Performance, Personality, and Energetics: Correlation, Causation, and Mechanism[*]

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ABSTRACT

The study of phenotypic evolution should be an integrative endeavor that combines different approaches and crosses disciplinary and phylogenetic boundaries to consider complex traits and organisms that historically have been studied in isolation from each other. Analyses of individual variation within populations can act to bridge studies focused at the levels of morphology, physiology, biochemistry, organismal performance, behavior, and life history. For example, the study of individual variation recently facilitated the integration of behavior into the concept of a pace-of-life syndrome and effectively linked the field of energetics with research on animal personality. Here, we illustrate how studies on the pace-of-life syndrome and the energetics of personality can be integrated within a physiology-performance-behavior-fitness paradigm that includes consideration of ecological context. We first introduce key concepts and definitions and then review the rapidly expanding literature on the links between energy metabolism and personality traits commonly studied in nonhuman animals (activity, exploration, boldness, aggressiveness, sociability). We highlight some empirical literature involving mammals and squamates that demonstrates how emerging fields can develop in rather disparate ways because of historical accidents and/or particularities of different kinds of organisms. We then briefly discuss potentially interesting avenues for future conceptual and empirical research in relation to motivation, intraindividual variation, and mechanisms underlying trait correlations. The integration of performance traits within the pace-of-life-syndrome concept has the potential to fill a logical gap between the context dependency of selection and how energetics and personality are expected to interrelate. Studies of how performance abilities and/or aspects of Darwinian fitness relate to both metabolic rate and personality traits are particularly lacking.

It can scarcely be denied that the supreme goal of all theory is to make the irreducible basic elements as simple and as few as possible without having to surrender the adequate representation of a single ... experience. (Einstein 1934, p. 165)

Individual differences are no accident. They are generated by properties of organisms as fundamental to behavioral science and biology as thermodynamic properties are to physical science. Much research, however, fails to take them into account. (Hirsch 1963, p. 1436)

Biological reality is so complex that we are very far from any reasonably mechanistic understanding of evolutionary processes. (Felsenstein 1988, p. 468)

The diversity and design of particular functional systems can be properly understood only from the selective, genetic and historical perspectives that evolution provides; and the evolutionary processes of selection and adaptation can be truly understood only when the mechanistic bases underlying functional systems are elucidated. (Bennett and Huey 1990, p. 251; citing Arnold 1983)

Introduction

Evolution can be studied in many ways. We can focus on what happened in the past through phylogenetic analyses of species and/or population differences, which can be highly informative even in the absence of information from the fossil record (Nunn 2011; Rezende and Diniz-Filho 2012). We can focus on the present by studying living populations in order to measure selection acting in the wild (Endler 1986; Kingsolver and Diamond 2011), perform quantitative genetic analyses (Roff 1997), and even attempt to identify the genetic and environmental factors underlying individual variation in traits within populations (Feder 2007; Visscher et al. 2008; Barrett and Hoekstra 2011). We can also look toward the future by use of selection experiments and experimental evolution (Garland and Rose 2009).

Although each of the foregoing approaches has its strengths, a complete and cohesive understanding of how evolution has shaped complex phenotypes requires a combination of approaches (Arnold 1983; Bennett and Huey 1990; Huey and Kingsolver 1993; Garland and Carter 1994). For example, to evaluate whether phenotypic differences among populations and species represent the outcome of adaptive evolution in response to natural selection, we must understand, at a minimum, (1) how different phenotypes perform selectively challenging tasks under various ecologically relevant conditions, (2) how different environmental conditions influence fitness, and (3) the extent to which phenotypic differences are genetically based, through the use of common-garden experiments (Rose and Lauder 1996; Irschick and Garland 2001; Mazer and Damuth 2001). In addition, even a clear understanding of steps 1–3 will not accurately predict the response to selection on a focal phenotypic trait if selection also acts on genetically correlated (and perhaps unmeasured) traits (Lande 1979; Lande and Arnold 1983; Houle 1991; Dochtermann and Roff 2010). Clearly, the study of evolution should be an integrative enterprise that both combines different approaches (Barrett and Hoekstra 2011) and crosses disciplinary barriers to study phenotypic traits that historically have been studied in isolation from each other.

Irrespective of the method used to study evolution, two facts are undeniable: individual variation (see table 1 for a glossary of terms) within populations is omnipresent, and many (if not most) evolutionarily relevant measurements are made on individual organisms. Although individual variation is usually seen as measurement error in comparative analyses of species differences (Ives et al. 2007), it is the keystone level of analysis in quantitative genetics and studies of selection in the wild. Individual variation is most commonly viewed as the raw material on which natural selection acts, but it can also be the result of selection itself, as both natural and sexual selection sometimes favor the coexistence of alternative morphs or strategies within a population (Wilson et al. 1994; Wilson 1998; Calsbeek et al. 2002; Dingemanse and Réale 2005; Oliveira et al. 2008; Corl et al. 2010). The study of individual variation can contribute to our understanding of evolution because it can be used to (1) determine the magnitude and consistency of the raw material on which selection can act, (2) measure selection in action, (3) determine heritabilities and genetic correlations of traits, (4) elucidate the mechanistic bases of higher-level traits, and (5) identify functional relationships among traits (Bennett 1987; Pough 1989; Friedman et al. 1992; Garland and Carter 1994). A renewed focus on individual variation can provide both challenges to conventional wisdom and tremendous opportunities for physiologists to contribute to evolutionary biology (Williams 2008; see "Mechanisms").

One main advantage of studying individual variation is that it has the potential to bridge many gaps in the study of morphology, physiology, behavior, ecology, evolution, and population biology (Bennett 1987). Most recently, the study of individual variation facilitated the integration of behavior into the pace-of-life-syndrome concept (Réale et al. 2010b) and

helped to crystallize study of energetics and personality (Careau et al. 2008; Biro and Stamps 2010). For example, it is intuitive to think about a scenario in which differences in boldness can be generated and maintained within a population, depending on how performance is affected by metabolic rate (see fig. 5 in Careau et al. 2008). In a high-risk environment (with predators), the ecologically relevant performance trait for bold individuals may be sprint speed (to escape predators), whereas for shy individuals it may be fasting endurance (to survive longer under protective cover). We therefore believe that further improvements in these areas of research must consider how performance relates to both energy metabolism and behavior and how all three together influence aspects of Darwinian fitness (see fig. 1).

Objectives

We first attempt to integrate performance with concepts related to the energetics of personality and the more general pace-of-life syndrome (for definitions, see table 1). After introducing the key concepts of performance, personality, and energetics, we review the rapidly growing literature on the energetics of personality. To place these recent developments into perspective and foster the integration of energetics and environmental contexts into the physiology-performance-behavior-fitness paradigm, we also offer a historical overview of the research on individual variation in nonprimate mammals and squamates. We consider only these groups because they reflect our own interests and expertise and because the study of individual variation in these groups has a long and surprisingly parallel history. Finally, we briefly discuss three of the many opportunities arising from integrative research on individual variation: motivation, intraindividual variation, and mechanisms.

The Physiology-Performance-Behavior-Fitness Paradigm in Relation to Energetics and Ecological Context

In an influential article, Arnold (1983, p. 352) suggested that "the problem of measuring the selection gradient becomes manageable if we break it into two parts." In the laboratory, we can study how whole-organism performance is related to underlying variation in morphology, physiology, or biochemistry (i.e., quantify the performance gradients). In the field, we can study the associations between performance and Darwinian fitness or components thereof (i.e., quantify the fitness gradients). Since Arnold (1983), it has become generally acknowledged that selection acts more directly on performance traits (e.g., maximum sprint speed, locomotor stamina, fasting endurance, milk output) than on lower-level traits that determine performance abilities (e.g., leg length, muscle-fiber type composition; e.g., Bennett 1989; Bennett and Huey 1990; Garland and Carter 1994; Garland and Kelly 2006) and that direct measures of organismal performance can provide a bridge between skin-in and skin-out biology.

Arnold (1983, p. 348) used morphology "as a shorthand for any measurable or countable aspect of structure, physiology or behavior." He may have lumped behavior in with other lower-

level traits because he mainly had aspects of motivation in mind. In contrast, Garland and Losos (1994) argued that behavior should be at a different level of biological organization than lower-level or subordinate traits (see fig. 1). In this expanded scheme, behavior is seen as a potential "filter" (Garland et al. 1990) between selection and performance capacities (Garland and Carter 1994). For example, an animal confronted with a particular predator might remain motionless rather than running away at top speed, which would obviate the selective importance of variation in sprint speed. In addition, animals can choose microhabitats that affect their performance abilities, as when a lizard allows its body temperature to fall below the optimal for sprinting ability or moves onto a substrate that reduces traction. However, the inclusion of behavior in this framework remains a matter of considerable discussion (Losos et al. 2004; Husak 2006; Irschick et al. 2008; Duckworth 2009; Adriaenssens 2010). Given the proliferation of conceptual studies on individual variation and empirical research on the physiological underpinnings of behavior, its heritability, and its relationships with Darwinian fitness (Dingemanse and Réale 2005; Sih and Bell 2008; Réale et al. 2010a), the time is ripe for further consideration.

The framework we propose in figure 1 and discuss at length in its caption is centered on performance and behavior but includes physiology (used as a shorthand for all lower-level traits that determine performance capacities), Darwinian fitness, energetics, and environmental context. In an ideal world, a researcher could gather data at all levels and implement a path analysis (structural equation model) on the complete diagram to test the implied causal relations (e.g., that natural selection generally acts most directly on behavior and/or energetics, less on performance abilities, and least directly on lower-level morphological, physiological, and biochemical traits). In reality, however, there will always be missing links (Bennett 1997), as huge effort is needed to obtain (repeated) measures for all trait categories in multiple environmental contexts, which involves using several different techniques and probably multiple field seasons. Moreover, wild animals can be kept in the laboratory only for short periods of time, as extended time in captivity may affect their phenotype and/or incur consequences on their subsequent release (e.g., loss of territory or food cache), which places additional constraints on the type and number of measures that can be taken. Therefore, trade-offs occur involving how many components (physiology, performance, behavior, and fitness), traits per component (e.g., measure one or many behaviors), individuals, and repeated measurements per individual the researcher wants to consider. Still, as Bennett (1997, p. 12) noted, "Getting partial answers may be better than waiting forever to discover the perfect system." In any case, a framework such as that shown in figure 1 is helpful to guide the design of future studies and to see the limitations of previous studies that inevitably include fewer than all possible components (and traits). Long-term, individual-based studies of a wild population of marked individuals offer many advantages for studying this framework, presuming that estimates of lifetime fitness measures can be derived and in-

dividuals can be recaptured to measure different aspects of their biology (Clutton-Brock and Sheldon 2010).

The framework depicted in figure 1 has the potential to bring together researchers with different backgrounds and interests. Typically, an ecologist would tackle the study of individual variation from the perspective of variation in ecological context (e.g., population density, food abundance, predation risk). At the other end of the framework, physiologists would start from individual variation in biochemical, morphological, and physiological traits. Interestingly, the place where ecologists and physiologists, starting from their own ends of the framework, will meet is behavior and/or energetics, making the study of energetics and behavior pivotal to the entire framework.

Animal Personality

Individual differences in behavior have been of great interest to psychologists for at least a century (Nettle and Penke 2010), and it is now generally accepted that human personality (Bouchard and Loehlin 2001) includes five primary factors (extraversion, openness, conscientiousness, neuroticism, and agreeableness), each of which includes a number of subordinate facets (Digman 1990; Costa and McCrae 1992; Koski 2011). By using questionnaires to sample these big five, psychologists have gained considerable knowledge about human personality and its ontogeny, heredity, stability in adults, differences between men and women, and other aspects (Digman 1990; Costa et al. 2001). Although psychological studies of personality were mainly restricted to humans (but see Tryon 1942) for the simple reason that it was difficult to administer a questionnaire to other species, psychologists have recently renewed their interest in studying animal personality (Gosling 2001, 2008) and have started to adopt an evolutionary perspective on human personality (Nettle 2006; Penke et al. 2007; Nettle and Penke 2010).

Behavioral ecologists also recently became interested in animal personality (Sih et al. 2004a, 2004b; Dingemanse and Réale 2005; Réale et al. 2007). Réale et al. (2010a) highlighted the different definitions of animal personality that have emerged in this field. Under the broad definition of personality, any repeatable behavior can technically be termed a personality trait, as repeatability implies that differences among individuals show at least some statistical consistency (Bell et al. 2009). In this case, it can be hard to see the advantage of using the word "personality" instead of "repeatable individual differences in behavior" other than to save words (or increasing the "sexiness" of the subject matter). Still, because the substance of science is intimately related to its expression (Gopen and Swan 1990), using "personality" as a word encapsulating several others can help the flow of thoughts and potentially clarify complex concepts. However, if the meaning of animal "personality" varies substantially among researchers, then it will ultimately hinder progress. Many important articles on interindividual variation in behavior published 20–30 yr ago do not contain the word "personality" (e.g., Bennett 1980; Arnold 1983; Arnold and Bennett 1984; Garland 1988, 1994b; Boake 1989).

In this review, we emphasize a narrow-sense concept of an-

Table 1: Definitions of key concepts and phenotypic traits

Term (abbreviation)	Definition
Activity	General level of physical activity of an individual in terms of muscular movement leading to locomotion (Réale et al. 2007), which can be measured in various ways (Garland et al. 2011b).
Aggressiveness	Individual's agonistic reaction toward conspecifics (Réale et al. 2007). Note that many other kinds of aggressiveness exist (e.g., predatory aggression; Gammie et al. 2003; Sadowska et al. 2008).
Animal energetics	Measurement and explanation of variations in energy expenditure. For detailed methods at the organismal level, see Speakman (1997) and Lighton (2008).
Basal metabolic rate (BMR)	Lowest MR of an adult endotherm, postabsorptive, nonreproductive, and inactive while in its thermal neutral zone and inactive phase of its daily cycle (McNab 1997).
Boldness	Individual's reaction to a risky but nonnovel situation. Docility, tameness, and fearfulness have been used in the specific context of reaction to human beings (Réale et al. 2007).
Daily energy expenditure (DEE)	Total MR of a relatively unrestrained animal summed over 24 h, usually measured by metabolizable food intake and/or respirometry in captivity or the doubly-labeled-water technique in the wild. DEE of free-ranging animals is commonly referred to as field metabolic rate (FMR; Speakman 1997; Nagy 2001, 2005).
Exploration	From Réale et al. (2007, p. 295): "An individual's reaction to a new situation. This includes behaviour towards a new habitat, new food, or novel objects. This situation can also be considered risky if, for example, a new object may represent a potential predator. We have deliberately not included neophobia and neophilia in our terminology because both are considered as part of exploration."
Individual variation	Differences among individuals within a population after variation related to age and sex (and sometimes body size) is accounted for.
Metabolic rate (MR)	Amount of energy expended by an animal in a given period, as measured by heat produced, O_2 consumed, or CO_2 produced (Speakman 1997; Lighton 2008).
Pace-of-life syndrome	Association between one or more traits from the slow-fast metabolic continuum and one or more traits from the slow-fast life-history continuum. Although historically studied at the interspecific and interpopulation levels, the pace-of-life syndrome can also be applied to study individual variation. Personality traits have recently been integrated within this concept, with the general expectation that activity, exploration, boldness, and aggressiveness occur in individuals that tend to be "fast" while the opposite suite of personality traits occurs in individuals that tend to be "slow" (Réale et al. 2010b).
Performance	Ability of an individual to conduct a task when maximally motivated. Best performances by individuals from a series of measurements are often analyzed, but this may not be the optimal approach from a statistical perspective (Head et al. 2012). Arnold (1983) specified that a performance trait should preferentially be ecologically relevant and phylogenetically interesting. How an organism performs in nature while accomplishing an ecologically relevant task can be termed "ecological performance" (Irschick and Garland 2001; Irschick 2003). Husak et al. (2009a) also recognized two primary categories: dynamic performance, which includes measurements of movements of the whole body or parts of the body (e.g., sprint speed, endurance, bite force), and regulatory performance, which includes measures of how well organisms regulate physiological processes of the whole body or withstand environmental conditions (e.g., regulation of salt and water, thermoregulation or thermal tolerance, growth, digestive capacity, immune responsiveness).
Personality (broad sense)	Repeatable individual differences in behavior (Réale et al. 2010a).
Personality (narrow sense)	Repeatable individual difference in activity, exploration, boldness, aggressiveness, and/or sociability (Réale et al. 2010a). In behavioral ecology, temperament is often used synonymously with personality (e.g., Réale et al. 2007; Martin and Réale 2008), as is behavioral syndrome (e.g., Sih et al. 2004a, 2004b; Sih and Bell 2008). The term "coping style" carries a connotation of variation in how individuals deal with stress, often involving different aspects of aggression and formerly thought to involve primarily the

Table 1 (*Continued*)

Term (abbreviation)	Definition
Personality (narrow sense; *continued*)	hypothalamic-pituitary-adrenal axis (Koolhaas et al. 2007; Coppens et al. 2010; Huntingford et al. 2010; Costantini et al. 2011; and references therein). It was recently defined by Coppens et al. (2010, p. 421) as "a correlated set of individual behavioural and physiological characteristics that is consistent over time and across situations" (note the explicit inclusion of physiology).
Repeatability (τ, r)	Proportion of total phenotypic variance within a population that is attributable to differences among individuals (Falconer and Mackay 1996), usually measured as the intraclass correlation coefficient (Lessells and Boag 1987), Pearson product-moment correlation (Hayes and Jenkins 1997), or individual identity as a random effect in a mixed model (Wilson et al. 2010). Note that one generally removes variation related to age and sex before calculating repeatability (see also "individual variation" above).
Resting metabolic rate (RMR)	Lowest MR of an endotherm while resting in its thermal neutral zone when one or more of the conditions required for measuring BMR cannot be met (adult, postabsorptive, nonreproductive, resting phase).
Routine metabolic rate	In fishes, the MR of postabsorptive, undisturbed animals that also includes the costs of random activity (e.g., swimming for ventilation in fishes) and the maintenance of posture and equilibrium (Jobling 1994; see also Killen et al. 2011).
Slow-fast life-history continuum	Suite of intercorrelated life-history traits (e.g., growth, age at first reproduction, fertility, longevity). The term apparently was first coined by Sæther (1987). The concept is rooted in MacArthur's (1962) r and K selection theory except that it does not imply a specific reason, such as selection related to density-dependent phenomena, for its existence (Jeschke and Kokko 2009). In many cases, it is important to determine whether these correlations remain after correlations with body size have been removed from all traits (e.g., Clobert et al. 1998; Jeschke and Kokko 2009).
Slow-fast metabolic continuum	First coined by Lovegrove (2000), a suite of intercorrelated traits related to heat loss and MR—such as body temperature, RMR, and DEE—after the statistical effect of body size has been removed from all traits (Lovegrove 2003).
Sociability	Individual's reaction (seek or avoid) to the presence of conspecifics, excluding aggressive behavior (Réale et al. 2007).
Standard metabolic rate (SMR)	Lowest MR of an ectotherm—postabsorptive, nonreproductive, and inactive while in its resting phase—measured at a specified ambient temperature.

imal personality. As presently construed, this definition emphasizes general activity, exploration, boldness, aggressiveness, and sociability (Réale et al. 2007) because these traits potentially underlie an individual's behavior in many different contexts (e.g., mating, parental care, agonistic interactions, foraging, dispersal). Moreover, narrowing personality to these behavioral domains helps make it intimately related to the way many workers measure behaviors under various standardized conditions that are intended to index aspects of personality, such as a home cage (activity), a novel environment (exploration and/or anxiety), a mirror test (aggressiveness), reaction to a predator (boldness), or reaction to a conspecific (sociability). Although a certain degree of overlap may occur between the behaviors measured in such tests (Réale et al. 2007), some clearly capture independent aspects of behavior (Garland et al. 2011b; Careau et al. 2012b; Novak et al. 2012).

The extent to which the five above-listed personality traits explain individual variation in behavior across contexts remains to be determined, but empirical studies on this topic are rapidly accumulating. The open-field, hole-board, and other novel-environment tests, for example, have gained popularity in behavioral ecology because it was found that they can provide insight concerning the behavior of animals in nature. Red squirrels *Tamiasciurus hudsonicus* that were more exploratory during a hole-board test were captured more frequently and at a greater number of different locations on the study grid (Boon et al. 2008), suggesting that behavior in the open-field test predicts risk taking in the wild. Similarly, Siberian chipmunks *Tamias sibiricus* that were more exploratory during a hole-board test were captured more frequently and at a greater number of different traps, which in turn was positively associated with their parasite (tick) load (Boyer et al. 2010). Radio-tagged great tits *Parus major* that more rapidly explored a novel environment (a sealed room of 4.0 m × 2.4 m × 2.3 m containing five artificial trees) responded to a sudden drop in food abundance by shifting to other areas more rapidly than slow explorers (van Overveld and Matthysen 2010), suggesting that behavior in the novel-environment test predicts the spatial response to changes in the natural environment. Individual killifish *Rivulus hartii* that took less time to cross a gap between two refuges in a
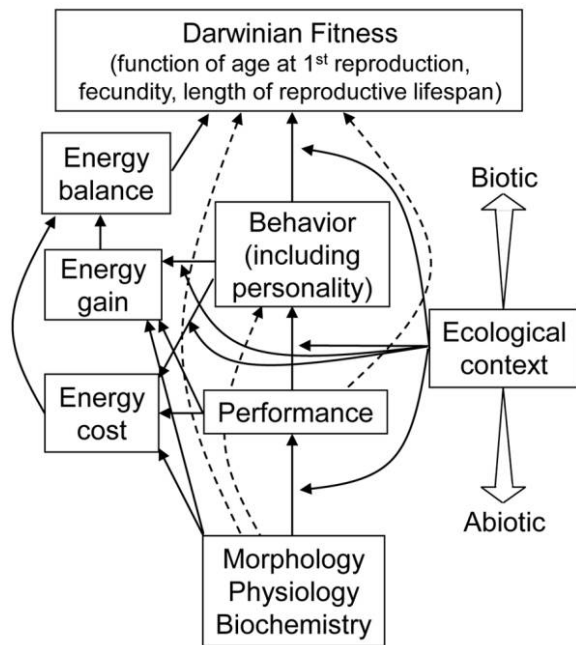
Figure 1. Physiology-performance-behavior-fitness paradigm, as expanded by Garland and Losos (1994; see also Garland 1994*b*; Garland and Carter 1994) from Arnold (1983) and to which we have added energetics (see also Arnold 1988; Biro and Stamps 2010) and ecological context. This path diagram highlights some of the conceptual and functional links between Darwinian fitness (i.e., lifetime reproductive success, largely determined by the three primary demographic parameters of age at first reproduction, fecundity, and length of the reproductive life span; Oufiero and Garland 2007), behavior (including "personality" traits, such as locomotor activity, exploration, boldness, aggressiveness, and sociability), performance (e.g., maximal sprint speed, stamina, fasting endurance), and lower-level traits in the realm of morphology/physiology/biochemistry. Assuming that organisms are maximally motivated to perform in some context (either in a laboratory test or in the wild), lower-level traits determine performance abilities. In turn, performance abilities set an "envelope" (or "performance space"; Bennett 1989) within which behavior is confined. The context dependency of the relationships between performance and behavior and between behavior and fitness is represented by arrows starting from the ecological context, which includes abiotic factors (e.g., ambient temperature, water and oxygen availability) that can directly modulate physiology/biochemistry and their effects on performance, as in Q_{10} effects caused by temperature variation. The ecological context also includes biotic factors (e.g., environmental productivity and predictability, predator density, parasites, interspecific competition, density-dependence mechanisms), which do not necessarily have acute effects on performance traits but can modulate the effect of behavior on fitness as, for example, in the context of foraging in the absence or presence of predators. Energetics must appear in this framework in several places, including an overall balance that is determined by energy gain and costs. Many behavioral choices may have no direct consequences for fitness, but they are indirectly subject to selection because they have consequences for energy balance. All behaviors require muscle action and thus cost energy. Some behaviors, such as foraging and basking in the sun, bring energy gain to the animal (Biro and Stamps 2010). The environment can also modulate the overall effect of behavior on energy balance. For example, the energetic gain of foraging can be high or low, depending on food availability and handling time. The energetic cost of behavior can be high or low,

small novel laboratory tank were captured farther away 24 h after being released back into their native stream (Fraser et al. 2001). These sorts of studies demonstrate that an individual's behavior in open-field and other novel-environment tests may correlate with its behavior in the field, including its ability to find new food sources and mates under natural conditions, which in turn may affect Darwinian fitness (Dingemanse et al. 2004; Boon et al. 2007).

The narrow-sense definition of personality used here therefore describes particular types of individual variation in behavior that are measured in more or less standardized ways among individuals and potentially among populations or spe-

for example, depending on ambient temperature, because of heat substitution (Chappell et al. 2004; Humphries and Careau 2011). If the heat produced by the muscles of an active animal can substitute for the heat otherwise required for thermoregulation when inactive, then the net energetic cost of behavior is reduced (see also fig. 2*D*). Performance traits also entail energetic cost (e.g., maximum thermogenic capacity), but some can also lead to energy gain (e.g., use of maximum sprint speed to catch a prey item). Lower-level traits have maintenance costs but in some cases also facilitate energy gain (e.g., larger digestive organs can provide greater energy assimilation capacity). Relationships that seem less likely are represented by dashed arrows. For example, it is unlikely that lower-level morphology/physiology/biochemistry directly influences Darwinian fitness, that is, without intermediate effects on performance, behavior, and/or energetics (see also Garland and Losos 1994). The use of arrows does not necessarily imply linear effects, and we have not attempted to depict interactive effects. Note that in the relations between lower-level traits and performance and even for relations among lower-level traits, relationships can also be nonlinear, hierarchical, and extremely complicated, including multifarious effects of variation in circulating hormone levels (e.g., Reilly and Lauder 1992; de Geus 2002; Ghalambor et al. 2003; Ketterson et al. 2005; Wainwright et al. 2005). In addition, effects of lower-level traits on performance may be nonobvious and not easily predictable (Bennett 1989), exhibiting emergent properties. All relationships have the potential to differ between the sexes and/or to vary ontogenetically (Vanhooydonck et al. 2005; Calsbeek 2008; Stamps and Groothuis 2010). In the context of individual variation, note that this diagram does not depict the effects of genetic variation and variation in environmental factors experienced since fertilization (or even before, in the case of some parental effects) that could cause variation in lower-level traits, performance, behavior, or components of fitness. As discussed elsewhere, this sort of conceptualization leads to the expectation that natural selection generally acts most directly on behavior and/or energetics, then on performance abilities, and least directly on lower-level morphological, physiological, and biochemical traits (e.g., Bennett 1989; Garland and Carter 1994; Garland and Kelly 2006), although patterns of correlational selection may cloud these distinctions (Sinervo and Calsbeek 2006; Calsbeek 2008). The same expectations would generally apply for sexual selection (Oufiero and Garland 2007), although in some cases (e.g., female choice and Fisher's runaway process), sexual selection could act rather directly on morphology (e.g., aspects of tail size, shape, or coloration; Garland and Losos 1994). For other diagrammatic considerations and further extensions of these relationships, see Bennett (1989), Pough (1989), Ricklefs (1992), Terwilliger and Göring (2000), de Geus (2002), Ricklefs and Wikelski (2002), Geber and Griffen (2003), Koteja (2004), Dishman et al. (2006), Kemp (2006), Nikinmaa and Waser (2007), Réale et al. (2007), Walker (2007, 2010), Buchwalter et al. (2008), Dishman (2008), Dalziel et al. (2009), Moore and Hopkins (2009), Houle et al. (2010), and Storz and Wheat (2010).

cies in order to allow comparative studies (reviewed in Réale et al. 2007; see also Careau et al. 2009, 2010a). Personality traits in the narrow sense (e.g., aggressiveness, boldness) may or may not be correlated among individuals, among populations, or among species (Dewsbury 1980; Bell 2005; Dingemanse et al. 2007; Martin and Réale 2008). This definition of personality also does not necessarily imply a link with human personality, which has traditionally been defined and quantified in other ways (see above and Wilson et al. 1994; Réale et al. 2007; Garland et al. 2011b; Koski 2011).

The narrow-sense conception of animal personality makes it slightly different from the concept of behavioral syndromes (Sih et al. 2004a, 2004b; Sih and Bell 2008), defined most simply by Sih et al. (2004a, p. 372) as "suites of correlated behaviors across situations." Even a single trait (e.g., exploration) can be studied in isolation from others (e.g., boldness) and still be termed a personality trait if it is statistically repeatable (from day to day or over longer time intervals). The two concepts are nonetheless closely related, in part because two measures of the same personality trait taken at different times or in slightly different contexts can be considered as two genetically different traits (Falconer and Mackay 1996; Dochtermann and Roff 2010). Behavioral syndromes may exist because underlying neural or endocrine axes affect more than one aspect of behavior (see "Mechanisms") and/or because they may evolve via correlational selection favoring particular combinations of traits (Jones et al. 2004; Arnold et al. 2008).

For some workers, personality and behavioral syndromes are also used synonymously with coping styles (Dingemanse and Réale 2005; Wilson and McLaughlin 2007; Fucikova et al. 2009; Garamszegi et al. 2009; Webster et al. 2009), yet "the precise way in which individual differences in stress coping and personalities are linked is unclear" (Carere et al. 2010, p. 728; see "Mechanisms"). The notion of coping styles emphasizes the need to consider individual variation as composed of several independent characteristics likely to reflect individual variation in the pattern of activity of underlying causal physiological mechanisms (Koolhaas et al. 2010). Coping styles are more frequently studied from the perspective of behavioral neuroscience, and these studies often attempt to describe the dimensions of animal personalities consistently with known (or expected) behavioral-control functions of particular brain structures or endocrine axes (Øverli et al. 2007; Coppens et al. 2010; Koolhaas et al. 2010; Costantini et al. 2011).

Animal Energetics and Slow-Fast Continua

Energetics is a very broad discipline, encompassing thermodynamics, chemistry, biochemistry, biology, ecology, and evolution (Speakman 1997). Animal energetics describes the properties of a biological process in terms of energy, commonly referring to their costs, such as the energetic costs of reproduction (e.g., Angilletta and Sears 2000; Bergeron et al. 2011), parasitism (e.g., Careau et al. 2010b), transport (e.g., Secor et al. 1992; Beck et al. 1995; Gleeson and Hancock 2002; Chappell et al. 2004; Rezende et al. 2009; Dlugosz et al. 2012), and other

physical activity (e.g., Garland et al. 2011b). Aside from body temperature, which influences heat loss as well as metabolic rate via Q_{10} effects, the most commonly measured energetic traits are daily energy expenditure (DEE), basal metabolic rate (BMR), standard metabolic rate (SMR) in ectotherms or routine metabolic rate in fishes, and the less rigorously defined resting metabolic rate (RMR). A positive correlation between DEE and BMR, forming a slow-fast metabolic continuum, has been shown repeatedly among species of birds and mammals (Drent and Daan 1980; Daan et al. 1990; Koteja 1991; Ricklefs et al. 1996; Speakman 2000; White and Seymour 2004). In contrast, several studies have reported no such relationship at the interindividual level (Meerlo et al. 1997; Peterson et al. 1998; Fyhn et al. 2001; Speakman et al. 2003). In fact, the only positive relationships found between DEE and RMR at the individual level were in reproductive individuals (Nilsson 2002; Tieleman et al. 2008; Careau et al., forthcoming).

From the first law of thermodynamics (energy cannot be created or destroyed), it follows that all of the energy an animal expends must be balanced by its intake of food to maintain a long-term energy balance. Since the publication of Fisher (1930), a central theme in evolution is the principle of allocation of energy to different functions (e.g., growth, reproduction, and maintenance), because animals generally do not have access to (or cannot process) an unlimited amount of food. This energetic constraint, in turn, may generate trade-offs, that is, situations in which one trait or function cannot increase unless another decreases (including the so-called Y-model of resource allocation). These sorts of trade-offs may, in turn, cause multiple life-history traits to covary along a slow-fast life-history continuum.

It is intuitive to expect that species or individuals that grow fast, mature early, have large litters, and die young expend energy at higher rates than those expressing opposite life-history traits (e.g., McNab 1980). Hence, the slow-fast life-history continuum should correlate with the slow-fast metabolic continuum among and within species. Although such associations have been found at the interspecific level in birds and mammals (Symonds 1999; Kalcounis-Rüppell 2007; Wiersma et al. 2007; Careau et al. 2009; Williams et al. 2010; but see Harvey et al. 1991), this is not the case at the interindividual level (Hayes et al. 1992; Johnston et al. 2007). In fact, the relationships between fitness-related traits and BMR appear to be context dependent at the level of individual variation (Burton et al. 2011), which is perhaps unsurprising, given that arguments can be proposed to predict positive, nil, and negative correlations between DEE, BMR, or RMR and life-history traits such as litter size and survival (Speakman 1997; Nilsson 2002; Blackmer et al. 2005; Boratyński and Koteja 2010), as explained in the next section.

Increased-Intake, Compensation, Independent, and Substitution Models

Here, we illustrate four different mechanistic models of how DEE, BMR, and some component of nonresting energy ex-

penditure might be related on first principles. For purposes of illustration, we consider physical activity as the main contributor to nonresting energy expenditure, but the same reasoning can be applied to any other energetically demanding process, such as reproduction (see above).

The increased-intake model (Nilsson 2002) predicts a positive relationship between DEE, BMR, and activity because active individuals need a greater "metabolic machinery" to support their higher activity level by increased assimilation of energy (fig. 2A). This idea is rooted in the aerobic-capacity model for the evolution of endothermy, which posits that selection for high activity levels entailed an increase in maximal aerobic metabolic rate, which in turn entailed an increase in SMR/RMR/BMR (Bennett and Ruben 1979; Hayes and Garland 1995; Nespolo et al. 2011). On the other hand, the compensation model assumes a fixed energy budget; hence, any energy-demanding activity has to be compensated for by a reduction in another component of the energy budget, that is, an energetic trade-off must occur (Olson 1992; Wieser 1994; Speakman 1997; Bayne 2000; Konarzewski et al. 2000; Nilsson 2002; Steyermark 2002; Blackmer et al. 2005; Piersma and van Gils 2011). This hypothesis predicts no relationship between activity and DEE, and a negative relationship between activity and BMR (fig. 2B). A third model, less frequently recognized, is the in-

dependent model, in which activity increases DEE but is independent of BMR (fig. 2C). One argument in favor of the independent model is that organs used heavily during physical activity (mainly heart and skeletal muscles) are not those that contribute the most to BMR or RMR (Selman et al. 2001; Speakman et al. 2004; Chappell et al. 2007; Russell and Chappell 2007). All of these models, of course, are extremely simplified representations of the energy budget of animals. It is possible to imagine more-complex scenarios as we split DEE into more categories (e.g., Garland et al. 2011b). For example, if we further divide nonresting energy expenditure as the sum of energy spent on thermoregulation and that spent on activity (fig. 2D), then the possibility of the substitution of the heat required for thermoregulation by the heat produced by activity introduces another potential route for compensation that varies according to ambient temperature (Chappell et al. 2004; Humphries and Careau 2011). In this substitution model, the energetic cost of behavioral activity is reduced for an endotherm below the lower critical temperature of its thermal neutral zone (fig. 2D).

Energetics and Animal Personality

The insights we can potentially gain by studying the energetic ramifications of personality are twofold (Careau et al. 2008).
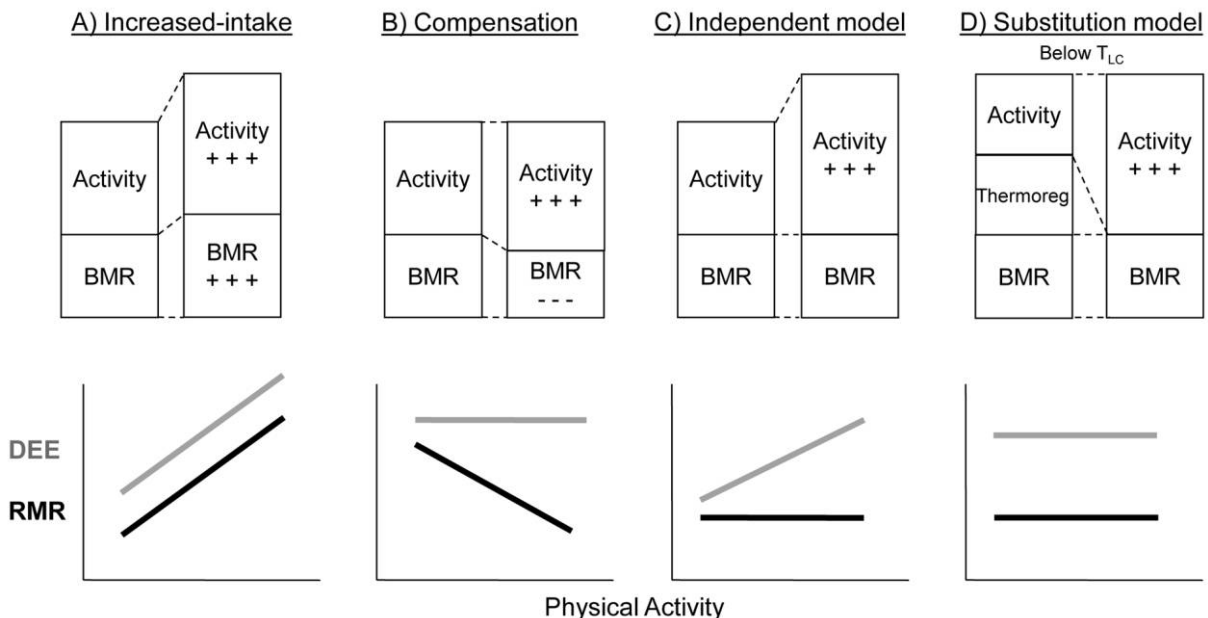

Figure 2. Hypothetical representations of the effect of increasing physical activity (plus signs; or any other energetically expensive process, such as reproduction) on the energy budget (height of the stack) and the predicted relationships between physical activity and daily energy expenditure (DEE) and basal metabolic rate (BMR), expanded from figure 4 of Careau et al. (2008). A, According to the increased-intake model, an increase in activity will entail an increase in BMR to support high DEE levels, as if BMR were the "engine" of the metabolic machinery (e.g., see Biro and Stamps 2010). B, According to the compensation model, an increase in activity will necessarily lead to a decrease in BMR (minus signs) because of the assumption that an animal has a fixed total amount of energy that must be allocated among competing processes, as if the BMR was the "competitor." C, The independent model assumes that BMR is independent of activity, which yields a positive relationship between DEE and activity but not between BMR and activity. D, Below the lower critical temperature (T_{LC}) of an endothermic animal, the substitution model further divides the nonresting energy expenditure into activity and thermoregulation, which generates a different prediction about the relationship between DEE and activity.

First, the energetics approach can help us understand why selection has sometimes generated and maintained variation in personality by revealing how various aspects of personality influence an individual's overall energy balance (Biro and Stamps 2010) or energetic state (Sih and Bell 2008). Second, aspects of personality can potentially explain part of the residual variation in DEE and RMR (Careau et al. 2008), a subject that has long puzzled evolutionary physiologists (e.g., Garland 1984; Speakman et al. 2004). Although it is intuitive to expect individuals that are more physically active, exploratory, aggressive, and bold will gain and expend energy at higher rates than those expressing the opposite suite of behavioral traits (Careau et al. 2008; Biro and Stamps 2010), the models elaborated above (fig. 2) indicate that these relations may not always exist. The numerous possible allocation and substitution mechanisms within the energy budget imply that measurements of multiple metabolic traits are required to better understand the energetic effects of personality (e.g., as it is for parasitism; Careau et al. 2012c).

One reason why energetics and personality might relate to each other is that both are also related to the slow-fast life-history continuum (Biro and Stamps 2008; Réale et al. 2010b). A literature survey indicated that activity, aggressiveness, and boldness are commonly positively related to growth, fecundity, and other life-history traits in a wide range of taxa (Biro and Stamps 2008). In addition, individuals with high rates of growth and fecundity should require high rates of food intake and, in turn, should bear relatively large morphological structures related to food assimilation and utilization, such as intestines and liver, which in turn can lead to a high RMR because these organs have high mass-specific metabolic rates and account for a substantial fraction of the overall metabolic rate when an animal is at rest (Biro and Stamps 2008, 2010; Piersma and van Gils 2011). In mammals, however, the effects of organ size on BMR or RMR can be quite variable (Speakman et al. 2004; Chappell et al. 2007; Müller et al. 2011; for a fish study, see Norin and Malte 2012). Therefore, the personality-organs-RMR chain of relationships may not be the sole pathway through which personality and energetics interact (see also Careau et al. 2008).

A recent literature review revealed that a positive relationship was found between BMR, RMR, or SMR and a behavioral trait (dominance, scrounging, aggressiveness, boldness, activity, home-range size, or mate calling) in 20 of 27 case studies (Biro and Stamps 2010). The number of case studies is much reduced, however, if we restrict these results to the narrow-sense definition of personality listed in table 1, which includes only activity, exploration, aggressiveness, boldness, and sociability. We also note that in the case study provided by Gębczyński and Konarzewski (2009a), only the line selected for high BMR had statistically higher home-cage activity, as compared with mice from four nonselected control lines, whereas the line selected for low BMR did not differ from the control lines (table 2). Moreover, neither selected line differed from the control lines in maximal oxygen consumption elicited by forced running (Gębczyński and Konarzewski 2009a). In addition, in a separate experiment, replicated selective breeding for high maximal oxygen consumption induced by swimming did not lead to correlated changes in either BMR or home-cage activity (Gębczyński and Konarzewski 2009b).

Here, it is crucial to note that some methods of measuring physical activity provide only a measure of duration or frequency of behavior, whereas others also provide indicators of the speed or intensity at which activity is conducted. Although most studies of wild animals lack a measure of the intensity of activity, research on laboratory rodents has shown the importance of distinguishing between different components of activity (i.e., duration and intensity; Garland et al. 2011b). We therefore note that although Sears et al. (2009) showed that BMR and distance run on wheels were positively correlated in deer mice *Peromyscus maniculatus*, the relationship with duration of activity was not statistically significant. In the same species, Chappell et al. (2004) showed that the relationship between RMR and wheel activity (both duration and distance run) is statistically nonsignificant at 3°C (fig. 3A) and 10°C (fig. 3B) but positive and significant at 25°C (fig. 3C), a compelling example of the context dependency of the relationship between RMR and activity. These differences and nuances taken into account, 9 of 21 case studies yielded a significant positive relationship between a personality trait and BMR, RMR, or SMR (see footnote a in table 2).

In addition to the studies described in Gębczyński and Konarzewski (2009a, 2009b), at least three other selection experiments are particularly relevant to relations between activity and metabolic rate of resting animals. Rundquist (1933) bred rats for either high or low levels of spontaneous locomotor activity, as measured by the total number of revolutions in rotating drum-type cages over a 15-d period. In generation 15 of the experiment, BMR was significantly higher in the rats from the high-activity line than the low-activity line (Rundquist and Bellis 1933; fig. 4). Another selection experiment bred mice for high or low heat loss (kcal kg$^{-0.75}$ d^{-1}) as measured by direct calorimetry over 15 h at night while mice had access to food but not water (Nielsen et al. 1997b). Selection clearly affected overall metabolism of the animals under normal housing conditions because it changed food consumption, body temperature, lean mass, and the relative size of metabolically active organs (reviewed in Swallow et al. 2009). Mousel et al. (2001) found that physical activity, as measured with implanted transmitters over 3 d in mice housed with at least one cage mate of the same sex, had clearly changed as a correlated response to selection on heat loss in both directions (mice bred for high and low heat loss were, respectively, more and less active than control mice; fig. 5).

As interesting as these results are, they bear some caveats. The method used by Rundquist and Bellis (1933) to measure BMR is questionable. In the metabolic chamber, the rats were maintained in place with a stiff flap of aluminum alloy, which allowed a minimum of movement. After a preliminary habituation period of 10 min, the "BMR" was averaged over the following 20 consecutive minutes. Although Rundquist and Bellis (1933) stated that the rats were usually sleeping during

Table 2: Summary of empirical studies (sorted by personality trait) on the relationships between animal personality traits (activity, exploration, aggressiveness, and boldness) and standard metabolic rate (SMR), resting metabolic rate (RMR), basal metabolic rate (BMR), heat loss, metabolizable energy intake (MEI), or routine metabolic rate (routine MR) according to housing conditions (lab, kennel, seminatural, or wild) and behavioral testing procedure

Personality trait and species	Housing	Test or apparatus to measure behavior	Metabolic trait	Group, condition, or level of analysis	Relation	Source
Activity:						
Brook charr (*Salvelinus fontinalis*)	Wild	Proportion of time spent moving	SMR		NS	Farwell and McLaughlin 2009[a]
Deer mouse (*Peromyscus maniculatus*)	Lab	Time spent/distance run on wheel	RMR	25°C	+/+	Chappell et al. 2004[a]
Deer mouse (*P. maniculatus*)	Lab	Time spent running on wheel	RMR	10°C	NS/NS	Chappell et al. 2004[a]
Deer mouse (*P. maniculatus*)	Lab	Time spent running on wheel	RMR	3°C	NS/NS	Chappell et al. 2004[a]
Deer mouse (*P. maniculatus*)	Lab	Time out of nesting box	BMR		NS	Sears et al. 2009[a]
Deer mouse (*P. maniculatus*)	Lab	No. wheel revolutions	BMR		+	Sears et al. 2009[a]
Gerbil (*Meriones unguiculatus*)	Lab	Time spent/distance run on wheel	BMR	Males	NS/NS	Chappell et al. 2007[a]
House mouse (*Mus musculus*)	Lab	Time spent moving in home cage	BMR	High BMR[b]	+	Gębczyński and Konarzewski 2009[a]
House mouse (*M. musculus*)	Lab	Time spent moving in home cage	BMR	Low BMR[b]	NS	Gębczyński and Konarzewski 2009[a]
House mouse (*M. musculus*)	Lab	Time spent/distance run on wheel	RMR	Males	+/+	Rezende et al. 2009[a]
House mouse (*M. musculus*)	Lab	Time spent/distance run on wheel	RMR	Females	NS/NS	Rezende et al. 2009[a]
House mouse (*M. musculus*)	Lab	Time spent moving in home cage	Heat loss	Low heat loss[c]	−	Mousel et al. 2001
House mouse (*M. musculus*)	Lab	Time spent moving in home cage	Heat loss	High heat loss[c]	+	Mousel et al. 2001
Rat (*Rattus norvegicus*)	Lab	No. revolutions on revolving drum cage	BMR	High vs. low activity[d]	+	Rundquist and Bellis 1933
Aggressiveness:						
Arctic charr (*Salvelinus alpinus*)	Lab	No. attacks toward another fish	SMR		+	Cutts et al. 2001
Salmon (*Salmo salar*)	Lab	Charge, chase, and nip displays	SMR	Group comparison[e]	+	Cutts et al. 1998[a]
Dogs (*Canis familiaris*)	Kennel	Questionnaires	MEI	Breed comparison[f]	+	Careau et al. 2010a
Boldness:						
Common carp (*Cyprinus carpio*)	Lab	Dispersal into potentially dangerous tank	SMR	Group comparison[g]	+	Huntingford et al. 2010[a]
European sea bass (*Dicentrarchus labrax*)	Lab	Activity after simulated attack	Routine MR	Fed	NS	Killen et al. 2011
European sea bass (*D. labrax*)	Lab	Activity after simulated attack	Routine MR	Food deprived	+	Killen et al. 2011
European sea bass (*D. labrax*)	Lab	Activity after simulated attack	Routine MR	Normoxic	NS	Killen et al. 2012
European sea bass (*D. labrax*)	Lab	Activity after simulated attack	Routine MR	Hypoxic	+	Killen et al. 2012
Salmon (*S. salar*)	Seminatural	Use of sheltered vs. exposed areas	SMR	Cover	NS	Finstad et al. 2007[a]
Salmon (*S. salar*)	Seminatural	Use of sheltered vs. exposed areas	SMR	No cover	+	Finstad et al. 2007[a]
Exploration:						
Deer mouse (*P. maniculatus*)	Lab	Hole board (2 min)	RMR	r_P[h]	NS	Careau et al. 2011
Deer mouse (*P. maniculatus*)	Lab	Hole board (2 min)	RMR	r_G[h]	+	Careau et al. 2011
Meadow vole (*Microtus pennsylvanicus*)	Wild	Open field (10 min)	RMR		NS	Timonin et al. 2011
Root vole (*Microtus oeconomus*)	Wild	Open field (5 min)	RMR	Reproductive	NS	Lantová et al. 2011
Root vole (*M. oeconomus*)	Wild	Open field (5 min)	RMR	Nonreproductive	+	Lantová et al. 2011
Root vole (*M. oeconomus*)	Wild	Open field (5 min)	RMR	Males	NS	Lantová et al. 2011
Root vole (*M. oeconomus*)	Wild	Open field (5 min)	RMR	Females	+	Lantová et al. 2011

Note. Studies on the energetics of sociability are lacking. Studies that have obtained different relationships in different groups (e.g., males and females), conditions (e.g., food deprived or not), or level of analysis (e.g., genetic vs. phenotypic correlations) are shown in consecutive rows; within a row, studies that tested the relationship between metabolism and different components of activity are listed sequentially and separated by a slash (e.g., duration vs. intensity of wheel running). Plus sign = positive relation; minus sign = negative relation; NS = not significant.

[a] Studies that were included by Biro and Stamps (2010).

[b] Activity was compared between lines selectively bred for high and low BMR versus their nonselected control lines.

[c] Physical activity of mice from lines artificially selected for high or low heat loss versus their nonselected control line (see fig. 5).

[d] BMR was compared between lines selectively bred for high versus low locomotor activity (see fig. 4).

[e] Aggressiveness was compared among groups that had high, medium, or low standard MR.

[f] Different breeds were compared.

[g] SMR was compared between risk takers and risk avoiders.

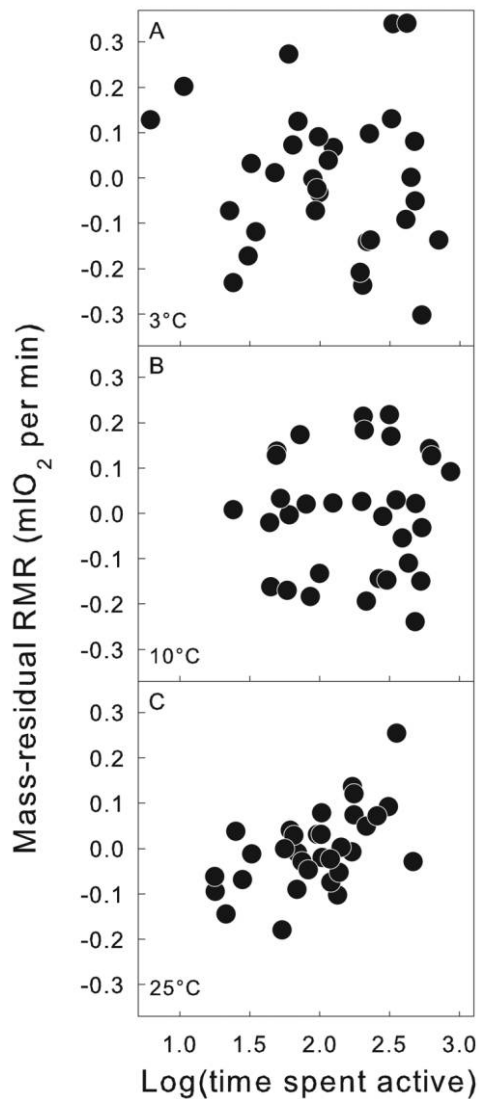[h] Phenotypic correlation (r_P) and genetic correlation (r_G).

ative to the putative pace-of-life syndrome. Indeed, the rat line bred for high activity seems to have developed a faster pace of life than the low-activity line, with slightly larger litters and more fertile matings in fewer days (Rundquist 1933). Similarly, the mouse lines bred for high heat loss have larger litter size at birth than lines bred for low heat loss, with control lines being intermediate (Nielsen et al. 1997*a*).

Swallow et al. (1998) selectively bred mice for high voluntary wheel-running behavior, which did not yield correlated changes in BMR (Kane et al. 2008), the traditional measures of open-field behavior (Bronikowski et al. 2001; Careau et al. 2012*b*) or life-history traits (Girard et al. 2002). However, mice from the four replicate selected lines had higher predatory aggression on crickets as compared with those from the four nonselected control lines (Gammie et al. 2003). Therefore, taken together, results from artificial-selection studies suggest that different evolutionary outcomes are common for behavioral traits and for physiologically complex traits ("multiple solutions" sensu Garland et al. 2011*a*).

Several new studies have been conducted on energetics and personality since the publication of recent conceptual articles on the topic (Careau et al. 2008; Biro and Stamps 2010; table 2). Across dog breeds, metabolizable energy intake (which must equal DEE in animals that maintain energy balance) was positively correlated with aggressiveness (Careau et al. 2010*a*). In the common carp *Cyprinus carpio*, bold individuals have higher routine metabolic rates (Huntingford et al. 2010; termed SMR in the original study). Other studies found variable results offering striking examples of the context dependency of the re-
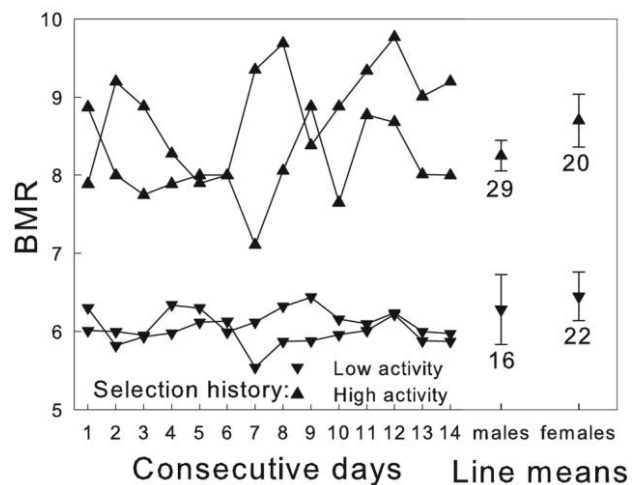

Figure 3. Relationship between resting metabolic rate (RMR; corrected for variation in body mass) and voluntary wheel-running activity in deer mice maintained at 3°C (*A*), 10°C (*B*), and 25°C (*C*) in metabolic chambers allowing nearly continuous measurements of metabolic rate (data from Chappell et al. 2004; M. A. Chappell, personal communication).

the 30-min test period, this procedure combined a constraining and novel environment, which most likely elicited a stress-induced rise in body temperature (Careau et al. 2012*d*). As for Nielsen et al.'s (1997*b*) experiment, individual variation in heat loss (as measured) could be related to individual differences in behavioral response when mice are put in the calorimetric chamber and isolated from external signals. Nielsen et al. (1997*b*) were aware of this and gave mice a 30-min habituation period in the chambers before heat loss was recorded, after which they were usually not physically active (M. K. Nielsen, personal communication). Irrespective of any shortcomings, results of these selection experiments are very interesting rel-

Figure 4. Basal metabolic rate (BMR; cal g^{-1} h^{-1} measured over 20 min while [usually sleeping] animals were maintained in place with a stiff flap of aluminum alloy, which allowed a minimum of movement) in rats from lines selectively bred for high or low spontaneous loco-motor activity (as measured by the total number of revolutions in rotating drum-type cages over a 15-d period). To the left are shown four individuals measured repeatedly across 14 consecutive days. To the right are shown the sex-specific averages ($\pm$ SE) in high and low lines, along with sample sizes (from Rundquist and Bellis 1933).
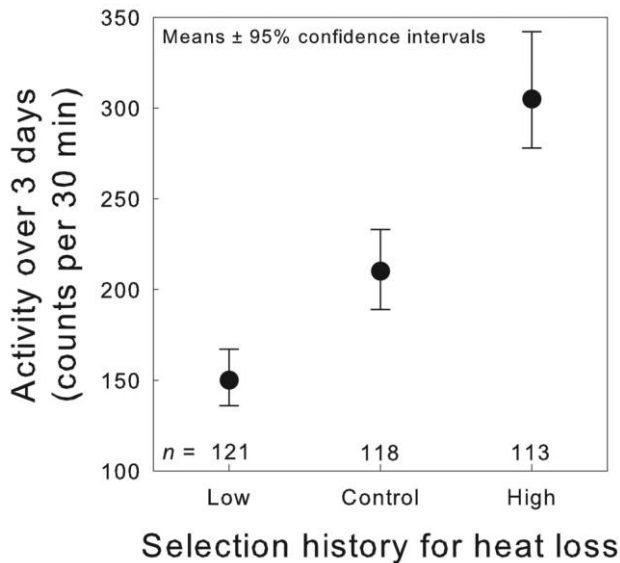
Figure 5. Average (±95% confidence intervals) activity counts per 30-min periods (averaged over 3 d) in mice artificially selected for low and high heat loss relative to randomly bred lines (control) from Mousel et al. (2001). Sample sizes are indicated below symbols.

lationships between metabolism and behavior. In European sea bass *Dicentrarchus labrax*, there was no relationship between routine metabolic rate and boldness except when individuals were food deprived (Killen et al. 2011) or exposed to hypoxic conditions (Killen et al. 2012). In deer mice, no phenotypic correlation was observed between RMR and exploratory behavior, but a quantitative genetic analysis revealed a positive genetic correlation (Careau et al. 2011).

The diversity of results obtained under laboratory conditions casts some doubt on our ability to detect statistically significant correlations in free-living animals (given that they really do exist), as there could be many more potentially confounding factors affecting these relationships in nature. For instance, Timonin et al. (2011) captured wild meadow voles *Microtus pennsylvanicus* and measured open-field behavior and RMR within 3 d of captivity. They found no significant phenotypic correlation between exploratory behavior and RMR (Timonin et al. 2011). Lantová et al. (2011) captured wild root voles *Microtus oeconomus* and measured open-field behavior and RMR on two consecutive days. Exploratory behavior was positively correlated with RMR in females but not in males and only during the nonreproductive season (Lantová et al. 2011). No study has yet attempted to relate open-field behavior with DEE measured on free-ranging animals, but such data are badly needed. Although the most intuitive expectation is that exploratory individuals have higher DEE compared with less exploratory ones, some complexity may arise because, for example, the open-field test is not a good indicator of general locomotor activity, at least in laboratory mice (Careau et al. 2012*b*). No study has yet attempted to relate sociability to energetics, despite preliminary evidence that social context can affect RMR or BMR in

two *Peromyscus* species (individuals housed with a conspecific tended to have higher BMR or RMR than those housed alone; Careau et al. 2011; Dlugosz et al. 2012).

It is becoming clear that a "universal" hypothesis about personality and energetics based on a single underlying mechanism has limited applicability. What may help in making sense of the diversity of results is the integration of concepts and measures of performance and their ecological effects on, for example, predator escape, food acquisition, mate attraction, and starvation resistance (see fig. 1). For example, Heg et al. (2011, p. 1232) argued that "it is quite likely that bold individuals have a higher net energy gain than shy individuals in certain contexts (e.g., under food monopolisability or high predation risk; Stamps 2007), whereas the reverse might be true in other contexts (e.g., under abundant food or low predation risk)." In order to fully explore this possibility, we need measures not only of metabolism and behavior but also of performance and the ecological effect of these traits on food acquisition and predator escape in each context. It is also important to understand the mechanistic bases of individual variation in BMR (Müller et al. 2011; Konarzewski and Książek 2012). To put these new developments into perspective and help integrate energetics and environmental contexts into a physiology-performance-behavior-fitness paradigm, we next take a step back and consider how the study of individual variation made its debut in physiological/ecological research with mammals and squamates. A historical appraisal of studies in these taxa is useful because their literature is largely parallel but mostly complementary. Indeed, in looking back over 40 yr of research on individual variation in physiology, performance, behavior, and fitness, we noticed that as a generality, studies of performance are currently lacking in mammals, whereas in squamates studies of energetics are lacking.

Historical Overview of Research on Individual Variation

Mammals

This section focuses on nonprimate wild-mammal studies that have been from the perspective of behavioral or physiological ecology, leaving aside the very large number of studies on laboratory rats and mice (e.g., Friedman et al. 1992; Lambert et al. 1996). A number of studies on mammals that were conducted in the 1970s and 1980s probably would have used the term "personality" had they been conducted today, because they were focused on individual variation and were based on typical personality tests, such as the mirror-image stimulation and open-field tests. These studies were mainly spurred by the idea that behavioral interactions among individuals were important in regulating population size (Chitty 1960, 1967). Their objective was, therefore, to relate individuality to ecological factors in order to help explain population dynamics (Krebs 1970; Smartt and Lemen 1980). It was recognized that individual variation and "behavioral types" were important for dispersal, but very little was known about the physiological causes of dispersal (Bekoff 1977). It was also known that some individual rodents become "trap happy," which could lead to inappro-

priate biases in capture-mark-recapture studies (Wilbur and Landwehr 1974).

Krebs (1970) used the open-field and neutral-fighting-arena tests to measure exploratory behavior and aggressiveness in two vole species (*Mictotus ochrogaster* and *Microtus pennsylvanicus*). Individual variation in exploration was related to neither home-range size nor longevity in either species. In *M. ochrogaster*, a high population growth rate was associated with low exploratory behavior (higher latency to enter arena) and high anxiety (number of fecal pellets deposited) in the open field. Interestingly, individual males of both species were more aggressive during population peaks than during other phases of the cycle. Krebs (1970) suggested that selection on aggressiveness may alternate through the cycle, referring to the *r*- and *K*-selection paradigm between low and high densities, respectively, which is in line with the recent pace-of-life-syndrome concept (Réale et al. 2010*b*) and illustrates how the ecological context affects the relationship between behavior and fitness (fig. 1). Myers and Krebs (1971) studied how exploration (measured in a maze over two nights) and aggressiveness differed between dispersing and resident voles within populations and found that dispersing male *M. pennsylvanicus* were more aggressive than residents during peaks of population density. They also found that dispersing males of both species were less exploratory than residents.

Fairbairn (1978) used a novel-environment test (dispersal maze for 10 min), neutral-arena encounters, and home-cage sensors to compare the exploration, aggressiveness, and general activity of residents with dispersers in deer mice *Peromyscus maniculatus*. Contrary to what was found in voles, resident males were more aggressive and dominant than dispersing males during neutral-arena encounters. Similar to the findings of Myers and Krebs (1971), dispersing deer mice of both sexes showed lower levels of exploration and higher levels of general activity than did nondispersing individuals in the same population.

Armitage and colleagues (Svendsen and Armitage 1973; Armitage 1986*a*, 1986*b*) used a novel-environment test (maze) and mirror-image stimulation to measure exploration and aggressiveness in yellow-bellied marmots *Marmota flaviventris*. In reviewing Armitage's work, Hayes and Jenkins (1997, p. 281) stated that his "results suggest that marmots have individual personalities." The scores produced using the mirror-image test were consistent with social interactions observed in the field (Svendsen and Armitage 1973; Armitage 1986*a*). In another study, however, Armitage (1986*b*) showed that mirror-image stimulation was not correlated with either social behavior in the field or lifetime reproductive success. As was found in *Microtus* and *Peromyscus*, dispersers were less active in the novel environment than residents (Armitage 1986*a*), suggesting the presence of common mechanisms linking exploratory behavior and dispersal in rodents and perhaps other groups in general (see also Duckworth and Badyaev 2007). These early findings on mammals are certainly interesting and relevant to the study of personality, yet some of them are currently unappreciated,

even in the context of population cycle and density (e.g., Korpela et al. 2011; but see Cote et al. 2010; Hoset et al. 2011).

After the publication of the seminal book chapter by Bennett (1987), many evolutionary physiologists documented repeatability of maximum aerobic performance (Hayes and Chappell 1990; Friedman et al. 1992; Chappell et al. 1995), RMR or BMR (Hayes et al. 1998; Fournier and Thomas 1999), and DEE (Speakman et al. 1994; Berteaux et al. 1996). At the same time, they studied whether individual variation in metabolic rate was related to life-history traits (Derting and McClure 1989; Hayes et al. 1992; Hayes and O'Connor 1999). These studies (before 2000) revealed to ecologically and evolutionarily oriented physiologists the great opportunities that the study of individual variation offers (Bennett 1987; Pough 1989; Friedman et al. 1992; Garland and Carter 1994) and laid the groundwork for subsequent studies on (1) the repeatability of BMR, RMR, or DEE in mammals (Speakman et al. 2004; Nespolo and Franco 2007; Russell and Chappell 2007; Szafrańska et al. 2007; Cortés et al. 2009; Duarte et al. 2010), (2) the quantitative genetics of metabolism (Dohm et al. 2001; Bacigalupe et al. 2004; Konarzewski et al. 2005; Sadowska et al. 2005, 2009; Wone et al. 2009; Careau et al. 2011; Zub et al. 2012), and (3) how energetics relates to fitness in the wild (Jackson et al. 2001; Boratyński and Koteja 2009; Boratyński et al. 2010; Larivée et al. 2010; Careau et al. 2012*a*). Surprisingly, as compared with the number of squamate studies (see "Squamates"), few studies of mammals have reported repeatable or heritable individual variation in locomotor performance (Djawdan and Garland 1988; Blumstein 1992; Djawdan 1993; Blumstein et al. 2010). Therefore, in mammals, the arrows to and from performance are the least documented of all in figure 1.

Numerous ecologically oriented studies of personality have appeared in the past 5 yr or so, involving a diversity of mammalian species. Some personality studies have been conducted in relatively large mammals, including fallow deer *Dama dama* (Bergvall et al. 2011), bighorn sheep *Ovis canadensis* (Réale and Festa-Bianchet 2003; Réale et al. 2009), and spotted hyenas *Crocuta crocuta* (Watts et al. 2010). Most studies of mammal personality, however, are conducted on small rodents, including laboratory house mice (Lewejohann et al. 2011) and lab rats (Koolhaas et al. 2007), wild marmots *Marmota marmota* (Costantini et al. 2011), red squirrels *Tamiasciurus hudsonicus* (Boon et al. 2007, 2008), chipmunks *Tamias striatus* and *Tamias sibiricus* (Martin and Réale 2008; Boyer et al. 2010; Patterson and Schulte-Hostedde 2011), kangaroo rats *Dipodomys merriami* (Dochtermann and Jenkins 2007), voles *Microtus oeconomus* and *M. pennsylvanicus* (Hoset et al. 2011; Lantová et al. 2011; Timonin et al. 2011), and mice *Scotinomys teguina* (Crino et al. 2010). Rodents lend themselves relatively well to novel-environment, mirror, and handling tests, which can be integrated into long-term studies of wild populations (e.g., Boon et al. 2007, 2008). Trapping data from long-term studies can also be used to estimate individual differences in the likelihood of entering a trap, or "trappability," which is often taken as an index of boldness (Réale et al. 2000; Boon et al. 2008) or activity (Boyer et al. 2010). Rodents are also practical to work with

when estimating the hormonal or metabolic underpinnings of personality (Costantini et al. 2011; Lantová et al. 2011) or performance (Girard et al. 2007; Malisch et al. 2008; Dlugosz et al. 2012). Hence, the integration of performance in future mammalian studies on personality and energetics has the potential to yield many important insights into how these traits interact to affect Darwinian fitness.

Squamates

While mammalogists of the 1970s and 1980s who studied individual variation focused largely on the links between ecology and behavior or morphology (Smartt and Lemen 1980), leaving the underlying physiology and proximate mechanisms relatively unexplored, herpetologists emphasized the links between physiology and performance, heritabilities, and how selection in the wild acted on performance and associated behaviors (see earlier review in Garland and Losos 1994). Many of these studies were spurred by Arnold's (1983) "morphology-performance-fitness" conceptual framework and how it could shed light on adaptation by natural selection. Here, we highlight some of the most pertinent studies to illustrate the parallel developments of studies of individual variation in squamates and mammals.

Many studies on squamates reported significant repeatability and broad-sense heritability estimates for performance traits in lizards and snakes (reviewed in Garland and Losos 1994). Because temperature influences almost every aspects of an ectotherm's physiology, it was crucial to evaluate early on whether individual differences in performance held across a range of temperatures (i.e., thermal repeatability). Bennett (1980) showed that thermal repeatability was statistically significant for both sprint speed and distance-running capacity for all six species of lizards studied. Significant thermal repeatability for aspects of locomotor performance was later found in other species of lizards (Huey and Dunham 1987; Van Berkum et al. 1989) as well as in amphibians (Putnam and Bennett 1981). Thus, individuals that have high locomotor performance at one temperature tend to have high locomotor performance at others (Angilletta et al. 2002). Moreover, there appears to be significant individual variation in preferred body temperature in the lizard *Pseudemoia entrecasteauxii* (Stapley 2006).

Although Arnold's (1983) paradigm did not include behavior (but see Arnold 1988) until it was later modified by Garland and Losos (1994), ironically, several studies at this time were focused on antipredator behavior (Arnold and Bennett 1984, 1988; Garland 1988; Brodie 1989, 1992, 1993). In their study of antipredator behavior in Mexican garter snakes, Herzog and Burghardt (1988) advocated that what psychologists referred to as personality traits was of special relevance to the study of consistency of behavioral differences through development (see also Martins 1991). They stated that "individual differences in defensive 'personalities' among newborn snakes are persistent" (Herzog and Burghardt 1988, p. 256). Herzog et al. (1989, p. 506) recognized that there was an increased interest in the significance of individual differences in animal behavior, stating that "the term 'personality' is even creeping into the literature."

This was in reference to a passage in Arnold and Bennett (1984, p. 1117): "while stimulus conditions affect antipredator responses, characteristic personalities are retained irrespective of external conditions and physiological state." Despite these early uses of the word "personality" in squamate literature, this term did not increase in popularity among herpetologists until after 2000 (see below).

Brandt (2003) used a mirror test to elicit push-up displays in side-blotched lizards *Uta stansburiana* and found that the total duration of threat posture was positively correlated with treadmill endurance. Brandt and Allen (2004) later found repeatable among-individual differences in components of the push-up display and reported that repeatability values did not change consistently between the rested and fatigued conditions (see also Martins 1991; Perry et al. 2004 for other studies on repeatability of push-up displays). Cox et al. (2009) also used a mirror test to elicit dewlap extensions, push-ups, and head bobs in the brown anole *Anolis sagrei* (see also Labra et al. 2007). Interestingly, the use of a mirror to elicit an individual's aggressive behavior mirrors (pun intended) what is used in some personality studies in mammals (e.g., Boon et al. 2008).

The number of studies in squamates that explicitly focus on personality or behavioral syndromes has recently increased. Stapley and Keogh (2004) found in water skinks *Eulamprus heatwolei* that "floater" individuals have a greater tendency to explore novel environments, are more likely to retreat in response to a simulated attack of a predator, and spend more time in the refuge after such an attack than territorial individuals. Although territorial males sire more offspring than floaters, the offspring of floaters are larger and thus may have higher survival (Stapley and Keogh 2005). Stapley (2006) showed that individual differences in preferred body temperature were positively correlated with aggressiveness in *P. entrecasteauxii*. Cote and Clobert (2007) measured attraction toward the odor of conspecifics on the day after their birth as a metric of social tolerance in the common lizard *Lacerta vivipara*. The attraction score was repeatable after 1 yr and correlated positively with dispersal probability in low-density but not in high-density populations (see also Cote et al. 2008). López et al. (2005) examined sources of variation in antipredator behavior of adult male Iberian rock lizards *Lacerta monticola* and quantified the use of refuges after simulating low- or high-risk attacks from a predator. They found that the correlations between boldness and body size, body condition, and T-cell immunocompetence were different in high- and low-risk attacks, again illustrating how the ecological context can affect the relationships to and from behavior (fig. 1). Rodríguez-Prieto et al. (2011) measured boldness (time to leave a refuge after being tapped on the tail), exploration (in a novel environment), and social tolerance (quantified as in Cote and Clobert 2007) in Iberian wall lizards *Podarcis hispanica*. They found that exploration but not boldness had a direct effect on habituation to predator exposure and that sociability had an effect on exposure to the predator, which led to habituation. Sinn et al. (2008) studied aggressiveness toward a conspecific model in White's skinks *Egernia whitii* and found that relative rank order of aggressiveness

among females was maintained from mating to pregnancy and postpartum periods. Moreover, female aggressiveness was not correlated with sprinting ability, body size, reproductive output, or offspring growth but was positively correlated with survival of their offspring in the field during the following year. Furthermore, in this species, aggressiveness is associated with a number of fitness-related traits, including the proportion of extrapair offspring (While et al. 2009). Carter et al. (2010) measured boldness (flight initiation distance; see also Rand 1964; Bulova 1994) in 30 male Namibian rock agamas *Agama planiceps* and found that it was repeatable and significantly positively correlated with time spent basking, feeding, and home-range size (although the two last correlations were weak). Moreover, bold individuals approached live food in a trap (clap net) more quickly than did shy individuals, with the two shyest individuals never entering the trap within 15 min, suggesting that individual differences in boldness may introduce sampling bias, depending on capture techniques (Carter et al. 2012).

These studies in squamates have considerably expanded our understanding of how personality is related to aspects of Darwinian fitness, ecology, morphology, and physiology. Given what we already know in squamates, studies of the pace-of-life syndrome in this group are highly promising. Indeed, over the past decade or so, there have been an impressive number of studies of selection in the wild in squamates, especially on performance and life-history traits (Sinervo and Svensson 2002; Irschick et al. 2007, 2008; Husak et al. 2009b; John-Alder et al. 2009). However, studies of individual variation in squamate energetics are rare in a life-history context (but see Marler et al. 1995). Many studies in squamates have been conducted to determine the energetic cost of reproduction (e.g., Angilletta and Sears 2000), feeding (e.g., Grimmond et al. 1994), and locomotion (e.g., Secor et al. 1992; Beck et al. 1995; see also Gleeson and Hancock 2002 for the cost of activity with consideration of the excess postexercise oxygen consumption). Other studies have estimated DEE and some of its components (Brown et al. 1992 and references therein). However, all of these studies were largely focused on the average energetic costs, and few have specifically focused on individual variation (but see Pough and Andrews 1984; De Vera and Hayes 1995; Peterson et al. 1998). Hence, in squamates, the arrows to and from energy balance are the least documented of all in figure 1. The integration of metabolic measures within studies on personality and performance has the potential to yield many significant insights as to how these traits interact and affect Darwinian fitness. Irschick et al. (2007) highlighted the enormous potential of long-term studies in the context of selection in the wild, yet such studies are rare in squamates compared with birds and mammals (but see Sinervo et al. 2000; Sinervo and McAdam 2008; Svensson et al. 2009).

Motivation

In performance studies, variation in motivational state can lead to underestimation of maximal abilities, introduce error variance, and reduce repeatability. Further, if motivation to perform is consistently affected by underlying individual characteristics (e.g., stress responsiveness, personality), then it could account for a portion of the repeatability observed (Losos et al. 2002). Just as individual variation in stress responsiveness can influence the measurement of BMR, which can have the effect of obscuring real relationships or creating artifactual ones (Careau et al. 2008), some personality types may be more or less inclined to perform at their maximal level during potentially stressful tests (e.g., of locomotor abilities) involving a novel apparatus. For example, this can be the case when endurance is evaluated by forced running on a treadmill. According to Copp et al. (2009), 10% of laboratory rats will turn and fight the treadmill belt for extended periods of time before settling into a normal running gait. Similar behavioral complication can occur for some individuals in certain species of lizards and snakes or can even be characteristic of entire species (Garland 1994b; T. Garland, personal observations). In these instances, it would seem that bolder and more aggressive individuals may fatigue prematurely because of energy expended at the initiation of the test, compared with shy and less aggressive individuals. Accordingly, individual lizards *Ameiva undulata* that were very "excited" during the first minute of a forced-running test on a treadmill had lower endurance (Steinberg et al. 1993). Acclimation to the apparatus, perhaps including initial trials at low speeds (e.g., Meek et al. 2009), may help reduce these effects, but this option may not always be possible when working with wild animals that need to be returned to the field as quickly as possible. Contrary to personality tests, in which individuals should have absolute freedom to choose how to behave quantitatively and qualitatively, performance tests should (ideally) not give individuals the freedom of choice of performing at submaximal levels; otherwise, they risk measuring "behavior" rather than "performance" (fig. 1).

In squamate research, it became clear that some individuals are just not motivated to run at their maximum (Losos et al. 2002). Ultimately, such individuals should be excluded from data analysis if the goal is to estimate performance gradients. However, if the goal is to estimate fitness gradients or the links between performance and personality traits, then those same individuals probably should not be excluded. Interestingly, many studies that combined field and laboratory measurements showed that individual lizards in the field often do not use their maximum locomotor capacity during such activities as (simulated) predator avoidance and foraging (Irschick and Garland 2001; Braña 2003; Irschick 2003; Irschick et al. 2005; Husak 2006; Husak and Fox 2006). Because differences in laboratory performance may reflect important behavioral (personality?) differences relevant to field behavior (Losos et al. 2002), data could be analyzed both with and without the individuals that consistently performed at a submaximal level. Husak (2006) highlighted that "behavior" is a broad and imprecise term and encouraged future workers to distinguish it from "ecological performance" (Irschick and Garland 2001; Irschick 2003; see "Performance" in table 1). We would add that personality traits, which are more narrowly defined than behavior, may help in making sense of relations between motivation and performance

abilities and how they undergo selection in the wild. For instance, bold and aggressive individuals may place themselves in situations (foraging close to a potential predator, engaging in many fights) that then require a greater proportion of their maximal performance abilities than do shy and unaggressive individuals (see also fig. 1 and its caption).

Intraindividual Variation

Interindividual variation is usually treated analytically as "error" in comparative studies of species or populations differences (Ives et al. 2007), and this role is relayed to intraindividual variation in studies of interindividual variation (Head et al. 2012). One problem arising from this is underestimation of the correlation between repeated measures of traits that have intraindividual variation (Adolph and Hardin 2007). However, intraindividual variation should not just be "corrected for" but should also be the focus of study, as it may contain important information on how two traits are functionally integrated across an environmental gradient or ontogeny or during acclimation and acclimatization (phenotypic plasticity). Therefore, the simultaneous estimation of the intra- and interindividual correlations may prove to be the most insightful approach to understanding the nature of correlations between traits (van de Pol and Verhulst 2006; van de Pol and Wright 2009). This may be especially true for metabolic, personality, and performance traits that are known to vary with age (Huey et al. 1990; Chappell et al. 2003; Broggi et al. 2010; Stamps and Groothuis 2010) or training (Garland et al. 1987; O'Connor et al. 2011). Individual differences in plasticity (the change in a trait over time or across environments; Garland and Kelly 2006; Piersma and van Gils 2011; Kelly et al. 2012) can be captured by the random regression approach (Dingemanse et al. 2010), a technique that has much to offer to studies on thermal repeatability and individual variation in Q_{10}.

Mechanisms

Physiologists have many opportunities to provide mechanistic understandings of key phenomena in evolutionary biology. Evolutionary biologists typically seek ultimate explanations for trait correlations, such as a correlational selection gradient that may have led to the evolution of a genetic correlation (Lande and Arnold 1983; Garland 1994*b*; Sinervo and Svensson 2002; Réale et al. 2010*b*). Physiologists, in contrast, look for proximate, mechanistic explanations, such as a common neuronal or hormonal system that links traits and that may facilitate or limit adaptive responses to (correlational) selection (Garland 1994*a*, 1994*b*; Garland and Carter 1994; Ricklefs and Wikelski 2002; Coppens et al. 2010; Garland et al. 2011*b*). Of course, physiological interconnections should also be observable as genetic correlations estimated by quantitative genetic analyses, so the two perspectives are dealing with two sides of the same coin. Ecological and evolutionary physiologists often attempt to understand both sides of that coin; that is, they seek both proximate and ultimate explanations for biological phenomena (Garland and Carter 1994; Feder et al. 2000, 2010).

As one example of such an attempt, Moore and Marler experimentally manipulated the behavioral phenotype of free-living male mountain spiny lizards *Sceloporus jarrovi* by use of testosterone (T) implants, which induced changes in territorial defense (a sexually selected trait), including a 3.5-fold increase in the rate at which aggressive behaviors were performed, an increase in the intensity of aggressive responses during encounters, and a 54% increase in time allocated for territory defense (Moore and Marler 1987; Marler and Moore 1989). However, the increased territorial aggression was accompanied by a significant decrease in survival, indicating fitness costs for males investing more in territorial defense as a consequence of T implants (Marler and Moore 1988). Further work showed that T-implanted males had lower food intake and less energy stored as lipids (Marler and Moore 1989) but that survival and stored-lipid levels of T-implanted males were higher than those of control males when the former were given supplemental food (Marler and Moore 1991), suggesting that the mechanism underlying the reduced survival was a lowered ratio of energy gain to cost (Marler and Moore 1991; fig. 1). To confirm this energetic explanation, Marler et al. (1995) used the doubly-labeled-water technique in wild lizards and found that T-implanted males had 31% higher DEE than control males. As T implants did not have an effect on SMR in a group of captive individuals, Marler et al. (1995) concluded that increased DEE (but not SMR) was a primary factor contributing to the trade-offs between increased territorial aggression and survival in this species. In a separate study of the eastern fence lizard *Sceloporus undulatus*, T-implanted males had higher endurance, larger home ranges, increased parasitism, and reduced growth rates and tended to have reduced survival, as compared with control males (John-Alder et al. 2009).

However, other studies have shown that the links between T and performance in lizards are not always straightforward (Cox et al. 2009; Husak and Irschick 2009; Huyghe et al. 2010; O'Connor et al. 2011). Furthermore, recent work has challenged the classic view that T promotes aggressiveness, suggesting that this relationship is highly context dependent and often not observed outside the mating season (reviewed in Adkins-Regan 2005). In line with this, While et al. (2010) found that in White's skinks *Egernia whitii*, repeatable baseline T concentration was negatively correlated with aggressiveness in males but not in females. Furthermore, studies examining how T influences DEE, BMR, RMR, or SMR have yielded variable outcomes (reviewed in Moore and Hopkins 2009).

Much of the work on the underlying mechanisms of personality and coping styles is based on mice, rats, pigs, and primates (reviewed in Carere et al. 2010; Coppens et al. 2010). Typically, proactive individuals (bold and aggressive) respond to stress with a strong sympathetic activation and increase in noradrenergic stimulation, whereas reactive individuals (shy and nonaggressive) respond to stress with strong hypothalamic-pituitary-adrenal (HPA) axis activation and a consequent increase in circulating glucocorticoid concentrations (Carere et al. 2010). This anchor of coping styles and personality in stress physiology implies that there must be mechanistic linkages with

other systems also affected by HPA reactivity and by the sympathetic and parasympathetic nervous systems. In birds, personality is related to corticosterone concentration in response to stress (Cockrem 2007; Baugh et al. 2012), which may be related to repeatable differences in body temperature during exposure to stress (Carere and van Oers 2004; Careau et al. 2012d). One might therefore expect to find that individual differences in metabolic rate (caused by variation in body temperature during exposure to stress) would be associated with coping styles (Careau et al. 2008), but whether or how this might translate to alterations in DEE or BMR is harder to predict. In fact, studies examining how glucocorticoids influence individual components of the energy budget have produced mixed results (reviewed in Moore and Hopkins 2009). For example, Dlugosz et al. (2012) found surprisingly few significant relationships among corticosterone, energy metabolism, behavior, and organ masses in California mice *Peromyscus californicus*, and these relationships differed between males and females.

As recently pointed out by Williams (2008), we still know little about the underlying neural or endocrine bases of individual variation in natural populations of vertebrates. Individual variation in a population can occur at single or multiple points along a given pathway and at various anatomical locations, and can involve diverse cellular processes, either early or late in the pathway. As a partial list of possibilities for the neuroendocrine system (as an example), variation might be present in one or more of many components, including the brain, the neural or neurochemical signaling from the brain to an endocrine gland, the secretion of a hormone from the gland, the distribution or abundance of receptors in target tissues, the neurotransmitter systems that might mediate the effects of hormones, the sensitivity of a negative-feedback system to circulating hormone concentrations, and the response of neurons or other target cells to the hormonal signal (e.g., on reproductive response to photoperiod, see Heideman 2004). The lack of consensus on the effects of hormones on energetics may stem from the focus on circulating (or, in some studies, excreted) hormone titers as the index of hormone function, which may not fully represent the biological activity of hormones (Williams 2008). For example, the bioactivity of corticosterone is determined not only by corticosterone concentrations in the circulation but also by levels of corticosteroid-binding globulin in the blood, the number and affinity of corticosteroid receptors in target tissues, and the availability of coactivator proteins within target cells (Malisch et al. 2008; Dlugosz et al. 2012). In addition, low repeatability of individual differences in circulating levels of some hormones (Ouyang et al. 2011) may limit our ability to demonstrate correlations with other traits.

We are still far from identifying one or more common underlying physiological mechanisms that would consistently tie together individual variation in life-history traits, performance, personality, and energetics (see also Moore and Hopkins 2009; Garland et al. 2011b). Yet, as indicated by the studies and review articles cited above, some pieces of the puzzle are falling into place. Clearly, the energetics approach can be useful for elu-

cidating the evolution of complex suites of traits, such as the slow-fast life-history continuum and personality traits, as energy can act as a constraint forcing trade-offs (see "Increased-Intake, Compensation, Independent, and Substitution Models"). Measurements of RMR and DEE, however, remain at the whole-animal level, and we lack clearly elaborated mechanisms through which these traits should correlate with personality. Although some candidate systems—such as the HPA axis, the hypothalamic-pituitary-gonadal axis, and the sympathetic and parasympathetic nervous systems—have been pointed out as potentially underlying relationships between energy expenditure and personality traits (Careau et al. 2008; Réale et al. 2010b), we lack empirical studies on this subject. As a result, we do not yet know how to deal with the variability of relationships obtained, such as in studies on the links between exploratory behavior in an open field and BMR (table 2).

Several indirect lines of evidence suggest an additional pathway worthy of investigation: the hypothalamic-pituitary-thyroid (HPT) axis. Thyroid hormones (i.e., triiodothyronine [T_3] and tetraiodothyronine, or thyroxine [T_4]) have key roles during development, growth, and adult metabolic function in various organs and organ systems (Yen 2001). In humans, for example, levels of thyroid hormones that are pathologically high (hyperthyroidism) or low (hypothyroidism) lead to differences in BMR (Goglia et al. 2002) and are associated with depression and anxiety (Sinai et al. 2009; Hage and Azar 2012). Such findings also extend to other vertebrate species. In fence lizards, for example, thyroidectomized individuals had a reduced SMR (Steinberg et al. 1993). In rats and mice, experimentally induced hypothyroidism was associated with low levels of exploratory behavior (Fundaro 1989; Sala-Roca et al. 2002; Pilhatsch et al. 2010) and low RMR (Moreno et al. 2002). However, results from individuals with "pathological" levels of thyroid function may tell us little about the effects of individual variation in thyroid status within the euthyroid range of variation (Johnstone et al. 2005; see also Girard et al. 2007 regarding variation in circulating leptin levels). Indeed, studies on the effect of T_3 on BMR have yielded mixed results in humans (reviewed in Johnstone et al. 2005). In men but not in women, T_4 (the precursor of T_3) was significantly positively correlated with BMR (Johnstone et al. 2005). In birds, a positive relationship was found between T_3 and BMR or RMR (Bobek et al. 1977; Chastel et al. 2003); in bats, however, no such correlation was found between T_3 and BMR (Richardson et al. 2009). Interestingly, individual variation in T_4 levels within the euthyroid range was positively correlated with exploratory behavior in rats (Helmreich and Tylee 2011). Furthermore, there appear to be links between the HPT axis and personality traits in healthy humans (Arqué et al. 1987; Balada et al. 1992; Frey et al. 2007). Finally, the HPT axis interacts with neurotransmitters, including serotonin and dopamine (Bauer and Whybrow 2002; Stipcevic et al. 2009). Therefore, individual variation along the HPT axis has the potential to link energetics with personality.

We urge physiologists (including neurobiologists and endocrinologists) to embrace integrative studies of personality with a goal of elucidating mechanisms that tie variation in

personality to variation in other complex traits. To integrate ecological and evolutionary approaches to animal personality with physiological approaches, it may be best to emphasize personality dimensions that reflect (largely) independent underlying causal mechanisms, but we do not yet have the knowledge to do this. Similarly, Moore and Hopkins (2009) argued for integrative studies of how hormones, immune functions, and energetics influence performance and ultimately lifetime reproductive success. It is also time to embrace a developmental perspective on the evolution of these suites of traits (Duckworth 2010; Stamps and Groothuis 2010), which is especially important, given the known organizational effects of hormones during development that can potentially lead to correlations among neural/behavioral and morphological/physiological traits observed in adulthood. Beyond this, on the genetic front (Bouchard and Loehlin 2001), brain-imaging methods (e.g., Schiller et al. 2009) are now being used to help identify genetic variants that have the potential to affect both personality and associated neural, physiological, or life-history traits (e.g., Buckholtz et al. 2008).

Conclusion

We have defined key concepts in the pace-of-life syndrome (table 1), reviewed the recent literature on the energetics of personality, highlighted some interesting parallels between research in mammals and in squamates, and attempted to integrate energetics and personality within a framework centered on performance (fig. 1). Many potentially interesting avenues remain to be explored both conceptually and empirically, including some that we have briefly discussed (motivation, intraindividual variation, and mechanisms). We come to the following conclusions.

(1) Although challenging, the study of individual variation can help to build bridges among disciplines, thus encouraging adoption of a holistic view of organisms that brings important synergy, compared with a separate focus on individual trait categories (Williams 2008). (2) A framework centered on performance is useful for integrating studies that span physiology, behavior, Darwinian fitness, energetics, and environmental context. (3) Although an increasingly large number of studies report links between energetics and life-history traits as well as a positive relationship between BMR and DEE among species, these associations are weakly supported at the level of individual variation. (4) No "universal" hypothesis (i.e., one based on a single underlying mechanism) can explain how energetics should relate to personality and fitness, and the multiple allocation and compensation mechanisms within an individual's energy budget imply that multiple metabolic measures are needed to fully understand the energetic consequences of individual variation in personality and life-history traits. (5) Performance fills a logical gap within the pace-of-life syndrome and has the potential to tie together the context dependency of selection and to illuminate the relationships between energetics and personality traits. (6) The term "personality" started to appear independently in behavioral-ecology studies of mammals and reptiles as if it expressed a concept that at least seemed easily understood by all, but future studies of animal personality must become more than phenomenological in nature. (7) Although research on individual variation has a long and rich history in both mammals and squamates, development of these research efforts occurred largely independently, and current research needs differ; studies on performance are currently lacking in mammals, whereas more studies on energetics are needed in squamates. (8) Although intraindividual variation and motivation can be seen as "nuisance" parameters in studies of performance, they can also become part of a comprehensive study of the relative importance of intra- and interindividual plasticity and consistency in correlations among traits. (9) More mechanistic studies are needed to resolve the common neural and endocrine pathways linking performance, energetics, and personality. However, studies that focus on hormone titers alone will likely provide an incomplete picture, as significant variation might be present in other components of neuroendocrine signaling systems, such as concentrations of hormone-binding proteins or the location, type, or abundance of receptors. (10) The HPT axis is worthy of additional attention as a possible mechanistic basis for associations between energy metabolism, performance, and personality.

Acknowledgments

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