Strategy evaluation of ecology and evolution by model selection: An overview

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Abstract
We present extensive literature reviews that demonstrate that temperament traits are heritable, and linked to fitness and to several other traits of importance to ecology and evolution. Furthermore, we describe ecologically relevant measurement methods and point to several ecological and evolutionary topics that would benefit from considering temperament, such as phenotypic plasticity, conservation biology, population sampling, and invasion biology. We propose that temperament can and should be studied within an evolutionary ecology framework and provide a terminology that could be used as a working tool for ecological studies of temperament. Our terminology includes five major temperament trait categories: shyness-boldness, exploration avoidance, activity, sociability and aggressiveness. This terminology does not make inferences regarding underlying dispositions or psychological processes, which may have restrained ecologists and evolutionary biologists from working on these traits.

Keywords: Temperament, personality, individual differences, behavioral syndromes, coping styles, context specificity

Introduction
Psychologists have long been interested in the study of human and animal temperament, which has led to significant theoretical and empirical developments (Wilson, 1994; Gosling, 2001; Boyce & Ellis, 2005) [40]. By contrast, ecologists and evolutionary biologists have generally shown little interest in the concept of temperament, although certain temperament traits perceived to affect fitness directly, such as aggressiveness and reaction to predators, have received substantial scientific attention (Clark & Ehlinger, 1987; Huntingford, Wright & Tierney, 1994; Wilson et al., 1994; Boissy, 1995; Clarke & Boinski, 1995; Greenberg & Mettke-Hofmann, 2001; Sih, Bell & Johnson, 2004a; Sih et al., 2004b; Ellis et al., 2006) [61, 45, 90, 27].

In recent years temperament has begun to receive theoretical and empirical attention from ecologists (Wilson et al., 1994; Clarke & Boinski, 1995; Greenberg & Mettke-Hofmann, 2001; Sih et al., 2004a, b; Dall, Houston & McNamara, 2004) [45, 90, 19]. However, ecologists generally do not perceive temperament as an important addition to our understanding of the ecology and evolution of animals. This is surprising given a growing body of evidence showing that temperament traits affect important ecological processes such as niche expansion, dispersal or social organization.

The reasons why temperament has not yet been integrated into ecological theory are diverse, and include difficulties in definition, in finding appropriate methods to quantify temperament, and in testing the significance of these traits in the field. Our goal here is to build a supporting conceptual and methodological framework for the ecological study of temperament that may help overcome these difficulties. Moreover, we review extensive evidence for the genetic basis of temperament traits and links between temperament and traits of importance to evolutionary ecology, such as reproductive rate and survival. Obviously, many important questions regarding temperament remain to be resolved before developing a general framework. Nevertheless, we hope that the proposed framework will serve to guide and encourage future research in the field.

How model selection works
Generating biological hypotheses as candidate models Model selection is underpinned by a philosophical view that understanding can best be approached by simultaneously weighing evidence for multiple working hypotheses. Consequently, the first step in model selection lies in articulating a reasonable set of competing hypotheses. Ideally, this set is chosen before data collection and represents the best understanding of factors thought to be involved in the process of interest.
Hypotheses that originate in verbal or graphical form must be translated to mathematical equations (i.e. models) before being fit to behavioral trait concepts in an ecological and evolutionary context. A character (or trait) can be considered as a characteristic of an organism shared by all or some of the individuals of a species that can vary, although not necessarily, among these individuals (we consider character and trait as synonyms; see Wagner, 2001 [3], on the diversity of the character concept). Measured individual values for that character are called phenotypes. A quantitative genetic framework can provide a biological definition of a trait. Quantitative genetic models, which have received some recent support, assume that the variance of phenotypic quantitative traits (i.e., the trait measured) is influenced by a relatively large number of genes, each with small individual effects, and by a series of environmental effects (Falconer & Mackay, 1996; Lynch & Walsh, 1998; Roff, 1997; Flint, 2003; Reif & Lesch, 2003) [32, 34, 84]. An important aspect of our definition is that two traits can be associated at the phenotypic level, illustrating their potential genetic or epigenetic links (Henderson, 1990; Wagner, 1996; Cheverud, 1996; Sih et al., 2004b) [34, 94].

Validating measures of temperaments traits Biological and ecological validity: For logistical and methodological reasons, temperament traits should be measured in an experimental context as we can rarely measure them by direct observation. Furthermore, the need for large sample sizes for estimation of heritability or selection pressures, means tests should be rapid and easy to perform. Direct observation of individuals and their ranking according to a predetermined scale has, however, been used by psychologists (Gosling, 2001) [40] but can be criticized because of the subjectivity of the interpretation of observations. The experimental approach is open to criticism since it places an animal in a situation that is irrelevant to its natural conditions.

**Measuring temperament traits**

When developing tests to measure temperament traits we expect to find three characteristics in the trait we measure: i.e. phenotypic variation and repeatability.

**Linking temperament with fitness**

We raised above the importance of past selection pressures on the organization of temperament traits. Few attempts have been made to study temperament and its functional consequences in natural populations (Wilson et al., 1994), meaning that the importance of temperament for fitness remains largely unknown (Clark & Ehlinger, 1987; Wilson, 1998; Dingemanse & Reale, 2005) [24].

**Temperament traits as adaptation**

Comparative studies To investigate temperament traits as adaptations, it is insufficient to show that the trait affects current fitness. The selective forces that have resulted in past evolutionary changes are not necessarily the same forces acting on contemporary populations (e.g., Bennett & Owens, 2002) [7], so to elucidate fully the ultimate explanations for links between temperament and ecology, we also need to know how present-day patterns result from historical events (Losos & Miles, 1994). This can be done using comparative approaches, based on the comparison of populations or species that differ in a given temperament trait or set of traits. Such an approach may also be useful in determining general principles regarding the potential evolutionary and ecological role of temperament that apply across taxa, as well as allowing tests of hypotheses otherwise difficult to examine (Losos & Miles, 1994).

**Conclusions**

Our aim was to build a general framework for the ecological and evolutionary study of temperament and to review the evidence that temperament traits are heritable, linked to fitness, and correlate with several other important traits. We hope this framework and compilation of evidence, combined with the growing general interest in the evolutionary ecology of temperament and the diversity of empirical approaches available, stimulates new progress. We predict that temperament will form an important part of future research on various ecological topics. Temperament appears to affect the various ways an individual interacts with its environment, whether in its reactions with predators, food sources, and habitat, or in its social or sexual interactions with conspecifics. Temperament phenotypes will be favored or disfavored by selection depending on the particular ecological conditions experienced by the population. Furthermore, individual differences in temperament may affect variation in habitat use or assortative mating, and thus will create conditions for non-random mating. Temperament may have important consequences for several ecological topics, such as: population dynamics and genetics (i.e., dispersal, individual movement, gene flow, and the genetic composition of meta-populations, landscape ecology (i.e., changes in the structure of the landscape will affect the movement of individuals differently according to their temperament, community ecology (i.e., individual variation in some sets of correlated temperament and morphological traits may be viewed as functional sub-categories in the organization of communities), invasion biology (i.e., could temperament be an important factor in the invasiveness syndrome?); and (e) speciation (i.e., temperament variation may be responsible for the geographic and reproductive isolation of individuals characterized by particular combinations of behavioral and morphological and life-history traits).

**References**


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