

# A framework for determining the fitness consequences of antipredator behavior

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A recent review by Lind and Cresswell (2005) noted some important difficulties with quantifying the fitness consequences of antipredator behaviors. In this paper, we discuss the conceptual and analytical tools available to behavioral ecologists for approaching the question of adaptive value in the broader context of whole organism performance and total fitness. Because these tools already exist, we feel that determining the fitness consequences of antipredator behavior, or any behavior for that matter, is not intractable. Instead, it seems that both the challenge and the solution lie in linking the theoretical concepts of evolutionary biologists to the empirical data typically collected by behavioral ecologists. We hope that this paper will help forge this link as well as serve as a reminder that when grounded in natural history and an appropriate quantitative, conceptual framework, empirical studies can still provide detailed answers to the increasingly complex questions we ask. *Key words*: antipredator behavior, fitness, multivariate selection analysis, path analysis, phenotypic integration. [*Behav Ecol*]

Behavioral ecologists have long been interested in understanding the adaptive value of antipredator behavior (Sih 1987; Lima and Dill 1990; Lima 1998). A recent review by Lind and Cresswell (2005), however, noted some important difficulties with quantifying the fitness consequences of antipredator behaviors. In essence, Lind and Cresswell suggest that most studies do not provide strong evidence on the adaptive value of antipredator behavior because they do not consider 1) trade-offs between antipredator and reproductive performance, 2) the abilities of organisms to avoid fitness losses associated with constraints on focal traits by employing behavioral alternatives (behavioral compensation), and 3) the effects of behavioral defenses at different stages of the predation sequence. The authors rightfully assert that an understanding of these issues can only be accomplished by measuring multiple traits and fitness components (i.e., survival and reproduction). Nevertheless, the question of how to integrate such data into a coherent analysis of adaptive value was left unclear. Our discussion therefore has 2 main goals: 1) to illustrate how the concerns addressed by Lind and Cresswell can be unified and generalized to include a variety of other issues under the conceptual framework of phenotypic integration and 2) to describe 2 quantitative techniques that exist within that framework for addressing the question of adaptive value. We begin by reiterating the main points made by Lind and Cresswell with a hypothetical example (illustrated in Figure 1).

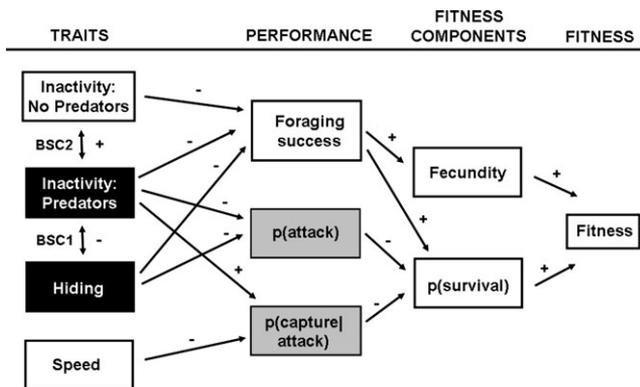
Imagine an aquatic invertebrate prey species coexisting with predatory fish. One response exhibited by these prey when they sense fish is to become inactive. By reducing the rate at which the prey encounter and are detected by predators, this behavior reduces the prey's overall probability of being attacked. With respect to predator avoidance, this behavior is clearly adaptive. However, inactivity also lowers encounter rates between prey and their resources. This leads to poor foraging performance in both the presence and absence of

predators. The result is a trade-off between predator avoidance and foraging success. Now imagine the prey species has 2 alternative behaviors, inactivity and hiding in refuges, which reduce its probability of being attacked by predators. Here, behavioral compensation can occur, wherein individuals that do not become inactive in the presence of predators can still avoid being attacked by hiding. The result is that the expected positive correlation of one trait (inactivity) with fitness is masked by the effect of the other trait (hiding), which confers high fitness irrespective of an individual's activity level (Figure 1, black boxes). Next, consider that behavioral traits can have different effects at different stages of the predation sequence (e.g., probabilities of attack and probability of capture given an attack, Figure 1, gray boxes). For example, while inactivity reduces an individual's probability of being attacked by a predator, performing this behavior means that escape responses are delayed. Thus, if attacked, inactivity increases an individual's probability of being captured. This example illustrates how a single trait can have different effects on fitness through alternative pathways and how multiple traits can interact to affect fitness. Recent studies of prey behavior show that these complex phenomena are common in nature (DeWitt et al. 1999; Hedrick 2000; McCarthy and Fisher 2000; DeWitt and Langerhans 2003; Ghalambor et al. 2003; Relyea 2004; Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004; Kishida and Nishimura 2005).

In the face of such complexity, determining the fitness consequences of antipredator behavior is indeed a difficult task. Nevertheless, there are relevant conceptual and analytical tools currently available for addressing integrated behavioral responses. Because these tools already exist, we feel that accounting for the complexity associated with understanding the fitness consequences of antipredator behavior, or any behavior for that matter, is not intractable. Instead, it seems that both the challenge and the solution lie in linking the theoretical concepts of evolutionary biologists to the empirical data typically collected by behavioral ecologists. In particular, the issues highlighted by Lind and Cresswell center around covariation between functionally related traits and can be unified under the conceptual framework of phenotypic integration. Phenotypic integration has been defined as "the pattern

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Received 18 December 2005; revised 19 May 2006; accepted 30 June 2006.



**Figure 1**

Path diagram showing how behavioral traits influence different stages of performance, including multiple stages of the predation sequence, which then influence the fitness of prey. The diagram illustrates the 3 main problems (1–3) outlined by Lind and Cresswell (2005), as well as, potential behavioral syndromes (4). 1) The trade-off between the probability of being attacked,  $P(\text{attack})$ , and foraging success can be seen by following the different paths (each represented by a series of arrows) leading from the trait inactivity: predators. The path traditionally emphasized is through  $P(\text{attack})$ ; however, another path leads through foraging success both directly and indirectly via the behavioral correlation with inactivity: no predators. 2) The black boxes indicate compensatory behaviors; both hiding and inactivity have a negative (–) effect on  $P(\text{attack})$ . 3) The gray “performance” boxes represent 2 stages in the predation sequence (probability of being attacked and probability of capture given an attack). Different behaviors, for example, inactivity: predators, have different effects at different stages. 4) The within (BSC1) and across (BSC2) context correlations that represent behavioral syndrome components are indicated by double-headed arrows.

of functional, developmental and/or genetic correlation (however measured) among different traits in a given organism” (Pigliucci 2003). There is a long and diverse history of approaches aimed at understanding how traits (particularly morphological traits) interact (Wright 1934; Olsen and Miller 1958; Berg 1960; Lande 1980; Lande and Arnold 1983; Crespi and Brookstein 1989; Wagner 2001; Arnold 2005). Within this framework, there are 2 closely related techniques for quantifying the degree and fitness consequences of interactions among traits: path analysis and multivariate selection analysis (MSA).

Path analysis is a multiple regression-based technique aimed at describing patterns of covariation among traits and their relative importance in explaining variation in performance and fitness. The relationships among traits, performance, and fitness are represented by arrows in a path diagram (see Figure 1). An important aspect of path analysis is that it is based on an a priori understanding of the causal interactions among traits and fitness (Kingsolver and Schemske 1991). Thus, path diagrams represent hypotheses and often multiple path diagrams are constructed and “tested” in much the same way as alternative verbal hypotheses. The validity of alternative path models can be directly assessed by designing experiments to demonstrate the causal mechanisms underlying the correlative relationships embodied in a given path diagram. In this way, path diagrams can serve as “experimental roadmaps,” for making predictions about experimental outcomes and highlighting areas that require further investigation (e.g., Wootton 1994; Sinervo and DeNardo 1996). Additionally, well-established statistical methods (e.g., using Akaike information criteria) exist for evaluating the relative fit of different models to observed data (Burnham and Anderson 2001; Hobbs and Hilborn 2006), including software designed to compare alternative path models (e.g., Amos; Arbuckle and Wothke 1999).

Another key feature of path analysis is its applicability to situations in which multiple traits affect fitness in a sequential manner (Wright 1931; Kingsolver and Schemske 1991). For example, in quantifying the effects of prey defenses on anti-predator performance, path analysis makes it possible to break down the predation sequence into progressive stages (e.g., Sih and Moore 1990); one of the concerns raised by Lind and Cresswell. It is then possible to quantify the effect of any number of different prey traits on the probability of encounter, detection, attack, capture, and consumption, in turn, and then look at each stage’s contribution to the overall probability of survival (Figure 1, gray boxes). In this way, path analysis allows the overall effect of a particular trait on fitness to be partitioned into separate pathways that correspond to different causal mechanisms. For example, using path analysis, it is possible to quantify the relative importance of the different pathways leading from “inactivity: predators” to “fitness” in Figure 1. The usual mechanism emphasized by behavioral ecologists is represented by the path leading through  $P(\text{attack})$  and  $P(\text{survival})$ ; however, other pathways lead through foraging success (both directly and indirectly via the behavioral correlation to inactivity in the absence of predators) and  $P(\text{capture|attack})$ . Depending on the relative contribution of different aspects of performance to various fitness components and ultimately to total fitness, the net fitness affect of inactivity: predators could be positive, negative, or neutral.

An example of the types of hypotheses that can be addressed using path analysis appears in Sih et al. (2002). In that study, path analysis was used to determine the relative contribution of 3 processes: male-male competition, male-female conflict, and female choice, to sexual selection on behavior and morphology in water striders. Each process was represented by a different path leading from traits to fitness, in this case mating success. Large males enjoyed increased mating success on account of being better competitors and more able to overpower resisting females. Females, however, preferred small males. As a result, the positive correlation of male size with mating success, and thus the strength of selection for larger males, was attenuated by female choice. Analyzed in this manner, it becomes easy to hypothesize about how net selection on size might vary in response to ecological and demographic factors influencing the relative strengths of male-male competition, male-female conflict, and female choice. A similar approach could be used to apply path analysis to antipredator behavior.

Path analysis does not, however, typically account for situations where fitness depends on interactive combinations of traits (Conner 1996). For this, a useful statistical technique is MSA. Here, multiple regression techniques are used to identify specific targets of selection (Lande 1980; Lande and Arnold 1983). Like path analysis, MSA allows you to examine the independent (i.e., assuming all other traits are fixed) and net effects of multiple traits on different stages of the predation sequence or components of overall fitness. The real power of MSA, however, lies in the ability to investigate whether the fitness consequences of a focal trait depend on the expression of other traits. In other words, by using MSA it is possible to quantify the interactive effects of traits on fitness (e.g., Brodie 1992; Forsman and Appelqvist 1998; Svensson et al. 2001). To understand the importance of this, think back to the aquatic invertebrate scenario above. Consider that some individuals are faster than others, and that rather than always becoming inactive, individuals of this species can modulate their activity in response to predators along a continuum from inactivity to fleeing. Fleeing increases the preys’ probability of being attacked by attracting the predators’ attention (opposite of inactivity) but decreases their probability of capture given an

attack. However, the advantage of fleeing depends on an individual's speed. For fast individuals, fleeing always results in higher fitness than inactivity due to the high probability of escape, despite being attacked. For slow individuals, however, fleeing will always reduce fitness because slow individuals will have a high probability of being both attacked and captured. In other words, fleeing and speed are complementary (*sensu* DeWitt et al. 1999); they work best when used in conjunction.

When the fitness effects of traits are interdependent, as in the above example, natural selection acts directly on combinations of those traits' values rather than on each trait independently. This form of multivariate selection, known as correlational selection, plays a central role in the evolution of genetic architecture (e.g., Sinervo and Svensson 2002) and phenotypic integration (e.g., Arnold 2005). A practical implication of correlational selection is that the fitness consequences of interactive traits, like fleeing and speed, cannot be determined independently of one another. Fortunately, MSA provides a way to quantify the joint effects of traits on fitness (see Arnold 1994 for a discussion of MSA targeted toward behavioral ecologists). It is worth noting, however, that MSA requires quantification of the genotypic or phenotypic relationships among traits (i.e., covariance matrices) across many individuals which is in and of itself a difficult task. Nevertheless, behavioral ecologists have successfully quantified covariance matrices that included behavioral traits for both natural and laboratory populations of organisms as diverse as nematodes (Estes et al. 2005), snails (Hoverman et al. 2005), crickets (Reale and Roff 2002), snakes (Brodie 1992), fish (Bell 2005), birds (van Oers et al. 2004), and mammals (Hayes and Jenkins 1997 and references therein).

Another advantage of MSA is the ability to visualize the relationship between traits with respect to fitness (Phillips and Arnold 1989; Brodie et al. 1995). This is done using a fitness surface generated from the joint regression of trait values on fitness. The surface depicts the relationship between an individual's multivariate phenotype and its expected fitness. If the trait values and fitness measures used to make this surface pertain to genotypes (as opposed to individuals), then it becomes possible to predict the evolution of traits and trait combinations in response to selection (Lande and Arnold 1983; Arnold et al. 2001; Sinervo and Svensson 2002; Steppan et al. 2002). Arnold (2005) asserts that fitness surfaces (and their relatives: selection surfaces and adaptive landscapes) remain the preeminent tools available for exploring the ultimate causes and consequences of phenotypic integration.

An additional challenge in assessing the adaptive value of antipredator behavior is accounting for individual differences. Lind and Cresswell allude to the fact that individual differences arise because individuals vary in the degree to which they can "afford" to allocate time and energy away from reproduction to predator avoidance. They suggest evaluating the relationships among prey traits in terms of the trade-off, or negative correlation, between predator avoidance and other behaviors. The importance of examining suites of correlated traits as a means of understanding individual differences is indeed an important one. However, differential allocation in response to reproductive trade-offs is only one of several possible mechanisms underlying individual differences in antipredator behavior.

An alternative approach to individual differences, which can include but is not limited to time and energy constraints, is the behavioral syndrome conceptual framework (Wilson et al. 1993; Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004). A behavioral syndrome exists whenever individuals exhibit consistent behavioral tendencies. When individuals differ in their behavioral tendencies, they are said to have different "behavioral types" (Sih, Bell, and Johnson

2004; Sih, Bell, Johnson, and Ziemba 2004). For example, an activity-aggression syndrome is characterized by the presence of individuals who are both more active and aggressive than others across a variety of contexts, where contexts represent functional behavioral categories such as foraging, competing for mates, parental care, etc. The result is that individuals' behaviors (e.g., activity and aggression) are correlated within and across contexts. For the hypothetical example illustrated in Figure 1, different behavioral syndromes are possible depending on the direction of the correlations between inactivity (when not hiding) and hiding in the presence of predators (Figure 1, BSC1) and inactivity in the presence and absence of predators (Figure 1, BSC2). Individuals could vary in the extent to which they are generally cautious (shy/risk averse), spending more or less time both hiding and being inactive when not hiding. Alternatively, inactivity and hiding could be negatively correlated. Different behavioral mechanisms can generate the latter syndrome. For example, individuals could compensate for being the generally active type by hiding more of the time. Or, individuals could compensate for time spent hiding by being very active (gathering resources) while out of refuge. Note, only this last scenario involves a trade-off between survival and reproduction. The syndromes literature emphasizes multiple, potentially interacting, mechanisms capable of generating this type of variation in behavioral types. They include differential allocation in response to time/energy budget conflicts (Sih, Bell, Johnson, and Ziemba 2004), variation in physiology and endocrinology (reviewed in: Boissy 1995; Koolhaas et al. 1999), variation in complementary morphological or life-history traits (DeWitt et al. 1999; Sih, Bell, Johnson, and Ziemba 2004), and differential early experience (reviewed in Stamps 2003).

Fortunately, regardless of the specific mechanisms involved, the correlations that define behavioral types are not fundamentally different than the other trait interactions we have discussed. Once the relevant traits are identified, they can easily be incorporated into path analysis or MSA where the performance and fitness of behavioral types can be evaluated. This approach has several implications for our understanding of the adaptive value of antipredator behaviors for which individual differences exist. First, it emphasizes that constraints and trade-offs are not the only means of generating individual differences. Secondly, it suggests that even when behavioral types are the result of underlying constraints, the syndrome as a whole may nevertheless be optimal within the confines of the constraint. Finally, and perhaps most importantly, the concept of behavioral syndromes has been instrumental in spurring behavioral ecologists to think in terms of adaptive individual strategies as opposed to in terms of population/species-level optima where the implication is that variation about the mean phenotype is nonadaptive "noise" (Wilson 1998).

No conceptual framework or statistical technique, however, can address all the challenges inherent in the study of antipredator or any other kind of behavior. In particular, solutions to the practical problems of observing rare behaviors in nature and of identifying traits and elements of realism that should be incorporated into experiments remain elusive. With respect to the former, there may well be little to be done but ensure that the system chosen to address a particular question can provide the information necessary to answer it. As for the call to incorporate more of the complexity of nature into experimental studies, we agree with Lind and Cresswell that when it comes to designing experiments there is no substitute for an intimate knowledge of your study system. In fact, the usefulness of path analysis and MSAs depend on the investigators' ability to identify the key traits and fitness components relevant to their specific system and question. Just as

importantly, however, having data on many traits is of little use in the absence of a conceptual and statistical framework for analyzing and interpreting those data as a whole. In other words, the goal is not simply to quantify many traits independently but rather to begin applying the information contained within the relationships among traits to the question of adaptive value in the broader context of whole organism performance and total fitness. The conceptual framework and techniques presented here have already proved to be very powerful in this endeavor for investigations of morphological (e.g., Cheverud 1982; Crespi and Bookstein 1989; Chernoff and Magwene 1999) and life-history trait integration (e.g., Sinervo and DeNardo 1996; Svensson et al. 2001) and are currently proving just as useful to understanding the adaptive value of integrated behavioral traits (e.g., Brodie 1992; Forsman and Appelqvist 1998; Sih et al. 2002).

In summary, behavioral ecologists must be careful not to lose sight of the entire organism, all of its traits over its entire lifetime. However, rather than being hopelessly complex, interactions among traits and different aspects of performance and fitness are often predictable, based on their functional significance (e.g., Olsen and Miller 1958; Berg 1960; Armbruster 2004; Pigliucci 2004), and measurable, using path analysis or MSA. We hope that this paper will open the door to the use of these techniques in behavioral ecology and serve as a reminder that when grounded in natural history and an appropriate quantitative, conceptual framework, empirical studies can still provide detailed answers to the increasingly complex questions we ask.

We thank Tim Caro and the members of his lab for bringing the manuscript to our attention and for the insightful discussions that motivated this paper. We also thank Will Cresswell and an anonymous reviewer for helpful comments on earlier drafts of the manuscript.

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