophysiology is the production of a catalog of macrophysiological patterns. This will require both the inevitably somewhat haphazard accumulation of a much larger body of published studies testing the occurrence of particular patterns for given species, taxa, and assemblages and also a more carefully targeted approach to determine the full breadth of species for, and circumstances under, which particular patterns do or do not emerge.

Unification

Given that all are drawn from the same $r \times c$ matrix and fundamentally depend on the same biological determinants (and hierarchies), intraspecific, interspecific, and assemblage patterns cannot be entirely independent. Conventional unifying principles in physiology would be those of energy, water, mass, and nutrient balance, and one can doubtless think of macrophysiological patterns in such terms. However, in the context of macrophysiology and its explicit links with ecology and evolution, a more appropriate unification, at least of observed spatial patterns, may be through the geographic ranges of species. Intraspecific patterns describe the structure of the geographic ranges of species, and the mechanisms underpinning those patterns are what structure ranges (Gaston 2003). Interspecific patterns are derived from the structure of the geographic ranges of individual species and variation in the location of the geographic ranges of species exhibiting differences in a particular trait. Finally, assemblage patterns are derived from the structure of the geographic ranges of individual species, variation in the location of the geographic ranges of different species, and also the number of ranges (the range overlaps) in an area (all of which may be influenced by species' interactions).

A unification of macrophysiological patterns around the structure of geographic ranges serves readily to link them, logically and to some extent mechanistically, to many other ecogeographic and ecotemporal patterns (Gaston et al. 2008). Not only can many of these latter patterns best be thought of in terms of the structure of geographic ranges, but range size plainly plays an important role in speciation processes and thus in the development of the phylogenetic dependencies of species traits (Gaston 2003). A focus on geographic ranges as a core unit of macrophysiology would also fit well with a more general increase in the attention that they are receiving (e.g., Brown et al. 1996; Gaston 2003, 2009; Holt et al. 2005; Eckert et al. 2008). This is particularly being driven by the demand for predictions of the likely responses of species' distributions to anthropogenic climate change (see Kearney and Porter 2009), and the resultant needs to understand the patterns of niche conservatism (the retention of ancestral ecological characteristics; Wiens and Graham 2005). Both are obviously highly relevant to macrophysiology.

One variable that appears frequently in discourses about large-scale physiological patterns but does not fit well within the above framework of intraspecific, interspecific, and assemblage patterns in physiological traits is that of body size. A similar argument can be made with regard to large-scale intraspecific, interspecific, and assemblage patterns in ecological traits, which principally concern variation in species occurrences and abundances (Gaston and Blackburn 2000). Indeed, body size might perhaps best be viewed as providing an important link between macroecological and macrophysiological patterns, which sits well with the metabolic theory of ecology (Brown et al. 2004) and the focus on allometric and other scaling relationships.

Table 1: Possible macrophysiological “rules”

	Generality/taxonomic constraint	IA	IR	AS	References
Thermal biology:					
Payne	Degree of cold hardiness increases with seasonal climatic variation (originally for insects but applies to all taxa)		✓	✓	Payne 1926; Allee et al. 1949; Scholander et al. 1950; Addo-Bediako et al. 2000
Brett	Less geographic variation in upper than in lower thermal limits (mostly terrestrial ectotherms, although originally proposed for fish)	✓	✓		Brett 1956; Snyder and Weathers 1975; Gaston and Chown 1999; Addo-Bediako et al. 2000; Klok and Chown 2003; Hoffmann et al. 2005; Ghalambor et al. 2006
Janzen	Increase in thermal tolerance range with increasing latitudinal position (animals; has been applied to altitude and extended to include relationship between thermal tolerance range and environmental temperature; marine systems are more complex, owing to polar stenothermy; Pörtner 2002)	✓	✓	✓	Janzen 1967; Snyder and Weathers 1975; Addo-Bediako et al. 2000; Klok and Chown 2003; Compton et al. 2007; Deutsch et al. 2008; Tewksbury et al. 2008
Vernberg	Positive relationship between extent of thermal acclimation and latitude (animals; marine systems are more complex, owing to polar stenothermy; Pörtner 2002)	✓	✓		Vernberg 1962; Janzen 1967; Ghalambor et al. 2006
Brattstrom	Positive relationship between thermal acclimation ability and geographic range size (ectothermic animals)	✓	✓	✓	Brattstrom 1968; Calosi et al. 2008*a*, 2008*b*
Bogert	Positive relationship between external reflectance and solar radiation (ectothermic animals; note that this is the opposite of Gloger’s rule for endotherms; a Bogert effect has also been named by Huey et al. [2003], which has to do with the influence of behavior on physiological evolution)	✓	✓	✓	Bogert 1949; Mani 1968; Clusella-Trullas et al. 2007, 2008
Metabolic rate and energetics:					
Krogh	No relationship or a slight negative relationship between mean standard metabolic rate and ambient environmental temperature (terrestrial animals and plants; also known as metabolic cold adaptation; typically not seen in marine organisms at the whole-organismal level, with exceptions in the subarctic)	✓	✓		Krogh 1916; Fox 1936; Prosser 1986; Clarke 1991, 1993, 2003; Huey and Berrigan 1996; Chown and Gaston 1999; Addo-Bediako et al. 2002; Steffensen 2002; Wikelski et al. 2003; Pörtner 2006; Enquist et al. 2007; White et al. 2007*a*; Jacobsen and Brodersen 2008
Dehnel	Small mammal body mass varies with season in north-temperate systems	✓			Dehnel 1949; Mezhzherin 1964; Stenseth 1978

Water and ionic balance:					
Mellanby	Negative relationship between desiccation resistance and water availability (ectotherms)	✓	✓	✓	Mellanby 1935; Bursell 1958, 1959; Edney 1977; Zachariassen et al. 1987; Hadley 1994; Addo-Bediako et al. 2001
Development:					
Moore	Negative relationship between development rate and habitat temperature or growing-season length (ectothermic animals; early statement of countergradient variation)		✓	✓	Moore 1942*a*; Conover and Present 1990; Conover and Schultz 1995; Gotthard and Nylin 1995
Other:					
Gause	Negative relationship between acclimation ability and extent of initial tolerance (ectothermic animals; initially proposed in the context of salinity, this work foreshadows work demonstrating the same effect for critical thermal limits)		✓		Gause 1942; Chown 2001; Stillman 2003
Baker	Invasive species have greater phenotypic plasticity and environmental tolerance than indigenous species		✓		Baker 1965; Daehler 2003; Chown et al. 2007; Brook 2008

Note: We indicate the author of the earliest demonstration of the generality of which we are aware or the researcher with whom it is most widely associated; any major taxonomic constraint on the generality; whether the generality is likely to be apparent at intraspecific (IA), interspecific (IR), or assemblage (AS) levels (see text for details; in the interests of brevity, these are not given separate entries in the table, although it is important to distinguish at what level any particular macrophysiological pattern is being explored); and the studies in which the generality was originally described and that report other empirical examples.

A key question then becomes the extent to which body size is treated as a given, from which other trait states follow (e.g., Brown et al. 2004; White et al. 2007*c*), or as a response to other trait states (e.g., Roff 1981; Bernardo 1994; Bernardo and Reagan-Wallin 2002; Etilé and Despland 2008) or whether it follows from a complex interplay between these two extremes (Chown and Gaston 1999; Kozłowski et al. 2004; Cabanita and Atkinson 2006; Bernardo et al. 2007; Kaiser et al. 2007). It is useful to consider each of these viewpoints, depending on the objectives of a macrophysiological study. Sometimes it is most helpful to view body size as an important determinant of physiological tolerances and capacities, sometimes as being influenced by these tolerances and capacities, and sometimes as a combination of both.

In a related vein, and secondarily, body shape may also play a significant role in linking macroecological and macrophysiological patterns. Although it is often overlooked in both contexts, in combination with body size, shape affects surface-to-volume ratios and thereby influences metabolic rate, desiccation, food and water requirements, sheltering behavior, locomotion, and spatial distributions (Gates 1980). Body size and shape are also constrained by the physical environments available to a species (e.g., fossorial or arboreal habitats). Morphological properties affect developmental times, potential growth rate, time to sexual maturity, movement distances, resource requirements, parts of the environment that an organism can use, and many other physiological and ecological aspects of species and their geographic ranges (see, e.g., Lovegrove 2001). The interactions and interconnections of morphological, physiological, and behavioral properties constrain the set of properties feasible for any given environment.

Form of Patterns

There is a perhaps inevitable predisposition on the part of investigators of large-scale physiological patterns to step directly from the observed patterns to considerations of how these are shaped and what they tell us about the typical ecophysiological mechanistic currencies of energy, water, mass, and nutrient balance (Prosser 1986; Hochachka and Somero 2002; McNab 2002; Chown and Nicolson 2004). However, particularly given the potential applied significance of some of these patterns, it also may be well worth dwelling on what can perhaps be regarded as an intermediate step, examining how these patterns are formed in much more general terms.

One potentially useful way of doing this (building on the work of Kunin 1997; Gaston 2006; Gaston et al. 2008; see also Darlington 1943) is to think of macrophysiological patterns in terms of three sets of processes: entry rules, exit rules, and transformations. Entry rules are biases in the processes that determine which individuals or species join a population or assemblage through immigration or speciation; exit rules are biases in the processes that determine which individuals or species leave a population or assemblage through emigration or extinction; and transformations are changes caused by environmentally induced or genetically based processes, such as shifts in resource profiles, behavior, or tolerance, that act on individuals or species when they are members of a particular population or assemblage at a given spatial location at a particular time. For example, the extent to which phenotypic plasticity in physiological or behavioral traits can promote or retard adaptation (Lee et al. 2003; Dybdahl and Kane 2005; Ghalambor et al. 2007) is an especially relevant, although underexplored, component of the ways in which transformation may lead to macrophysiological patterns and their subsequent consequences for ecological and evolutionary variation.

All macrophysiological patterns are effectively shaped by one or more entry rules, exit rules, or transformations. For example, consider a simple interspecific gradient of decreasing critical thermal minimum temperatures (CT_{min}, the temperature that defines the lower limit of normal physiological, behavioral, and ecological function) from low to high latitudes (Snyder and Weathers 1975; van Berkum 1988; Addo-Bediako et al. 2000; Deutsch et al. 2008). First, it could be generated because species with lower CT_{min} invaded areas at higher latitudes or speciation in those areas gave rise to organisms with lower CT_{min} (entry rules). Second, it could arise because species that did not have lower CT_{min} at higher latitudes emigrated or became extinct in those areas (exit rules). Finally, the gradient could arise because variation in selection with latitude resulted in those species that were present acquiring systematically different CT_{min} either through acclimatization or adaptive evolution (transformations).

Plainly, human activities have influenced all three of these sets of rules. Chown and Gaston (2008) highlighted how a macrophysiological approach can help elucidate the impacts of the major drivers of biodiversity loss and sources of concern for human well-being (climate change, habitat destruction, invasive species, overexploitation, and pollution). Taking each of these drivers in turn, it can be argued that the effects of habitat destruction on macrophysiological patterns are so profound because they result in large influences on entry and exit rules and transformations (e.g., Brooks et al. 2002; Brook et al. 2003; Angilletta et al. 2007; Cheptou et al. 2008). The effects of climate change are more spatially variable, particularly on entry and exit rules, although they have a widespread influence on transformations (e.g., Umina et al. 2005; Huey and Tewksbury 2009; Huey et al. 2009). Conversely, introductions tend to have a spatially variable effect on transformations but a generally large effect on entry rules (in large part the introductions themselves) and a smaller effect on species-level exit rules (with extinctions driven by introductions being relatively low, at least regionally; e.g., Sax and Gaines 2003; Chown et al. 2007; Gilchrist and Lee 2007). Finally, both overexploitation and pollution, unless particularly severe, tend to act disproportionately through their effects on transformations (e.g., Coltman et al. 2003; Darimont et al. 2009).

Mechanisms

Investigators of large-scale variation in physiological traits typically seek mechanisms for this variation at lower levels in the biological hierarchy. This tradition has led to considerable success in understanding the underlying basis of the response of organisms to their environments and, for many, remains the raison d'être of comparative physiology. Today, exhortations are not uncommon for physiologists to pursue such investigations to the level of transcription products and the genes underlying them. For example, Dow (2007, p. 1632) recently argued for the "redefinition of integrative physiology as the investigation of gene function in an organotypic context." Little doubt exists that such work is essential and has a major role to play in improving understanding of the mechanistic basis of physiological variation (Storey 2006; Feder 2007*a*). Nonetheless, evolutionary physiologists have argued that its value can be broadened considerably when considered in light of the evolutionary origins of such variation and the conditions that are required to maintain it (Garland and Carter 1994; Feder et al. 2000). In much the same way, the currency of mechanistic physiology can be much broadened by extending its exceptional insights to macrophysiological questions. Several means of so doing can be identified, of which the following strike us as particularly significant.

First, broadening of the evolutionary array of organisms to which these tools are applied would go a considerable way to assist with understanding the basis of the physiological diversity that plays out at large spatial and temporal scales. While model organisms by necessity must form the foundation of much of the initial work at the cellular and genomic levels, determining the extent to which the lessons learned from them are more general is essential for considering the basis of broadscale physiological variation (Feder 2007*b*; Pertoldi and Bach 2007). This is particularly true because model organisms tend to be of intermediate size (for convenience of handling), eurytopic (so they survive experimental manipulation), and relatively common (for reasons of ease of acquisition and sometimes ethics). More attention should be given to include in studies rarer, non-laboratory-tolerant species and also "less charismatic" clades, which have not been historically favored. This will increase the likelihood of a thorough understanding of extant (and, through the use of phylogenetic tools, extinct) biodiversity. Previously such suggestions were much more easily made than actually taken up, but the challenges of adopting genomics-based approaches for nonmodel organisms are constantly lessening as technological advances occur in gene-expression profiling and cost reduction in DNA sequencing. In many cases, genomic resources generated for one organism may be applied to studies of related species (e.g., heterologous microarray hybridization; Buckley 2007). Those investigating physiological variation have an important role to play in drawing the attention of more mechanistically minded physiologists to the diversity they seek to understand (Chown and Storey 2006).

Second, in addition to broadening the array of organisms, broadening the array of traits studied would be valuable. The choice of the physiological traits traditionally studied, in part, reflects a historical legacy of the development of the field and mainly comprises those that are easy to measure. With the advent of molecular techniques (particularly molecular genetics), it is now possible to analyze the variation in many other traits likely to constitute and drive large-scale patterns, such as variation in cadmium susceptibility (Buchwalter et al. 2008), major histocompatibility gene complexes (Summers et al. 2003), or immune defenses, which might, for example, help explain why only some introduced populations become invasive (Lee and Klasing 2004).

Third, just as physiological mechanisms underlying significant macroecological patterns can themselves be considered patterns (e.g., variation in thermal limits thought to underpin variation in geographic range size; Stevens 1989; Gaston and Chown 1999; Cruz et al. 2005; Bernardo et al. 2007; Calosi et al. 2008*a*, 2008*b*; Naya et al. 2008), so too might gene-expression characteristics be considered broadscale patterns that can explain macrophysiological variation. Genome-scale expression fingerprints of organisms allow a higher-resolution assessment of physiological states than an emergent property, such as thermal limits, and yield data that inform how organisms may be partitioning energy and thus provide necessary details for addressing questions of ecological energetics (Teranishi and Stillman 2007; Cheviron et al. 2008; De Salvo et al. 2008; Place et al. 2008; St. Cyr et al. 2008; Stillman and Tagmount 2009). Moreover, much stands to be gained from investigating not only which genes might be underlying particular responses but also how evolutionary potential (e.g., copy number, promoter complexity) of candidate genes might underpin variable expression (e.g., Lucassen et al. 2006) and thereby constrain physiological change in the face of either natural or anthropogenic environmental variation. It is also important to recognize that the environment has an important role to play in genetic expression through methylation of DNA, which alters gene and protein expression during the lifetime of an organism and sometimes for multiple generations (i.e., epigenetic inheritance; Anway et al. 2005). There is increasing evidence that methylation "software" controls genetic "hardware." Thus, the interaction between environments and the organisms that exist in them can lead to variable phenotypes across the landscape, even though the underlying genotypes may be very similar or even identical. Yet, how such variation in gene expression contributes to adaptive evolution remains largely speculative.

Fourth, and perhaps most readily achievable for many macrophysiologists, further focus needs to be given to the relationship between physiological mechanisms and demographic parameters. At the population level, the only way in which physiological variation can have ecological implications is through its effect on birth, death, immigration, and emigration rates. Although this causal connection has long been recognized (Andrewartha and Birch 1954) and reemphasized in a variety of contexts (Huey and Stevenson 1979; Kingsolver 1983, 1989; Bale 1987; Dunham et al. 1989; Lawton 1991; Dunham 1993; Kingsolver and Huey 1998; Porter et al. 2000), framing physiological investigations in such a manner is not undertaken to the extent it perhaps should be. In particular, efforts need to be made to examine multiple populations (ideally large numbers and certainly substantially more than two), although the challenges of doing so at very large scales may be formidable (Garland and Adolph 1991). Recent work is beginning to demonstrate the considerable insights that can be gained from such an approach (Kearney and Porter 2004, 2009; Ludwig et al. 2004; Loeschcke and Hoffmann 2007; Pörtner and Knust 2007; Kristensen et al. 2008). Even so, additional emphasis needs to be given to sublethal effects (Bernardo and Spotila 2006; Layne and Peffer 2006; Hance et al. 2007; Chown et al. 2008), especially to loss of performance (Peck et al. 2004; Pörtner and Knust 2007; Pörtner and Farrell 2008), including the significance of reproductive failure (e.g., Rinehart et al. 2000; Jørgensen et al. 2006) rather than failure to survive a given set of conditions, and to the ways in which dispersal influences variation in physiological traits (Chown and Terblanche 2007).

Fifth, difficult as it may be for physiologists (who are often trained in the tradition of keeping all variables constant, save for the one of key interest), varying several factors simultaneously and determining their influence on survival and reproduction must be more commonly undertaken. Organisms routinely face changes to more than a single environmental variable at a time (many of which markedly covary), and understanding whether such variation acts in an additive or multiplicative fashion is essential (Bernardo and Reagan-Wallin 2002; Meynard and Quinn 2007; Pörtner and Farrell 2008; Widdicombe and Spicer 2008). Experimentally, this obviously creates substantial challenges in attaining sufficient levels of replication, particularly for studies on animals, although these are not insurmountable (e.g., McNab 2003).

Sixth, and in a related vein, while determining the influence of typical environmental variables, such as temperature and humidity for terrestrial habitats and temperature and salinity for marine ones, is achievable and has been the subject of some work (e.g., Hayward et al. 2001; Juliano et al. 2002; Appel et al. 2004), physiologists rarely consider other such combinations. For example, thermal tolerances may be very different in resource-deficient versus fed animals or in the presence of a predator that induces considerable differences in behavior, morphology, and components of the physiological phenotype (Zangerl et al. 1997; Miner et al. 2005; Hoverman and Relyea 2007).

Finally, integrated laboratory and field experiments (e.g., Sears et al. 2006), the combination of laboratory-based selection and acclimation treatments with field tests (e.g., Kristensen et al. 2008), and the use of micro- and mesocosms (Relyea 2006; Warren et al. 2006) provide a means of reintegrating other, typically more ecological, pressures (e.g., predator pressures, resource patch location requirements) with the kinds of variables typically assessed in the laboratory. These kinds of approaches are often better developed for plants, through common garden experiments (e.g., Clausen et al. 1948; Alvarez-Uria and Körner 2007; van Kleunen and Johnson 2007), than they are for animals (perhaps with the exception of *Drosophila melanogaster*, but see, e.g., Niewiarowski and Roosenburg 1993; Conover et al. 1997; Billerbeck et al. 2001). Nonetheless, in both cases, substantial benefits could be realized from common gardens that are exposed to local conditions and that realistically (inasmuch as this can be done) replicate field conditions (see, e.g., discussion in van Loon et al. 2005).

Obviously, pursuing all of these recommendations would be extremely challenging. In the face of limiting resources, hard decisions will be required to determine which are the more important.

Conclusions

The distinctions that rapidly arose between the subdisciplines of physiological ecology and ecology allowed for the marked advances in mechanistic understanding that did much to fuel their development. However, this also resulted in highly reductionist perspectives that paid little attention to the large geographical and temporal-scale patterns that had underpinned much early work. The emergence of macrophysiology is a recognition of the importance of the continuing need to document geographical and temporal-scale patterns and their implications and in so doing to reunify physiological and ecological approaches, as well as include evolutionary ones. In large part, this reflects the significance of these patterns for understanding some of the major environmental issues currently facing humankind. Such a reunification will require improved collaboration between researchers working on related taxa in different parts of the world to establish the protocols and approaches that will enable them to document macrophysiological patterns and how these are formed. It will also require better collaboration between physiologists and ecologists to determine the mechanisms giving rise to those patterns, particularly the interplay between levels of explanation that have typically been regarded as either physiological or ecological, and the implications of both the patterns and their mechanistic bases. From an applied or conservation perspective, a much-improved predictive framework should result for anticipating which populations or species are likely to be most affected by habitat change, climate change, overexploitation, and biological invasions. The success of such endeavors might well be measured in terms of the emergence of genuine macrophysiologists.

Acknowledgments

We are grateful to the Marine Institute University of Plymouth, Company of Biologists, Society for Experimental Biology, Royal Entomological Society, British Ecological Society, Fisheries Society of the British Isles, and Marine Biological Association of the United Kingdom for support for the first meeting to address macrophysiology explicitly, which brought the authors together and sparked the writing of this manuscript. K.J.G. holds a Royal Society–Wolfson Research Merit Award; S.L.C. is a recipient of National Research Foundation incentive funding; P.C. is a research fellow of the Research Council, United Kingdom; M.K. is supported by Ministry of Science and Higher Education grant N304 3902 33; E.L.R. is a Ramón y Cajal Fellow supported by the Spanish Ministry of Science and Innovation; and J.H.S. is supported by National Science Foundation grant ESS 0533920. We are grateful to D. B. Miles and two anonymous reviewers for their comments on a previous version of the manuscript.

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Associate Editor and Editor: Mark A. McPeek