The role of quantitative genetic studies in animal physiological ecology

El rol de los estudios genético-cuantitativos en ecología fisiológica animal

PAULINA ARTACHO[1], LUIS E. CASTAÑEDA[1] & ROBERTO F. NESPOLO[1*]

[1] Instituto de Ecología y Evolución, Facultad de Ciencias, Universidad Austral de Chile,
Casilla 567, Valdivia, Chile;
* Corresponding author: robertonespolo@uach.cl

ABSTRACT

Evolutionary physiology is a new discipline with roots in comparative physiology. One major change in the emergence of this discipline was an explicit new focus on viewing organisms as the evolutionary products of natural selection. The shift in research emphasis from comparative physiology to evolutionary physiology has resulted in physiological traits becoming important elements in broad research programs of evolution and ecology. Evolutionary quantitative genetics is a theory-based biological discipline that has developed the quantitative tools to test explicit evolutionary hypotheses. The role of quantitative genetics has been paramount, in studying the microevolution of morphology, behavior and life history, but not comparative physiology. As a consequence, little basic information is known such as additive genetic variation of physiological traits and the magnitude of genetically based trade-offs (i.e., genetic correlations) with other traits. Here we explore possible causes for such gap, which we believe are related with the inconsistency of what we call physiological traits across taxonomic and organizational divisions, combined with logistical problems of pedigree–based analyses in complex traits.

Key words: evolutionary physiology, heritability, directional selection differential, response to selection, fitness.

RESUMEN

La fisiología evolutiva es una nueva disciplina con raíces en la fisiología comparada. Uno de los principales cambios introducidos con esta disciplina es un enfoque donde los organismos son analizados en forma explícita como el producto de selección natural. Este cambio de énfasis desde fisiología comparada a fisiología evolutiva ha resultado en que los rasgos fisiológicos son elementos importantes en el programa de investigación de la evolución y la ecología. La genética cuantitativa evolutiva es una disciplina biológica con bases teóricas que ha desarrollado las herramientas cuantitativas para someter a prueba hipótesis evolutivas en forma explícita. El rol de la genética cuantitativa ha sido notable en el estudio de la microevolución de la morfología, comportamiento e historia de vida, pero no en fisiología comparada. Como consecuencia, existe escasa información básica sobre variación genética aditiva de rasgos fisiológicos y posibles compromisos genéticos (i.e., correlaciones genéticas) que puedan tener estos con otros rasgos. En este comentario exploramos las posibles causas de este vacío, las cuales creemos están relacionadas con la inconsistencia de lo que llamamos rasgos fisiológicos entre las divisiones taxonómicas y organizacionales, a los que se agregan problemas logísticos inherentes a los análisis genealógicos en rasgos complejos.

Palabras clave: fisiología evolutiva, heredabilidad, diferencial de selección direccional, respuesta a la selección, adecuación biológica.

INTRODUCTION

Biology has always differed from chemistry and physics in the sense that fundamental theories and laws that aim to predict every phenomenon (as in the later) are unlikely to exist (Murray 2001). There are many reasons for that, most of them related with the fact that (1) what we call biological phenomena are complex frameworks of processes occuring across several levels of organization, and (2) there is an important amount of stochasticity or environmental "noise" added in each level of organization (Weber 2000). However, biological sciences are diverse; some fields are more formalized in terms of theories and laws than others. This is

probably due to historical, as well as practical reasons. Disciplines that are mostly experimental are less theoretical and are essentially grounded on empirical patterns and processes, an aspect that inspired their first researchers. We suggest comparative physiology is an example of this. The legacy of former comparative physiologists was a change in the way of thinking in order to consider organisms as the evolutionary product of natural selection (Schmidt-Nielsen 1995, McNab 2001). This aim was commonly addressed by the experimental comparison of physiological capacities between organisms from extreme environments.

Conversely, disciplines that arose from the interest to test explicit theoretical formulation such as the Darwinian evolutionary theory, have developed a more theoretical construct preceding empirical patterns. An example of the later is evolutionary quantitative genetics (Weber 2000). In times of interdisciplinary fusion and meta-analyses, the percolation of quantitative genetic procedures into comparative physiology would contribute greatly to the understanding of the explicit evolutionary causes and consequences of physiological traits. However, as we have searched in the literature, very few of these interdisciplinary approaches have been carried out so far. In this commentary we discuss the potential of evolutionary quantitative genetics to explore the underlying causes of physiological adaptation, the probable causes for its absence in comparative physiology, and possible solutions for such missing link.

PHENOTYPE-BASED MICROEVOLUTION

Evolutionary population geneticists such as Fisher (1930), Haldane (1932) or Wright (1932) addressed quantitatively the problem of selection and its evolutionary response in natural populations (i.e., microevolution). To solve their theoretical questions, they developed statistical methods for correlational and randomized experiments, that are now of common usage in biological sciences such as the analysis of variance, path analysis and related analytical procedures. The concept of fitness, as the reproductive potential of an individual (R_0), is owed to Fisher (1930, see also Huey & Berrigan 2001) who stated that the

mean fitness of a population is equal to the additive genetic variance in relative fitness in this moment. This was called "the fundamental theorem of natural selection" (Ewens 1989), which is part of a more general expression, the Robertson-Price identity (Lynch & Walsh 1998, also known as the "secondary theorem of natural selection", Caswell 1989) that equates the selection differential (S = the difference in the mean value of the trait within generations) with the covariance of any trait and relative fitness (w = R_0 / mean R). The predictability of microevolution is encapsulated in the breeder's equation (Henderson 1984), which relates the response to selection in any trait (R = the difference in the mean value of the trait between generations) to the product of narrow-sense heritability (h^2 = the ratio between additive genetic variance and phenotypic variance) and S (= the directional selection differential, see Fig. 1):

$$R = h^2 S \qquad (1)$$

For many traits that are interrelated through genetic correlations (i.e., correlations that persist across generations), Lande & Arnold (1983) developed the multivariate selection theory that basically changed the equation (1) to a matrix equation. This new equation relates Δz (vector of the response to selection in a suit of traits which replaces R) with G (the variance – covariance additive genetic matrix which replaces h^2) and β (the directional selection gradient, which replaces S),

$$\Delta z = G\beta \qquad (2)$$

This basic framework is a statistical approach to dissect genetic variation completely based on phenotypic measures and known pedigrees. Contrarily to what common knowledge regarding molecular genetics could lead to believe, there is no better procedure to determine the heritable variation in a trait in natural populations.

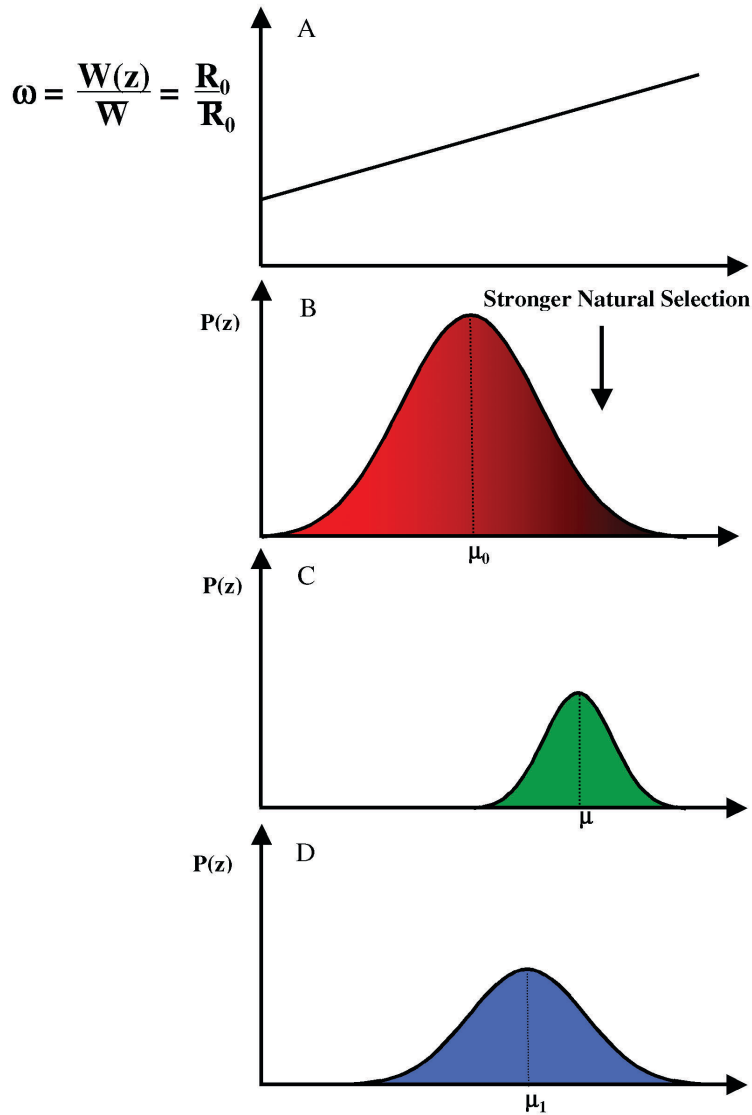## THE CONFLICTING EVIDENCE: PHYSIOLOGICAL TRAITS

Elements of the above equations as well as the use and statistical comparisons of whole

equations have become very sophisticated after the income of computer-intensive likelihood and Monte Carlo methods (Boldman et al. 1995, Roff 1997, Steppan et al. 2002). A broad scope of organisms and types of traits are known from this perspective and hence, a great amount of predictable (micro) evolution is possible (Mousseau & Roff 1987, Stirling et al. 2002). In fact, one of the general findings of evolutionary genetics is that genetic variation is abundant and the vast majority of traits respond to selection (Mousseau et al. 2000). However, the heritability of traits of interest to comparative physiologists has rarely been measured. Some progress has been made with bioenergetic traits of endotherm. Hayes & O'Connor (1999) presented evidence supporting that the directional selection differential (S) could be high in thermoregulatory maximum metabolic rate (MMR) of a rodent. Dohm et al. (1996) and Dohm et al. (2001) showed that aerobic endurance, basal metabolic rate (BMR) and maximum metabolic rate (MMR) in *Mus* exhibit low h^2 thus suggesting that these traits have low potential for response to selection. Besides, current estimates of heritabilities of metabolic rate in animals have low statistical power (Dohm et al. 2001, Nespolo et al. 2003, Bacigalupe et al. 2004). All this view may change soon as we are aware of at least two research programs currently in progress that are recording large and significant heritabilities of mammalian metabolic traits (Ksiazek et al., Nespolo et al. unpublished results; Sadowska et al. unpublished results).

The relevance of maternal effects, including the influence of parental care on the performance of young, formerly considered unimportant to adaptive evolution, have been reconsidered recently as determinant for the response to selection thanks to quantitative genetics (Mousseau & Fox 1998). Several bioenergetic traits of mammals have presented high maternal-non additive genetic effects such as nonshivering thermogenesis (NST), sustained metabolic rate (SusMR), and mass of metabolically active organs (Nespolo et al. 2003, Bacigalupe et al. 2004). However, the adequate separation of maternal effects themselves from common environmental variance remains as an open question. On the other hand, the genetic correlation among bioenergetic traits and life history traits, that is, the components of the G- matrix that predict evolution of the integrated phenotype appear to be significantly different from zero in several cases (Nespolo, Bustamante, Bacigalupe & Bozinovic unpublished results). Indirect analyses suggest that metabolism may be heritable in vertebrates because metabolic rates (VO_2) are repeatable (Hayes & Chappell 1990, Speakman et al. 1994, Chappell et al. 1995, Berteaux et al. 1996, Hayes & O'Connor 1999), because an underlying trait (e.g., hemoglobin polymorphism, brown adipose tissue) presents heritable variation (Snyder 1978, Chappell & Snyder 1984, Lynch et al. 1988, Sorci et al. 1995), or because VO_2 shows high broad-sense heritability (Garland et al. 1990). However, it should be noted that (1) high repeatability is not a guarantee of high heritability (Lessels & Boag 1987, Dohm 2002), (2) underlying variables are expected to be more heritable than whole-organism traits because the latter are less influenced by environmental variance (Price & Schluter 1991, Kruuk et al. 2003), and (3) broad-sense heritability includes maternal and common environmental effects, hence it is larger than h^2 (Falconer & Mackay 1997).

Clearly, the few quantitative genetic studies of physiological traits in natural populations of vertebrates have given mixed results that claim for more research with more statistical power. The scarcity of data about genetic variances and genetic correlations in physiological traits is paradoxical considering the long tradition in research of comparative physiologists. Almost in parallel, evolutionary quantitative geneticists have studied the dynamics of all components of equations (1) and (2) for life histories, morphology and behavior in birds (Barbraud 2000, Szekely et al. 2000, Merila et al. 2001), mammals (Boonstra & Hochachka 1997, Kruuk et al. 2000, Thomas et al. 2000), reptiles (Janzen 1993, Shine & Shetty 2001, Sinervo & Zamudio 2001), amphibians (Van Buskirk & Schmidt 2000, Watkins 2001, Uller et al. 2002), fishes (Reznick et al. 1997, Brooks & Endler 2001, Karino & Haijima 2001), insects (Fox et al. 1999, Begin & Roff 2001, Stirling et al. 2002), mollusks (Parsonage & Hughes 2002), crustaceans (Pfrender & Lynch 2000) and bacteria (Travisano et al. 1995, Rileay et al. 2001).

$$\omega = \frac{W(z)}{W} = \frac{R_0}{R_0}$$

A

B

Stronger Natural Selection

P(z)

μ_0

C

P(z)

μ

D

P(z)

μ_1

Physiological trait (z) (e.g., metabolic rate, evaporative water loss, sprint speed, endurance, sustained metabolic rate)

Fig. 1: Simplified diagram showing the analysis of the response to directional selection in a physiological trait, in a population. In this example, directional selection, evidenced by a positive correlation between relative fitness (ω: the ratio between absolute and mean lifetime reproductive potential, R_0, see Huey and Berrigan, 2001) and the mean fitness of the population, is acting on the right tail of a distribution of the trait (A and B). Red and green curves represent the distribution of the trait before and after selection within a generation, respectively (B and C). Shaded area in the red curve represent individuals with increased survival and/or differential reproduction, according to the fitness function. Similarly, μ_o and μ represent the mean populational values before and after selection, respectively. The mean of the trait in the descendents of the selected individuals (i.e., between generations) is μ_1. In this case, directional selection differential ($S = \mu - \mu_o$) and response to selection ($R = \mu_1 - \mu_o$) in a hypotetical trait with narrow-sense heritability (h^2) of intermediate value (i.e., $h^2 \sim 0.5$) is reflected in the fact that although selection is strong (the displacement of the green curve from the red curve), its evolutionary response is intermediate (the displacement of the blue curve from the red curve). The progresively shadowed (or the slope of the curve in A) area in the red curve represent, in a diagramatic form, the Robertson – Price identity: the selection diffe-

There are obvious logistical problems related with developing quantitative genetic studies in comparative physiology. One major difficulty is to measure hundreds of individuals, as any pedigree-based design requires. Another problem relates to the fact that "physiological traits" are variables that are not functionally consistent across species. For some animals, many physiological traits (e.g., dessication resistance in insects, Hoffman, 2000) are functionally different from traits classified as "physiological" in other animals (e.g., oxygen carrying capacity by haemoglobin in mammals, Chappell & Snyder 1984). Hence, heritability estimates of physiological traits may not be readily used to infer values in other physiological traits. Thus the scarcity of estimates and the breadth of variation within the physiological category make it difficult to reach firm conclusions regarding the range of heritabilities in this type of traits. These complications could be avoided, or at least ameliorated, by means of: (1) comparing estimates of different physiological traits obtained during the same experiments and measured to the same individuals, and (2) considering a common physiological trait in very different organisms. To sum up, much experimental work is needed to attain this objective, followed by an appropriate synthesis in the form of a meta-analysis to decide finally if physiology has the same microevolutionary potential than morphology, behavior and fitness.

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rential is equivalent to the covariance between relative fitness and the trait, $S = Cov(\omega, z)$. In other words, natural selection could be determined by regressing relative fitness with the value of the physiological trait in a sample of organisms from a population. See text for details.

Diagrama simplificado que muestra el análisis de la respuesta a la selección direccional en un rasgo fisiológico, en una población. En este ejemplo, la selección direccional, evidenciada por una correlación positiva entre la adecuación biológica relativa (ω: razón entre el potencial reproductivo individual absoluto y el potencial reproductivo promedio, R_0, ver Huey & Berrigan 2001) y la adecuación biológica promedio de la población, está actuando en la cola derecha de la distribución del rasgo (A y B). La curva roja y verde representa la distribución del rasgo antes y después de la selección dentro de una generación, respectivamente (B y C). El área sombreada en la curva roja representa los individuos con la sobrevivencia y/o reproducción diferencial aumentada, de acuerdo a la función de la adecuación biológica. Similarmente, μ_0 y μ representan los valores poblacionales promedio antes y después de la selección, respectivamente. La media del rasgo en los descendientes de los individuos seleccionados (i.e., entre generaciones) es μ_1. En este caso, el diferencial de selección direccional ($S = \mu - \mu_0$), y respuesta a la selección ($R = \mu_1 - \mu_0$), en un rasgo hipotético con heredabilidad en sentido estricto (h^2) de valores intermedios (i.e., $h^2 \sim 0.5$), es reflejado en el hecho que aunque la selección es fuerte (el desplazamiento de la curva verde desde la curva roja), su respuesta evolutiva es intermedia (el desplazamiento de la curva azul de la curva roja). El área progresivamente sombreada (o la pendiente de la curva en A) en la curva roja representa, en forma diagramática, la identidad de Robertson-Price: el diferencial de selección es equivalente a la covarianza entre la adecuación biológica relativa y el rasgo, $S = Cov(\omega, z)$. En otras palabras, la selección natural podría ser determinada realizando una regresión entre la adecuación biológica relativa y el valor del rasgo fisiológico, en una muestra de organismos de la población. Ver texto para detalles.

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