New Directions for Studying Selection in Nature: Studies of Performance and Communities

Duncan Irschick[1,*]
Joseph K. Bailey[2]
Jennifer A. Schweitzer[2]
Jerry F. Husak[3]
Jerry J. Meyers[1]

[1]Department of Biology, Organismic and Evolutionary Biology Program, University of Massachusetts, 221 Morrill Science Center, Amherst, Massachusetts 01003; [2]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996; [3]Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

ABSTRACT

Natural and sexual selection are crucial factors in the evolutionary process, yet recent reviews show that researchers have focused narrowly on this topic, with the majority of research centered on the morphological traits of single species. However, in the past several years, several bodies of work have emerged that have examined both selection on performance capacity and selection in a community context, and our goal is to highlight these two growing areas and point toward future directions. Recent studies of selection on performance capacity point toward directional selection favoring high levels of performance, and we detected less evidence for selection favoring intermediate (i.e., stabilizing) or bimodal (i.e., disruptive) kinds of performance levels. Studies of selection in a community context, using the paradigm of indirect genetic effects, show significant community heritability and strong capacity for evolution to occur in a community context via the force of natural selection. For future directions, we argue that researchers should shift toward longer-term studies of selection on both individual species and communities, and we also encourage researchers to publish negative selection results for both performance and community studies to act as balancing influences on published positive selection results.

* Corresponding author; e-mail: irschick@bio.umass.edu.

Introduction

Studies of natural selection have formed a cornerstone of evolutionary studies for at least the past 50 yr. Recent reviews have showcased the importance of understanding the role of natural selection in driving microevolutionary change within natural populations (Hoekstra et al. 2001; Kingsolver et al. 2001) and have shown that natural selection in nature is pervasive, often strong (Endler 1986; Reznick et al. 1997), and prone to varying from year to year (Grant 1999). Laboratory studies, often with microorganisms (e.g., Bennett et al. 1990; Lenski and Travisiano 1994; Bohannan and Lenski 2000), have also been valuable for testing key ideas about the effects of strong and varying selection on adaptive processes and genetic outcomes. Further, selection studies examining the interactive role of genetics, morphology, and social behavior for influencing the formation of alternative male morphs have been illuminating (Sinervo and DeNardo 1996; Sinervo and Lively 1996).

Given the large number of selection studies already completed, a relevant question is how researchers in this area should invest their time. Several recent reviews (Hoekstra et al. 2001; Kingsolver et al. 2001) concluded that the vast majority of field studies of selection have been conducted on morphological traits, with a smattering of studies on behavior, performance, and other such traits. Among others, two resonant conclusions were (1) we understand remarkably little about how selection operates on higher-level organismal traits, such as performance and behavior, and (2) there is little information on how selection acts on more than one interacting species (i.e., especially >2 species). In short, the vast majority of selection studies were completed on the morphological traits of single species in isolation. Our aim is not to critique these studies but quite the opposite; we feel that such data form a crucial foundation that is needed before we expand into other arenas. Rather, our goal in this review is to build a framework for studying two promising and growing areas of research, namely, studies of selection on whole-organism performance and studies of selection on communities. We note that ideas about studying selection on higher-level traits and communities are not new (Wilson 1980; Arnold 1983), but we argue that the rapidly and recently growing number of studies in these areas merits reexamination.

We review these two areas using the following outline. First, we review several recent studies from our own work that touch

on these two areas, and second, we attempt to synthesize previously published research in these areas, much of which has been published since 2001, when Kingsolver et al. (2001) and Hoekstra et al. (2001) completed their reviews. We begin each section (selection on performance and selection on communities) by providing a brief justification for why researchers should study these two important areas; we then proceed to a more detailed examination of prior studies.

Selection on Performance

Many researchers have examined selection on morphology, with the implicit understanding that morphology should show strong links with performance (Arnold 1983). The strength of this assumption has occasionally been challenged as researchers have realized that relationships among morphology and performance are sometimes weak and occasionally even nonexistent (Garland and Huey 1987). The reasons for why such weak links sometimes exist among organismal "design" and performance are varied but include the facts that morphological traits have often evolved for use in multiple settings (i.e., multiple functions; Lauder 1996) and that behavior acts as a filter between morphology and performance (Huey 1982; Kingsolver and Watt 1983; Garland and Losos 1994; Irschick and Garland 2001; Huey et al. 2003).

Therefore, there is a great need for us to understand the nature of selection on functional traits themselves, as opposed to merely extrapolating from morphological traits to performance. Other authors have already provided rationales for why researchers should study selection on performance directly (e.g., Arnold 1983; Bennett and Huey 1990; Miles 2004; Lailvaux and Irschick 2006). In essence, selection is expected to act on performance first and on morphology only secondarily (Bartholomew and Tucker 1964; Garland and Losos 1994). Consider the example of a lizard species that runs to avoid a predator; long-limbed (and hence fast) lizards will more effectively avoid predators, and selection will favor individual lizards that are fast and possess long limbs. However, in this case, selection first favors fast lizards that happen to have long limbs. This shift in emphasis also opens the door to a whole range of exciting new questions: Does selection always favor extreme (i.e., high) performance values, or does selection sometimes favor intermediate performance values (Hertz et al. 1988; Bennett and Huey 1990; Huey et al. 2002)? Does selection favor the same kind of performance every year, or, alternatively, are different forms of selection favored in different years, as has been shown for morphological traits (Grant 1999)? Finally, does selection operate differently on morphology versus performance (Ricklefs and Miles 1994)? This final pattern might occur if behavior acts as a filter between the two kinds of traits, for example. In short, there are myriad reasons to study selection on performance directly, not the least of which is that doing so will open up new doors to a wide range of new and inter-

esting topics to help us better understand the role of selection in natural systems. Moreover, a central message of this article is our suggestion to adopt an integrative approach toward studying selection by examining many traits (morphology, performance, and behavior) simultaneously. Below, we provide two recent examples of an attempt at this approach in *Urosaurus* and *Crotaphytus* lizards.

Selection on Performance in Urosaurus *Lizards*

Mark-recapture studies of the ornate tree lizard (*Urosaurus ornatus*) have recently been undertaken to allow understanding of the nature of selection on morphology and performance (Irschick and Meyers 2007). This small, ubiquitous, and insectivorous lizard is native to the Southwestern desert regions of the United States and Mexico. We were primarily interested in two performance traits (bite force and sprint speed) and morphological variables associated with these variables (head shape and limb length, respectively). These two kinds of performance play a key role when lizards interact with congeners and with other species and the environment generally. Male lizards readily bite one another in agonistic social interactions, and lizards with high bite forces tend to be dominant over male lizards with lower bite forces (Lailvaux et al. 2004; Huyghe et al. 2005). Whether males with high bite forces are more likely to exhibit high survival rates simply because they are high-quality males or to exhibit low survival rates because of risky overaggressive behavior is unclear. We also note that in both *Urosaurus* and *Crotaphytus*, discussed in the next section, bite forces in adult males appear more closely tied to agonistic interactions than feeding (J. J. Meyers, unpublished data). Sprint speed has been widely studied as an important trait for eluding predators and capturing prey, two activities that are crucial to long-term survival (and hence overall fitness).

Irschick and Meyers (2007) marked and measured bite force and sprint speed in 100 *Urosaurus* lizards (57 males and 43 females) during the breeding season of 2005 (May and June) at a field site in northern Arizona and resampled the lizards during the fall of 2005 (the nonbreeding season, which was September and October in our case). All 100 lizards were initially measured for performance and morphology, marked, and then released at their original point of capture. An essential point of this design was that the same traits (morphology and performance) were measured both before and after selection. Since the lizards were all large adults at their initial sampling period and did not undergo significant growth to the nonbreeding period, we were able to successfully measure both selection on initial trait values and plasticity of morphology and performance.

We found that selection appeared to favor high sprint speeds in male but not female lizards. However, although we detected a significant directional trend favoring high sprint speeds in male lizards, we also detected a nonsignificant ($P = 0.07$) sta-

Table 1: Proposed definitions of different aspects of temporal variability in morphology and performance across time

Term	Definition
Repeatability	Variation in measurement taken by a single person or instrument on the same trait and under the same conditions
Relative repeatability	Variation in the relative rank order of measurements of morphology or performance over time
Developmental plasticity	Changes in physical structures or performance over development as a result of environmental influences (e.g., temperature)
Seasonal plasticity	Changes in physical structures or performance for adult individuals across different seasons (e.g., spring, fall)

bilizing component disfavoring the very fastest sprinters. We note that the intensity of selection was reasonably strong based on its having a number of Darwins (a standardized unit of evolutionary change; about 213,000) relative to other microevolutionary studies of "rapid" evolution (Hendry and Kinnison 1999). We caution that such measures are heuristic and say little about the long-term evolutionary influence of selection, which is driven by the genetic basis of traits as well as by the strength of selection. By contrast, there was no evidence of significant selection on performance in females, which supports the general view that selection can act differently on different sexes (Darwin 1871). An analysis of how selection proceeded on the other performance variable (bite force) showed a different pattern; there was no significant selection on initial values of bite force for either males or females within *Urosaurus*. A closer examination showed that substantial seasonal plasticity in bite force (and associated head shape variables) may be an important factor mediating this relationship. A consistent pattern was that numbers of individual lizards with high bite forces during the breeding season declined to the nonbreeding season, whereas numbers of individuals with low bite forces during the breeding season increased to the nonbreeding season, in some cases by as much as 40%. This seasonal change in bite force was mirrored by a change in head width, which fluctuated by up to 10%, resulting in heads shrinking and increasing in size. Other studies have documented seasonal changes in body morphology across seasons (e.g., beak size in birds [Smith et al. 1986], body size in marine iguanas [Wikelski and Thom 2000]), although we are not aware of studies that have addressed concomitant changes in functional capacities. Although the mechanistic basis of this seasonal change in head shape is not completely understood, temporal hypertrophy and atrophy of head muscles may be relevant, as has been documented in skinks (Cooper and Vitt 1985).

One overarching lesson from this work is that analysis of only the initial (preselection) values of performance and morphology is misleading because neither morphology nor performance was static within an individual, which is a key assumption of selection studies (but see Garland and Else 1987).

From an evolutionary perspective, seasonal plasticity in performance and morphology can mediate and potentially even obviate the traditional role of selection as a culler of poor performers. In this system, individuals are apparently not constrained to remain at a constant low or high state of performance their entire lives but rather can increase (or, more paradoxically, decrease) their performance dramatically in a relatively short period of time (although the rate of change is poorly understood; see Irschick et al. 2006). While the need to increase in performance would seem to provide a potential benefit, the reason for why animals should decrease in performance is less obvious; the balancing of increases and decreases in performance imply that high performance comes at a cost, in an energetic form or perhaps even in a behavioral form. At this point, we cannot definitively attribute an adaptive basis to this plasticity, and we are continuing to study underlying reasons for the seasonal change in plastic traits as well as the potential underlying physiological (e.g., hormonal) mechanisms.

It is important to distinguish plasticity in morphology and performance from a simple lack of repeatability among consecutive measures. Repeatability represents the tendency for an organism to be consistent in its performance capacities when measured multiple times in the same general time frame (e.g., across hours or days), and low repeatabilities can limit the influence of selection on performance traits (Huey and Dunham 1987). Whereas low repeatabilties are typically manifested as short-term, and often random, fluctuations in performance, performance plasticity is less random, manifests itself over longer time periods, is more permanent, and is typically more substantial (Garland and Else 1987; Irschick et al. 2006). One must also distinguish plasticity from temporary (e.g., hours, days) changes in performance resulting from environmental effects, such as increased food (see Garland and Losos 1994 for a review) or the consumption of toxic prey (Brodie and Brodie 1991). Table 1 provides some simple definitions of these different concepts.

A recurrent debate in the evolutionary literature concerns whether morphological traits can act as effective surrogates for

functional capacities (Ricklefs and Miles 1994). Contrary to the view that morphology and function will always be tightly related, we found generally different patterns of selection on morphology and performance. For example, in the case of sprint speed, there was no evidence of selection on hindlimb length in *Urosaurus* lizards, despite a fair amount of evidence showing that elongated hindlimbs are correlated with speed among and within lizard species (Bonine and Garland 1999). This result underscores the need to simultaneously quantify selection on performance and morphology, not just on morphological traits that are presumably linked with performance.

Natural and Sexual Selection on Performance in *Crotaphytus* Lizards

It is intuitively appealing to consider maximal locomotor performance as a trait likely to be under strong natural and sexual selection (Snell et al. 1988). Many animals use fast speeds during various ecological tasks, including escaping predators, capturing prey items, and chasing rivals during territorial disputes. Hence, a large proportion of performance selection studies have focused on "maximum" locomotor performance (see "Other Studies"). However, behavior can act as a filter between performance and fitness (reviewed in Hertz et al. 1982; Garland et al. 1990; Garland and Losos 1994; Irschick and Garland 2001), complicating interpretation of selection studies. Further, prior studies have noted the importance of considering ontogenetic and sex effects on how selection operates (see also Jayne and Bennett 1990).

Husak et al. (2006a) have examined these issues in collared lizards (*Crotaphytus collaris*), a common species in the southwestern United States and one in which behavior varies between sexes and throughout ontogeny. Females in the study population of collared lizards do not actively defend territories (Husak and Fox 2003), whereas males actively do so from their second year onward (Baird et al. 1996). For the first year of life, males are sexually mature but are socially suppressed and do not defend territories (Baird et al. 2001). By comparison, males older than 1 yr actively defend territories. Hence, whereas prey capture and predator escape may be relevant selection pressures for all age classes, selection for territory defense (i.e., sexual selection) may be more relevant for territorial adult males.

Husak and colleagues (Husak 2006a, 2006b; Husak and Fox 2006; Husak et al. 2006a, 2006b) studied a population of collared lizards (*C. collaris*) in Oklahoma to understand the relative roles of natural and sexual selection on locomotor performance. Adult lizards were captured, marked, and measured for maximal sprint speed early in the breeding season, so that survival to the next breeding season could be determined (sprint speed does not change across the active season; Husak et al. 2006b). They also determined whether these same age classes used maximal sprint speed in nature (i.e., ecological performance; Ir-

schick 2003) by having the lizards engage in capturing simulated prey, escaping a simulated predator, and responding to a rival introduced into their territory/home range (Husak and Fox 2006). They then determined whether survival of these groups depended on maximal capacity or ecological performance used in nature while completing the above ecological tasks. Husak and colleagues also examined selection on maximal sprint speed in hatchling lizards, a group that emerges in the fall (August–October) and that has not yet been through a round of selection as free-ranging individuals.

Several findings were notable. First, there was significant directional selection on maximal sprint speed only for hatchlings and not for sexually mature individuals (Husak 2006a). For sexually mature adults (yearlings and adults), there was directional selection for both sexes on ecological performance while animals escaped a simulated predator (i.e., no sex effect). That is, survival depended on how fast lizards actually ran while escaping predators, not how fast they were capable of running. This finding implies selection for a threshold, adequate speed that individuals must attain to accomplish the task of escaping a predator (Husak 2006b), underscoring that evolution need only be "good enough" for an organism to survive in its population. Second, these results were in agreement with the examination of field speeds in the three ecological contexts: no age class used more than 80% of their maximal capacity when capturing prey (25%–45% of maximal used) or escaping a predator (60%–80% of maximal capacity), but adult males used more than 90% of their maximal capacity while responding to an intruding rival male (Husak and Fox 2006). Further, poor maximal performers of all demographic groups compensated for their poor performance by increasing the percentage of their maximal capacity used when capturing prey and escaping predators; however, the compensation had a limit such that most individuals had field speeds that were similar in a given ecological context (Husak and Fox 2006). Gravid females compensated for reduced locomotor ability by staying closer to refugia and not by increasing the percentage of maximal capacity that they used (Husak 2006a). The fact that adult males used near-maximal capacity while responding to rivals reinforced our results that faster males were better able to defend a larger territory, show more overlap with females (Peterson and Husak 2006), and sire more offspring.

The selection analysis revealed ontogenetic and sex differences in the nature and strength of selection operating on sprint speed. The approach of examining selection on ecological performance provides a powerful complement to selection studies on "maximum" performance; knowledge of how performance is used in nature (and not under "optimal" laboratory conditions) can assist in developing a priori hypotheses about the direction and strength of selection. However, researchers should determine whether ecological performance as measured in nature is an accurate reflection of how individuals choose to perform during a given situation or an artifact of constraints

imposed by the physical environment. The above work raises the question of whether selection does not necessarily favor high performance but may rather favor performance that is simply good enough (i.e., meets some threshold). In this regard, we advocate a shift from measuring selection on only maximum locomotor performance to measuring selection on percentage of maximum capacity, or what an animal actually does relative to what it can do (Hertz et al. 1988).

Other Studies

Although researchers have long been interested in selection on performance, research in this area has recently blossomed. Le Galliard et al. (2004) examined selection on maximum loco-motor performance in a lacertid lizard (*Lacerta vivipara*) as individual juvenile lizards matured from very young lizards to more mature subadults. Beyond examining the role of selection on initial traits alone, they examined how the role of food causes individual lizards to compensate for initially poor performance by eating more (and hence improving). Contrary to the prediction of strong directional selection, they detected only weak selection on initially high values of endurance. They explained this weak relationship as occurring because initially poor performers can rapidly increase in endurance capacity by increasing food rate. This study is consistent with other data (Irschick and Meyers 2007) showing that performance may be more labile than previously thought. Another study (Miles 2004) examined selection on sprint speed and morphology in a cohort of juvenile *Urosaurus* lizards. Miles (2004) showed significant directional selection favoring high sprint speed in these lizards as well as morphological variables associated with sprint speed (e.g., hindlimb length). O'Steen et al. (2002) used an innovative experimental design to examine survival in *Poecilia* guppies from low- and high-predation environments. They showed that fish from high-predation environments generally had higher survival and better performance than low-predation fish in response to a dangerous predator (a cichlid fish, *Crenicichla alta*). Further, in common-garden experiments, they showed that escape ability showed a genetic basis, indicating that the differences among populations are not manifested as a purely plastic response. We also point out that other work has documented significant repeatability (Huey and Dunham 1987) and heritability for sprint speed in squamate reptiles (Garland et al. 1990).

In other work, Watkins (1996) used a predator (a garter snake, *Thamnophis*, that eats tadpoles) in a tank with different tadpoles (individuals of *Pseudacris regilla*) of known swimming capacity. He found strong evidence for directional selection favoring high swimming capacity in tadpoles because snakes were more likely to consume tadpoles that had low speeds and that were relatively nonevasive. Jayne and Bennett (1990) examined selection on sprint speed in a large cohort of juvenile garter snakes as well as ontogenetic changes in speed and sta-

mina. The individual juvenile garter snakes were initially measured for both performance (burst speed and endurance) and morphology and then were released into the wild. The authors detected significant selection favoring both fast speeds and high endurance values in juvenile snakes, although these findings were not always consistent across their sampling periods.

An emerging picture from these studies indicates that, with some exceptions, selection typically favors high levels of performance and rarely seems to select for a bimodal distribution (i.e., disruptive selection; Smith 1993) or even for intermediate trait values (Miles 2004). We note that few studies have examined selection on performance across more than one sampling period (but see Jayne and Bennett 1990), and hence, we cannot determine whether selection favors the same kind of performance every season or every year. Evolutionary biologists have always been interested in foreseeing future trends, and while the current set of studies implies that performance can evolve quickly, we question whether this pattern would hold if one were to examine selection on performance across longer time periods. Long-term studies with Darwin's finches have shown that strong directional selection over short time periods can be counterinfluenced by opposing selection the following year, resulting in stasis over even relatively short ecological time periods (Grant 1999). Finally, we emphasize the conclusion from Kingsolver et al. (2001) that selection is often weak and therefore may pass undetected if sample sizes are small.

Further, our review of the literature revealed at least three heretofore-neglected factors in studies of selection on performance. The first concerns whether the published data sets are actually representative of the true biology of most organisms. Researchers are well known for attempting to publish exciting positive results (i.e., those in which there is a significant link between fitness and the trait of interest) and not publishing (or perhaps attempting to publish but not succeeding) negative results (i.e., no link between a trait and fitness). While there is no way to know how many negative selection studies of performance exist, we know of such data for at least two species (*Sceloporus occidentalis* and *Sceleporus merriami*; R. Huey, personal communication), and others probably exist. However, negative selection results are, in many ways, just as valuable as positive results. For example, an intriguing study was completed by Kingsolver (1999), who artificially reduced the size of the wings of different individuals of a butterfly species (*Pontia occidentalis*) and found no significant effects on field survival, despite laboratory evidence showing significant effects of the wing alteration on wing kinematics. This work highlighted a key point: biologists should appreciate that there may not be a 1 : 1 relationship between morphological structures and fitness because many traits are multifunctional and may be important in other contexts (in the case of butterflies, thermoregulation; Huey and Stevenson 1979). Hence, we encourage authors, editors, and reviewers to be open-minded when con-

sidering negative selection studies, which necessarily act as an important counterbalance to published positive results.

Selection on Communities

Organisms exist in frequently intricate and interlinked communities, and therefore a focus of community ecology has been to understand the nature and strength of species interactions within a community. However, only recently have evolutionary ecologists begun to consider the fitness consequences of natural selection in a community context (i.e., how the morphology or behavioral syndrome of one species may act as an agent of natural selection on other interacting species within that community). This process is generally termed "diffuse coevolution" or "community heritability." While both diffuse coevolution and community heritability are the study of evolution in a community context, they differ in that diffuse coevolution suggests that it is difficult to understand the evolution of one species without understanding its interactions with many species (Stinchcombe and Rausher 2001; Strauss and Irwin 2004). Community heritability supports the theory of diffuse coevolution but extends the theory by providing a mechanism for evolution in a community context, and this is referred to as indirect genetic effects (Shuster et al. 2006).

Recent work (Strauss and Irwin 2004; Johnson and Agrawal 2005; Bailey et al. 2006; Shuster et al. 2006) suggests that the time is ripe for researchers to focus their attention more fully on how selection proceeds on groups of coexisting species. This avenue of research is timely because of the increasing impact of global climate change, invasive species, and general anthropogenic factors directly impacting ecological communities. We do not argue that studies of selection on single species are not useful; quite the contrary—in fact, some of the coauthors of this article are currently undertaking such studies (i.e., the previous section of this article). Nevertheless, we suggest that a more integrative and community-based approach toward selection will ultimately be needed for the field of evolutionary biology to move in new directions.

Prior syntheses of natural selection have focused on the debate over whether selection operates only on individuals, which is widely accepted, or additionally at levels above the individual (i.e., community or ecosystem level). This focus on the community is an important advance because species do not live or evolve in a vacuum but are part of a tangled web of interactions (Goodnight 1990a, 1990b; Iwao and Rausher 1997; Mauricio and Rausher 1997; Moore et al. 1997; Agrawal et al. 2001; Strauss and Irwin 2004; Agrawal 2005; Strauss et al. 2005) that vary at different genetic (Maddox and Root 1990; Marquis 1990; Hochwender and Fritz 2004) and geographic scales (Thompson 2005). Because variations in species interactions are often constrained by the nutrients or energy available in a system, that selection may occur in an ecosystem context as well (Whitham et al. 2006). However, selection beyond the

individual has not been widely incorporated into ecological or evolutionary studies or models primarily because of the debate over the proper units of selection (i.e., individuals, groups). However, recent empirical and theoretical work has shown that natural selection can act at levels higher than that of the individual and that group fitness is not a requirement even for selection to occur in a community context (Shuster et al. 2006). Therefore, we take a neutral view of the controversial field of group selection and group fitness and instead focus on understanding selection on individual species in a community context and provide a recent example examining this concept.

Indirect genetic effects (IGEs) are one important mechanism by which selection occurs in a community context (Moore et al. 1997; Agrawal et al. 2001; Shuster et al. 2006). In their simplest form, IGEs occur when the genotype of one individual indirectly affects the phenotype of another individual, creating a selection gradient that affects the fitness of both interacting individuals (Moore et al. 1997; Agrawal et al. 2001; Shuster et al. 2006). This is in contrast to the ecological definition, where the effects of one individual on another are mediated by a third. While intraspecific IGEs are important in a social evolution context, only recently has this theory been extended to the interspecific level of plant-animal interactions (Shuster et al. 2006; Whitham et al. 2006).

Based on theory established by Shuster et al. (2006), interspecific IGEs (IIGEs) have been implicated in recent studies documenting how species interactions (in this case with arthropods) are a predictable consequence of the plant genotype with which they are associated. In other words, variation in species interactions (i.e., communities) is dependent on and consistent among genotypes. Shuster et al. (2006) examined arthropod communities on replicated genotypes of *Populus fremontii*, *Populus angustifolia*, and their natural hybrids. Quantifying a diverse arthropod herbivore community, they found that community composition was significantly different on the foliage of different replicated *Populus* genotypes (Fig. 1, *top*). Some genotypes had diverse communities with many individuals, while others had almost no associated arthropods. When measured with standard quantitative genetic approaches, the species interactions among plant genotypes showed significant heritability. A finding of significant arthropod community heritability indicates that there are shared fitness effects among the interacting species arising from IIGEs and that natural selection has occurred in a community context, and it is evidence of evolution in a community context (Shuster et al. 2006). It is important to emphasize that these studies of community heritability are based on individual measures of trait expression and fitness and do not imply that communities themselves have fitness or that communities evolve like populations (Whitham et al. 2006).

Current examples of community heritability range from microorganisms to vertebrates, indicating that the theory has broad generality. For example, using 10 replicated (i.e., cloned)
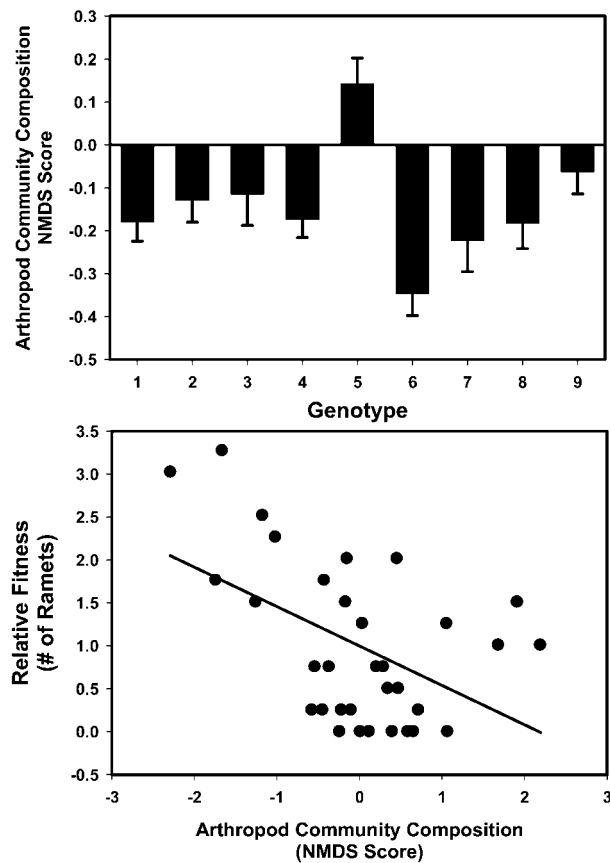
Figure 1. Community heritability and community level selection in *Populus*. Using nonmetric multidimensional scaling ordination (NMDS), the arthropod communities of nine replicated *Populus angustifolia* genotypes were summarized. There were significant differences in arthropod community composition among cottonwood genotypes. Sixty-three percent of the variance in community composition was related to plant genetic factors (*top*). Based on a phenotypic correlation between relative plant fitness and arthropod community composition, there was also strong selection acting on the arthropod community via the plant (*bottom*). The relative fitness of the plant genotypes, measured as the total number of ramets of a particular replicate genotype, was related to arthropod community composition, indicating that there was directional selection. However, the positive or negative direction of selection cannot be determined because NMDS scores are relative to one another and represent a point in space; thus, β can be used only to determine the strength and form of selection.

P. angustifolia genotypes that were planted randomly in a common garden in northern Utah, Schweitzer et al. (2007) found that different *P. angustifolia* genotypes had different associated soil microbial communities based on phospholipid fatty acid biomarkers that represent broad microbial groups. Such apparent specificity of microbial communities to individual replicated plant genotypes is consistent with the recent studies of the heritability of canopy arthropods (described above). Similarly, Bailey et al. (2006) showed that interactions within a simple trophic community of *P. angustifolia*, a galling herbivore, and avian predators also varied by plant genotype. These results indicate that there are fitness consequences of interactions among associated species that are important to how communities become structured by plant genetic factors. Together, these studies suggest that plant genetic factors have a strong impact on many aspects of community formation and potentially on ecosystem function. Across the three studies described above, heritability of community composition (H_C^2) ranges from 0.60 to 0.80, indicating that 60%–80% of the variation in community composition was related in some way to additive, dominant, and epistatic plant genetic factors and their interactions with associated species. Because community heritability summarizes the interactions among species that are related to IIGEs, it indicates that individual species must create environmental variation related to their own phenotypes, which affects the phenotype and fitness of other interacting species within the community (i.e., selection gradients). These examples therefore all demonstrate the possibility for selection to operate in a community context.

Using the arthropod herbivore canopy data from the above example (Shuster et al. 2006) of heritable communities of *Populus* trees, we regressed the relative fitness (i.e., the number of asexually derived clonal ramets) of the same trees used in the arthropod study against the arthropod community composition and found a strong relationship (Fig. 1, *bottom*; $r^2 = 0.67$, $F_{1,8} = 12.44$, $P = 0.012$). A significant correlation between relative cottonwood fitness and arthropod community composition indicates that there were differential fitness consequences for the plant, depending on the arthropod community composition ($\beta = 0.82$; see Conner and Hartl 2004). These results indicate that *P. angustifolia* evolves in the environment of a community of interacting species. Whether the arthropod community is directly or indirectly related to variation in plant fitness is still unknown. Our estimate of selection is strong relative to other estimates of selection as reviewed by Kingsolver et al. (2001), which generally found that selection varied between 0 and 0.40 and supports the hypothesis of diffuse coevolution (natural selection acting in a community context).

Diffuse coevolution and community heritability have not been widely incorporated into evolutionary studies; however, emerging research (Stinchcombe and Rausher 2001; Strauss and Irwin 2004; Agrawal 2005; Thompson 2005; Bailey et al. 2006; Shuster et al. 2006) indicates that selection across higher levels of organization is probably common and may be stronger than selection at the individual level. Studies of selection in a community context may reveal unique mechanisms for (1) the evolution of species interactions such as competition or facilitation, as well as parasitism, mutualism, or predation; or (2) the ecological functions that ecosystems provide (e.g. soil fertility, biodiversity, or productivity).

Future Directions

Our intent in this review was to highlight new directions for how researchers can study selection in nature. We focused on two areas that we felt represented emerging paradigms; each independently complements the quite large body of work on selection on morphological traits of single species (Hoekstra et al. 2001; Kingsolver et al. 2001, which also includes reviews of studies on other traits). Beyond showing that such studies are achievable, our review also raises a host of new research topics for researchers to consider in future studies. Examples include the relative roles of plasticity and selection in performance, selection on ecological performance, and the role of community heritability in determining the pace and direction of evolutionary change within communities.

In the context of studies of selection on performance, we suggest that long-term (i.e., across multiple seasons and years) studies of selection that simultaneously quantify selection and plasticity in performance would be especially useful. Although researchers have long appreciated the role of plasticity (especially in plants; e.g., Schmitt et al. 2003) for morphological traits, there has not been similar attention paid to plasticity in performance and its potential role in mediating selection. We suggest that plasticity in performance may be an important reason (among others) for why one might not always expect significant selection on performance. Long-term studies may reveal differing strategies for different individuals; some individuals may exhibit peak performance during one time of year (i.e., beginning of breeding season), whereas other individuals may exhibit peak performance later in the breeding season, just as the first set of animals are declining in performance. Moreover, the ecological context of performance may become especially relevant when examined over longer time periods, as we may begin to understand whether selection more often acts on absolute levels of performance or relative (i.e., percentage of maximum) values of performance. Long-term studies are needed because we understand little about whether the pace of selection on performance is the same across different seasons or years. An inspection of the results presented here implies that selection is generally strong relative to other selection studies, suggesting the potential for performance to evolve rapidly. Whether counteracting selection in alternative years might result in ecologically static performance is unknown, however.

In the context of selection on multiple interacting species, we suggest that a logical extension would be to examine selection not on phylogenetically divergent sets of species in a single community but rather on closely related groups of species (i.e., within the same genus) within a single community or across presumably convergent communities. The phylogenetic revolution, which has transformed many other areas, including ecology, conservation biology, and epidemiology, among others, has not infiltrated our understanding of natural selection. However, a phylogenetic approach toward natural selection can go a long way toward resolving basic unresolved issues in evolutionary biology. For example, one debate concerns the nature of convergence. Do species of different phylogenetic relatedness experience the same direction and intensity of selection when they occupy similar environments (Ricklefs and Schluter 1993)? Tests of convergence have usually focused on examining whether the divergent species exhibit the same morphological and/or behavioral features despite their distant relationships. Do closely related species that occur within the same environment tend to experience divergent selection pressures that might, in turn, be a key ingredient of adaptive radiation? These and other questions represent new vistas for future research.

With respect to diffuse coevolution and community heritability, we are only beginning to scratch the surface. Basic studies on the strength of selection, variation in selection in the environment of other species (neighborhood effects), and variation in selection across genetic scales represent open avenues of research that will provide further insight into how evolution occurs in a community context, how species coevolve, and how processes emerge from these evolutionary interactions. Much of the work discussed here focused on plants and invertebrates, and it would be informative to extend this approach to a wider range of organisms, preferably those that are not clonal, as many plants are. Finally, research on the formation and evolution of communities will also provide a powerful counterpoint to ecological hypotheses on community structure and formation, such as the neutral theory of biodiversity (Hubbell 2001) or the resource ratio hypothesis (Tilman 1985), that generally lack an evolutionary basis.

Acknowledgments

Literature Cited

Agrawal A.A. 2005. Natural selection on common milkweed (*Asclepias syriaca*) by a community of specialized insect herbivores. Evol Ecol Res 7:651–667.

Agrawal A.F., E.D. Brodie III, and M.J. Wade. 2001. On indirect genetic effects in structured populations. Am Nat 158:308–324.

Arnold S.J. 1983. Morphology, performance, and fitness. Am Zool 23:347–361.

Bailey J.K., S.C. Wooley, R.L. Lindroth, and T.G. Whitham. 2006. Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. Ecol Lett 9:78–85.

Baird T.A., M.A. Acree, and C.L. Sloan. 1996. Age and gender-related differences in the social behavior and mating success of free-living collared lizards, *Crotaphytus collaris*. Copeia 1996:336–347.

Baird T.A., C.L. Sloan, and D.K. Timanus. 2001. Intra- and inter-seasonal variation in the socio-spatial behavior of adult male collared lizards, *Crotaphytus collaris* (Reptilia, Crotaphytidae). Ethology 107:15–32.

Bartholomew G.A. and V.A. Tucker. 1964. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. Physiol Zool 37:341–354.

Bennett A.F., K.M. Dao, and R.E. Lenski. 1990. Rapid evolution in response to high-temperature selection. Nature 346:79–81.

Bennett A.F. and R.B. Huey. 1990. Studying the evolution of physiological performance. Oxf Surv Evol Biol 7:251–284.

Bohannan B.J.M. and R.E. Lenski. 2000. Linking genetic change to community evolution: insights from studies of bacteria and bacteriophage. Ecol Lett 3:362–377.

Bonine K.E. and T. Garland Jr. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. J Zool (Lond) 248:255–265.

Brodie E.D., III, and E.D. Brodie Jr. 1991. Evolutionary response of predators to dangerous prey: reduction of toxicity of newts and resistance of garter snakes in island populations. Evolution 45:221–224.

Conner J.K. and D.L. Hartl. 2004. A Primer of Ecological Genetics. Sinauer, Sunderland, MA.

Cooper W.E. and L.J. Vitt. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. Can J Zool 63:995–1002.

Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. J. Murray, London.

Endler J. 1986. Natural Selection in the Wild. Princeton University Press, Princeton, NJ.

Garland T., Jr., A.F. Bennett, and C.B. Daniels. 1990. Heritability of locomotor performance and its correlates in a natural population. Experientia 46:530–533.

Garland T., Jr., and P.L. Else. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. Am J Physiol 252:R439–R449.

Garland T., Jr., and R.B. Huey. 1987. Testing symmorphosis: does structure match functional requirements? Evolution 41:1404–1409.

Garland T., Jr., and J.B. Losos. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pp. 240–302 in P.C. Wainwright and S.M. Reilly, eds. Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago.

Goodnight C.J. 1990a. Experimental studies of community evolution. I. The response to selection at the community level. Evolution 44:1614–1624.

———. 1990b. Experimental studies of community evolution.

II. The ecological basis of the response to community selection. Evolution 44:1625–1636.

Grant P.R. 1999. Ecology and Evolution of Darwin's Finches. Princeton University Press, Princeton, NJ.

Hendry A.P. and M.T. Kinnison. 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. Evolution 53:1637–1653.

Hertz P.F., R.B. Huey, and T. Garland Jr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles Olympians or Boy Scouts? Am Zool 28:927–938.

Hertz P.F., R.B. Huey, and E. Nevo. 1982. Fight versus flight: body temperature influences defensive responses of lizards. Anim Behav 30:676–679.

Hochwender C.G. and R.S. Fritz. 2004. Plant genetic differences influence herbivore community structure: evidence from a hybrid willow system. Oecologia 138:547–557.

Hoekstra H.E., J.M. Hoekstra, D. Berrigan, S.N. Vignieri, A. Hoang, C.E. Hill, P. Beerlii, and J.G. Kingsolver. 2001. Strength and tempo of directional selection in the wild. Proc Natl Acad Sci USA 98:9157–9160.

Hubbell S.P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

Huey R.B. 1982. Temperatures, physiology, and the ecology of reptiles. Pp. 25–91 in C. Gans and F.H. Pough, eds. Biology of the Reptilia. Vol. 12. Academic Press, London.

Huey R.B., M. Carlson, L. Crozier, M. Frazier, H. Hamilton, C. Harley, A. Hoang, and J.G. Kingsolver. 2002. Plants versus animals: do they deal with stress in different ways? Integr Comp Biol 42:415–423.

Huey R.B. and A.E. Dunham. 1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. Evolution 41:1116–1120.

Huey R.B., P.E. Hertz, and B. Sinervo. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. Am Nat 161:357–366.

Huey R.B. and R.D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am Zool 19:357–366.

Husak J.F. 2006a. Does speed help you survive? a test with collared lizards of different ages. Funct Ecol 20:174–179.

———. 2006b. Does survival depend on how fast you can run or how fast you do run? Funct Ecol 20:1080–1086.

Husak J.F. and S.F. Fox. 2003. Spatial organization and the dear enemy phenomenon in adult female collared lizards, *Crotaphytus collaris*. J Herpetol 37:211–215.

———. 2006. Field use of sprint speed by collared lizards (*Crotaphytus collaris*): compensation and sexual selection. Evolution 60:1888–1895.

Husak J.F., S.F. Fox, M.B. Lovern, and R.A. Van Den Bussche. 2006a. Faster lizards sire more offspring: sexual selection on whole-animal performance. Evolution 60:2122–2130.

Husak J.F., A.K. Lappin, S.F. Fox, and J.A. Lemos-Espinal. 2006b. Bite-force performance predicts dominance in male

venerable collared lizards (*Crotaphytus antiquus*). Copeia 2006:301–306.

Huyghe K., B. Vanhooydonck, H. Scheers, M. Molina-Borja, and R. Van Damme. 2005. Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. Funct Ecol 19:800–807.

Irschick D.J. 2003. Studying performance in nature: implications for fitness variation within populations. Integr Comp Biol 43:396–407.

Irschick D.J. and T. Garland Jr. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. Annu Rev Ecol Syst 32:367–396.

Irschick D.J. and J.J. Meyers. 2007. An analysis of the relative roles of plasticity and natural selection on morphology and performance in a lizard (*Urosaurus ornatus*). Oecologia 153: 489–499.

Irschick D.J., M. Ramos, C. Buckley, J. Elstrott, E. Carlisle, S. Lailvaux, N. Bloch, A. Herrel, and B. Vanhooydonck. 2006. Are morphology-performance relationships invariant across different seasons? a test with the green anole lizard (*Anolis carolinensis*). Oikos 114:49–59.

Iwao K. and M.D. Rausher. 1997. Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. Am Nat 149:316–335.

Jayne B.C. and A.F. Bennett. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. Evolution 44:1204–1229.

Johnson M.T.J. and A.A. Agrawal. 2005. Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). Ecology 86:874–885.

Kingsolver J.G. 1999. Experimental analyses of wing size, flight, and survival in the western white butterfly. Evolution 53: 1479–1490.

Kingsolver J.G., H.E. Hoekstra, J.M. Hoekstra, D. Berrigan, S.N. Vignieri, C.E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. Am Nat 157:245–261.

Kingsolver J.G. and W.B. Watt. 1983. Thermoregulatory strategies in *Colias* butterflies: thermal stress and the limits to adaptation in temporally varying environments. Am Nat 121: 32–55.

Lailvaux S., A. Herrel, B. Vanhooydonck, J.J. Meyers, and D.J. Irschick. 2004. Performance capacity, fighting tactics, and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). Proc R Soc B 271:2501–2508.

Lailvaux S.P. and D.J. Irschick. 2006. A functional perspective on sexual selection: insights and future prospects. Anim Behav 72:263–273.

Lauder G.V. 1996. The argument from design. Pp. 55–91 in M.R. Rose and G.V. Lauder, eds. Adaptation. Academic Press, San Diego, CA.

Le Galliard J.F., J. Clobert, and R. Ferriere. 2004. Physical per-

formance and Darwinian fitness in lizards. Nature 432:502–505.

Lenski R.E. and M. Travisiano. 1994. Dynamics of adaptation and diversification: a 10,000-generation experiment with bacterial populations. Proc Natl Acad Sci USA 91:6808–6814.

Maddox G.D. and R.B. Root. 1990. Structure of the encounter between goldenrod (*Solidago altissima*) and its diverse insect fauna. Ecology 71:2115–2124.

Marquis R.J. 1990. Genotypic variation in leaf damage in *Piper arieianum* (Piperaceae) by a multispecies assemblage of herbivores. Evolution 44:104–120.

Mauricio R. and M.D. Rausher. 1997. Experimental manipulation of putative selection agents provides evidence for the role of natural enemies in the evolution of plant defense. Evolution 51:1435–1444.

Miles D.B. 2004. The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. Evol Ecol Res 6:63–75.

Moore A.J., E.D. Brodie III, and J.B. Wolf. 1997. Interacting phenotypes and the evolutionary process. I. Direct and indirect effects of social interactions. Evolution 51:1352–1362.

O'Steen S., A.J. Cullum, and A.F. Bennett. 2002. Rapid evolution of escape ability in Trinidadian guppies (*Poecilia reticulata*). Evolution 56:776–784.

Peterson C.C. and J.F. Husak. 2006. Locomotor performance and sexual selection: individual variation in sprint speed of collared lizards (*Crotaphytus collaris*). Copeia 2006:216–224.

Reznick D.N., F.H. Shaw, F.H. Rodd, and R.G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934–1937.

Ricklefs R.E. and D.B. Miles. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. Pp. 13–41 in P.C. Wainwright and S.M. Reilly, eds. Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago.

Ricklefs R.E. and D. Schluter. 1993. Species Diversity in Ecological Communities. University of Chicago Press, Chicago.

Schmitt J., J.R. Stinchcombe, M.S. Heschel, and H. Huber. 2003. The adaptive evolution of plasticity: phytochrome-mediated shade avoidance responses. Integr Comp Biol 43:459–469.

Schweitzer J.A., J.K. Bailey, S.C. Hart, and T.G. Whitham. 2007. The role of plant genetic variation in determining above- and belowground microbial communities. In S.E. Lindow and M. Bailey, eds. Phyllosphere Microbiology. American Phytopathological Society Press, St. Paul, MN (forthcoming).

Shuster S.M., J.K. Bailey, S. C. Hart, and T.G. Whitham. 2006. Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. Evolution 60:146–158.

Sinervo B. and D.F. DeNardo. 1996. Costs of reproduction in the wild: path analysis of natural selection and experimental tests of causation. Evolution 50:1299–1313.

Sinervo B. and C.M. Lively. 1996. The rock-scissors-paper game and the evolution of alternative male strategies. Nature 340: 240–246.

Smith J.N.M., P. Arcese, and D. Schluter. 1986. Song sparrows grow and shrink with age. Auk 103:210–212.

Smith T.B. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. Nature 363:618–620.

Snell H.L., R.D. Jennings, H.M. Snell, and S. Hartcourt. 1988. Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. Evolutionary Ecology 2:353–369.

Stinchcombe J.R. and M.D. Rausher. 2001. Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory *Ipomea hederacea*. Am Nat 158:376–388.

Strauss S.Y. and R.E. Irwin. 2004. Ecological and evolutionary consequences of multispecies plant-animal interactions. Annu Rev Ecol Syst 35:435–466.

Strauss S.Y., H. Sahli, and J.K. Conner. 2005. Toward a more trait centered approach to diffuse (co)evolution. New Phytol 165:81–89.

Thompson J.N. 2005. The Geographic Mosaic of Coevolution. University of Chicago Press, Chicago.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am Nat 125:827–852.

Watkins T.B. 1996. Predator-mediated selection on burst swimming performance in tadpoles of the Pacific tree frog, *Pseudacris regilla*. Physiol Zool 69:154–167.

Whitham T.G., J.K. Bailey, J.A. Schweitzer, S.M. Shuster, R.K. Bangert, C.J. Leroy, E.V. Lonnsdorf, et al. 2006. Community and ecosystem genetics: a framework for integrating from genes to ecosystems. Nat Rev Genet 7:510–523.

Wikelski M. and C. Thom. 2000. Marine iguanas shrink to survive El Niño: changes in bone metabolism enable these lizards to reversibly alter their length. Nature 403:37–38.

Wilson D.S. 1980. The Natural Selection of Populations and Communities. Benjamin/Cummings, Menlo Park, CA.