Notes and Comments

The Pace of Life under Artificial Selection: Personality, Energy Expenditure, and Longevity Are Correlated in Domestic Dogs

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ABSTRACT: The domestic dog has undergone extensive artificial selection resulting in an extreme diversity in body size, personality, life-history, and metabolic traits among breeds. Here we tested whether proactive personalities (high levels of activity, boldness, and aggression) are related to a fast "pace of life" (high rates of growth, mortality, and energy expenditure). Data from the literature provide preliminary evidence that artificial selection on dogs (through domestication) generated variations in personality traits that are correlated with life histories and metabolism. We found that obedient (or docile, shy) breeds live longer than disobedient (or bold) ones and that aggressive breeds have higher energy needs than unaggressive ones. These correlations could result from either human preference for particular trait combinations or, more likely, correlated responses to artificial selection on personality. Our results suggest the existence of a general pace-of-life syndrome arising from the coevolution of personality, metabolic, and life-history traits.

Keywords: activity, aggression, correlated change, correlational selection, docility, life-history traits.

Introduction

Animal species and individuals differ greatly in key demographic and life-history traits, notably in growth rate, body size, and longevity. These traits tend to cluster along a "fast-slow" continuum and covary with the rate of energy expenditure, such that species or individuals with fast life histories also have high levels of energy expenditure (Symonds 1999; Lovegrove 2003; Wiersma et al. 2007). Identification of the proximate and ultimate causes of variation along the fast-slow life-history and metabolic continua is a pivotal topic in current ecology and evolutionary biology (Ricklefs and Wikelski 2002).

Personality, or the proactive-reactive continuum, has recently emerged as a promising new facet of the life-history/metabolic nexus (Biro and Stamps 2008; Careau et al. 2008). Proactive individuals—or by extension species—are expected to live fast and die young, whereas reactive personality types should live slow and die old (Wolf et al. 2007; Careau et al. 2009). For example, the fitness benefit of risk-taking behavior (e.g., boldness or docility toward humans) should covary with longevity, such that long-lived individuals or species are theoretically predicted to be shy, docile, or risk averse (Wolf et al. 2007). Natural selection should favor the integration of life-history, metabolic, and personality traits to optimize overall organisms' performance—or fitness—creating a suite of linked traits that can be referred to as a "pace-of-life" syndrome.

A large-scale artificial selection experiment was unwittingly initiated thousands of years ago and now allows us to evaluate the effects of artificial selection on personality (Swallow et al. 2009). The first animal species to be domesticated, the dog (*Canis familiaris*), has been shaped by artificial selection into more breed categories than any other living animal, with >400 breeds now recognized (Clutton-Brock 1999). Humans exerted selection on specific personality traits, such as activity, aggressiveness, and obedience (or docility), to shape each breed to a specific task (e.g., tracking, herding, guarding, fighting, or companionship). Therefore, other traits genetically linked with personality should have been changed as a correlated response to artificial selection on personality, such as the appearance of piebaldness in response to selection on tameness (Belyaev 1978). An alternative explanation to the presence of trait correlations among breeds is that, during domestication, humans could have favored combinations of traits and thus applied artificial correlational selection (Sinervo and Svensson 2002).

Dogs have long been the subject of scientific curiosity because of their close relationship with humans and their

great diversity in multiple aspects of their biology, especially body size (from the ∼2-kg Chihuahua to the >100-kg Saint Bernard; Kirkwood 1985; Jones and Gosling 2005). The result is a rich literature on breed-specific personality, life-history, and energetic traits. Yet dog breeds remain an overlooked resource for comparative genetic research on behavior (Wayne and Ostrander 2007; Swallow et al. 2009). Here, we use the striking behavioral differences among dog breeds to offer preliminary evidence for the pace-of-life syndrome.

Methods

We searched the literature for information on breed-specific personality, life histories, and energy expenditure. A complete data set and associated references are presented in table A1 in the online edition of the *American Naturalist*. The most complete and reliable data set on breed-specific personality was found in work by Draper (1995), who produced three uncorrelated personality traits from a factorial analysis on 56 breeds. In an effort to be consistent with the terminology used by behavioral ecologists (Réale et al. 2007), we labeled these traits as (*a*) activity, because the two main factors defining this trait were general activity and excitability; (*b*) aggressiveness, because the two main factors defining this trait were territorial defense and aggression to dogs; and (*c*) trainability, because the two main factors defining this trait were obedience training and ease of house-training. With regards to *c*, Svartberg (2002) showed that the broad personality dimension called shyness-boldness predisposes to trainability in general and can predict behavioral response in the home environment. Because obedience training and ease of house-training were the two most important factors that influenced trainability, this trait shares some aspects with docility and the shyness-boldness personality dimension.

Subsequent literature searches for reliable data on breed-specific life-history traits and energy expenditure were restricted to the 56 breeds listed by Draper (1995). We obtained adult body mass for all breeds from Evans and White (1988). Most published studies on breed-specific growth patterns provide limited data on a single breed over a particular time frame or in a particular environmental setting, which impedes comparisons among studies. Hawthorne et al. (2004), however, compared the growth curves of 12 differently sized dog breeds housed in a standardized kennel environment, nine of which are included in the personality data set.

Although a large number of existing studies report breed-specific median age at death (Bronson 1982; Patronek et al. 1997; Michell 1999; Proschowsky et al. 2003), these studies do not provide reliable estimates of longevity because they were based on either a small sample size or a skewed database derived from teaching hospitals. The most reliable estimates of longevity were found by Bonnett et al. (1997), who analyzed data for over 222,000 dogs registered for life insurance. Every breed included in this study had a sample size of >500 dog years at risk. Bonnett et al. (1997) produced valid population-based estimates of mortality rate for 19 breeds in common with the personality data set. Even though breed-specific mortality rates and longevity are different variables, they are intrinsically related; the odds of dying within, for example, the first 10 years of life are inversely proportional to longevity.

We found data on metabolizable energy intake (MEI) for nine popular breeds maintained in kennels, a standardized environment. When multiple MEI data were available for a given breed, we simply averaged all estimates (see table A1). Veterinarians and nutritionists most commonly reported MEI divided by body mass raised to the 0.75 exponent (e.g., in $kJ \cdot kg^{-0.75} \cdot day^{-1}$) without providing the associated body mass. All MEI measurements were made on nonreproductive adult individuals that neither significantly gained nor lost mass over the course of the sampling periods. Because dogs were in energy balance (i.e., neither gaining nor losing mass), MEI can be treated as a measure of energy expenditure (Koteja et al. 1999).

Statistical Analysis

Because data for all traits were available for only very few breeds, the unbalanced design of our data set restricted us to a univariate approach. We used Pearson product-moment correlations to test whether personality traits (activity, aggressiveness, and trainability) were correlated with growth rate, mortality rate, and MEI (all log transformed). Because body mass (square root transformed) was positively correlated with log-transformed mortality rate ($r_p = 0.64$, $N = 19$, $P = .003$), we present partial correlation estimates. To illustrate the relationship, however, we computed residuals from the regression of mortality rate and body mass (referred to as mass-adjusted mortality rate). We adjusted critical *P* values by correcting for the false discovery rate (Verhoeven et al. 2005). Sex differences within breeds could not be examined because most data obtained consisted of males and females combined.

In a parallel analysis, we incorporated information on the phylogenetic relatedness of different dog breeds to partially control for nonindependence in comparative analyses (Garland et al. 2005). On the basis of a modified phylogeny from Parker et al. (2004), we used phylogenetic least square regressions to estimate the phylogenetic signal (λ; Freckleton et al. 2002) present in all variables included in this study. We also retested the statistical significance of all models while adjusting optimally for the degree of phylogenetic signal. An important limitation in phylogeny-based comparative analysis of dog breeds is that their evo-

lutionary history is not well represented by a bifurcating tree model. Although modern pure breeds are maintained as genetically isolated populations by breed standards, they are frequently derived from mixtures of previous breeds (Galis et al. 2007), which introduces reticulate elements in the phylogeny (Posada and Crandall 2001). On the basis of currently available phylogenetic information (Parker et al. 2004), most breeds are not characterized by significant phylogenetic structure and are therefore best represented as polytomies (fig. A1 in the online edition of the *American Naturalist*). This lack of elucidated phylogenetic structure among many dog breeds reduces the likelihood of detecting significant phylogenetic influence on the traits we study and obtaining different results with standard and phylogeny-based analyses.

Results

Bivariate correlations are presented in table 1. After correcting critical *P* values for false discovery rate, each personality trait was related to a different life-history or metabolic trait. Activity was strongly and negatively related to body mass (fig. 1*a*). Interestingly, activity tended to be positively correlated with growth rate, indicating that active breeds grow fast but over a shorter period. Mass-adjusted mortality rate was negatively related to trainability (fig. 1*b*), such that obedient breeds live longer than disobedient ones. Although sample size for MEI was relatively low ($n = 9$), it was strongly and positively correlated with aggressiveness (fig. 1*c*). The inclusion of a resolved phylogenetic structure in the analysis did not change any of the statistical conclusions reported above (table A2 in the online edition of the *American Naturalist*).

Discussion

To our knowledge, this is the first report of a relationship between energy expenditure and aggressiveness in endotherms (see Cutts et al. 1998; for studies on fishes, see Lahti et al. 2002). Our results suggest that aggressiveness, or the willingness to engage in potentially dangerous aggressive interactions, covaries with physical and physiological traits (metabolic capacity). Indeed, the fitness payoff of aggressiveness should covary with the metabolic

machinery needed to prevail when aggressiveness escalates into aggression (Briffa and Sneddon 2007). As a result, any fitness advantages of high aggressiveness may be intrinsically linked to the fitness disadvantages of increased energy expenditure (Careau et al. 2008). We also found that, once adjusted for body mass, variation in longevity among dog breeds is related to their trainability. Given that trainability is inversely related to boldness in dogs (Svartberg 2002), this shy and long-lived versus bold and short-lived pattern supports the theoretical model proposed by Wolf et al. (2007). These potential energetic and longevity trade-offs affecting the evolution of aggression and boldness, respectively, could generate and maintain variation in behavior, life history, and metabolism, depending on food abundance, risk-taking opportunities, and competition (Lahti et al. 2002; Biro and Stamps 2008; Careau et al. 2009). The correlations we found among personality, life-history, and metabolic traits offer support to current theories on the evolution and maintenance of personality (Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008; Careau et al. 2008).

Behavioral differences among dog breeds have a genetic basis (Saetre et al. 2006) and are often regarded as remnants from past selection targeted at personality (Svartberg 2006). The remarkable diversity of modern dog breeds primarily reflects a radiation from a common founder stock in the 1800s that served to create most modern European breeds (Parker et al. 2004). Controlled breeding practices to maintain purebred standards (i.e., the pedigree barrier) reduced effective population size and increased genetic drift within breeds, resulting in the loss of genetic diversity within breeds and greater divergence among them (Wayne and Ostrander 2007). Modern dog breeds represent distinct genetic units because the mean genetic distance among breeds is high ($F_{ST} = 0.33$), and the variation among breeds accounts for 27% of total genetic variation in dogs (as opposed to only 5%–10% among human populations; Parker et al. 2004). In some breeds, genetic variation has been further reduced by historical bottlenecks (Ostrander et al. 2000; Ostrander and Wayne 2005). To the extent that life-history traits and energy expenditure have not been primary targets of selection in the development of dog breeds (Galis et al. 2007), the genetic com-

Table 1: Correlation coefficients among breed-specific personality traits (activity, aggressiveness, and trainability) and growth rate (log transformed; $n = 9$), body mass (square root transformed; $n = 56$), mortality (log transformed; partial correlation estimate with body mass as covariate; $n = 19$), and metabolizable energy intake (MEI; log transformed; $n = 9$) in dogs

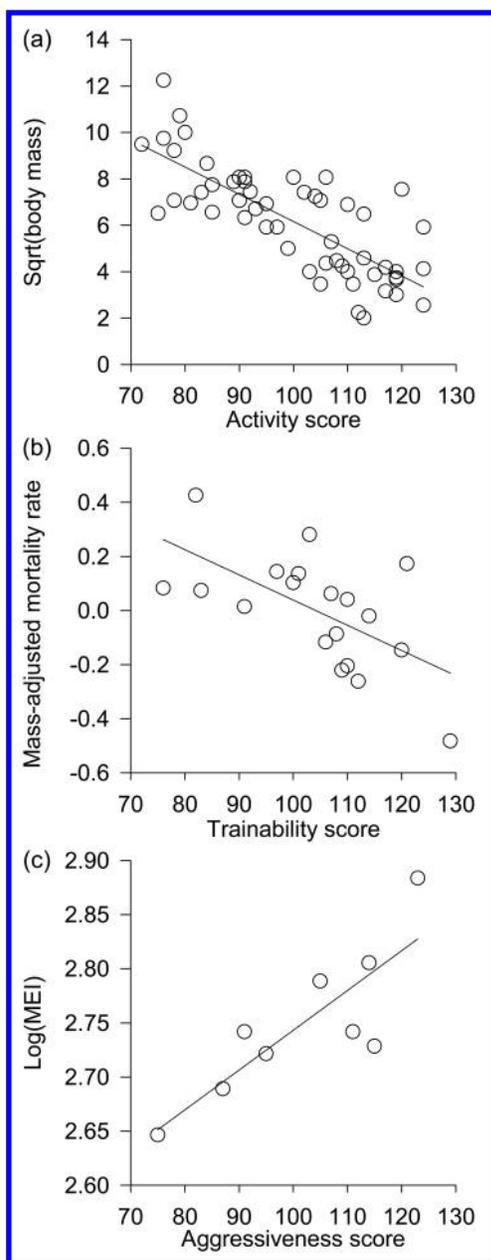|	Log (growth rate)		Square root (body mass)		Log (mortality rate)		Log (MEI)	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Activity	.72	.082	−**.77**	**.001**	−.25	.156	.50	.290
Aggressiveness	−.08	.846	−.10	.552	.24	.451	**.83**	**.022**
Trainability	−.17	.727	.26	.125	−**.61**	**.022**	−.51	.290

Figure 1: Correlations between breed-specific (*a*) activity score and body mass (square root transformed), (*b*) trainability score and mass-adjusted mortality rate (residuals from a regression of mortality rate [deaths 10,000 dogs^{-1} year^{-1}; log transformed] against square root of body mass), and (*c*) aggressiveness score and metabolizable energy intake (MEI; in kJ kg$^{-0.75}$ day^{-1}) in dogs. Detailed statistical results are given in table 1.

the correlations reported here are likely to have a stronger genetic component (Swallow et al. 2009)—our ability to generalize the pace-of-life syndrome to widely different taxa remains limited. The extent to which our results apply to ectotherms, for example, represents a particularly interesting question to address, especially because temperature (hence metabolic rate via Q_{10} effect) strongly influences ectotherm activity, aggressiveness, and boldness (Biro et al. 2010). Future studies should also examine how the extent of sexual dimorphism influences the pace-of-life syndrome since mate choice is known to promote genetic integration among traits (Svensson et al. 2009). As more species-specific tests of the pace-of-life syndrome become available, we will be better able to assess the extent to which relationships depend on (i) the level of biological variation involved (e.g., species, breeds, populations, genders, individuals) or (ii) the function of each personality trait in each gender or species (Biro and Stamps 2008), as well as whether these correlations (iii) are determined environmentally (e.g., Careau et al. 2009) versus genetically and (iv) differ in natural versus domesticated species (Adriaenssens and Johnsson 2009).

As noted above, the identified relationships could result from correlated responses to artificial selection on particular traits or from correlational selection exerted by humans on multiple traits simultaneously. The key distinction is whether these relationships emerged because humans selected for a single trait and other traits changed with it (correlated response to selection) or humans simultaneously selected multiple traits (correlational selection). For correlational selection to apply, two traits have to be under simultaneous selection, and the direction of selection on one trait has to consistently vary according to the other trait (Sinervo and Svensson 2002).

The activity versus body mass relationship (fig. 1*a*) could plausibly have arisen either through a correlated response to human selection on size or simultaneous correlational selection by humans on size and activity. We know that body mass is under intense artificial selection because various measures of body size are included in all breed standards (see American Kennel Club Web site, http://www .akc.org). Through creation of breeds, humans could have simultaneously and consistently selected for large body mass and low-activity level because high activity might progressively become undesirable as a dog's size increases (Draper 1995). However, it is unclear why humans would have necessarily selected for high activity in small breeds, as low or high levels of activity could be equally desirable in small-sized dogs. This could suggest, then, the alternative, that activity differences emerged incidentally as a correlated response to human selection on body size. Artificial selection on activity has been shown to lead to decreased body mass at maturity in mice (Swallow et al. 1999).

ponent of correlations identified here should be relatively high (Swallow et al. 2009).

Even though the particular associations of traits we report in this note are in general agreement with the literature reviewed by Biro and Stamps (2008)—except that

The most parsimonious explanation for the trainability versus longevity and aggressiveness versus MEI relationships (fig. 1*b*, 1*c*) is that longevity and energy expenditure changed as a correlated response to artificial selection on dog behavior since longevity and food intake are not included in any breed standards. For correlational selection to apply, not only would longevity and energy expenditure have to be under selection but also there would need to be consistent selection—throughout the independent creation of breeds spanning multiple continents, centuries, and breeding purposes (Clutton-Brock 1999)—applied to particular combinations of trainability or aggressiveness and longevity or MEI, respectively, to align breeds along the correlation. Consistencies in the circumstances under which dog breeds have been created could still impose unintentional correlational selection on trait combinations. For instance, if dogs are housed in groups and there is aggressive competition for limited food, less aggressive dogs with high energy requirements would be at a disadvantage. Under circumstances such as these, where correlational selection on multiple traits is unintentional, the distinction between correlational selection on multiple traits versus correlated responses to selection on a single trait becomes less clear.

Studies are needed to evaluate whether unintentional correlational-selection forces generally act in the same direction as natural correlational selection and maintain naturally existing genetic correlations or whether human-made environments unconsciously generate new artificial genetic coupling between behavioral, life-history, and physiological traits. Given the crucial importance of plant and animal domestication in human evolutionary history, it is surprising how little we know about the unintentional selective forces acting through domestication, especially in animal domestication (Zohary et al. 1998). Our results open new questions on the relative roles of correlated response to selection versus human preferences for particular trait combinations as major drivers of among-breed trait correlations in domesticated animals.

The selection process is termed "artificial" when human preferences or influences have a significant effect on the evolution of a particular population or species. Yet many evolutionary biologists view domestication as a type of natural selection and adaptive change that occurs as organisms are brought under the control of human beings (Ross-Ibarra et al. 2007; Driscoll et al. 2009; Garland and Rose 2009). Viewed this way, it is interesting to note that particular trait combinations that are expected to coevolve by means of natural selection (the pace-of-life syndrome) could have been selected in a correlated fashion through domestication, consciously or not. Alternatively, the presence of genetic correlations among personality traits, life histories, and energy expenditure can be considered either as a constraint on the independent evolutionary response of the traits involved or as an adaptation resulting from past natural selection pressures (Roff 1997; McGlothlin and Ketterson 2008). Therefore, the correlated-response scenario equally supports the constraint and the adaptive views of personality (Wolf et al. 2007). From the constraint point of view, our results indicate that selection along the fast-slow life-history and metabolic continua could potentially lead to apparently maladaptive behavior (Sih et al. 2004). From the adaptive point of view, behavioral variation might be maintained by trade-offs generated by genetic correlations between personality, life history, and energy metabolism (Stamps 2007; Biro and Stamps 2008; Careau et al. 2008).

Acknowledgments

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