

Chapter 10

Tradeoffs and Negative Correlations in Evolutionary Ecology

Anurag A. Agrawal, Jeffrey K. Conner, and Sergio Rasmann

Hairless dogs have imperfect teeth; long-haired and coarse-haired animals are apt to have, as is asserted, long or many horns; pigeons with feathered feet have skin between their outer toes; pigeons with short beaks have small feet, and those with long beaks large feet. Hence, if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly unconsciously modify other parts of the structure, owing to the mysterious laws of the correlation of growth (Darwin 1859: 11–12).

...as Goethe expressed it, 'in order to spend on one side, nature is forced to economise on the other side.' I think this holds true to a certain extent with our domestic productions: if nourishment flows to one part or organ in excess, it rarely flows, at least in excess, to another part; thus it is difficult to get a cow to give much milk and to fatten readily. The same varieties of the cabbage do not yield abundant and nutritious foliage and a copious supply of oil-bearing seeds. When the seeds in our fruits become atrophied, the fruit itself gains largely in size and quality. In our poultry, a large tuft of feathers on the head is generally accompanied by a diminished comb, and a large beard by diminished wattles. With species in a state of nature it can hardly be maintained that the law is of universal application; but many good observers, more especially botanists, believe in its truth. I will not, however, here give any instances, for I see hardly any way of distinguishing between the effects, on the one hand, of a part being largely developed through natural selection and another and adjoining part being reduced by this same process or by disuse, and, on the other hand, the actual withdrawal of nutriment from one part owing to the excess of growth in another and adjoining part (Darwin 1859: 147).

Why Are We Interested in Tradeoffs?

Tradeoffs have played a prominent role in evolutionary thinking for many reasons, most of which are directly tied to the factors that limit the adaptive

potential of organisms. Why is it that few plants are free from herbivory and that most animals cannot tolerate polar and equatorial climates? The answer accepted by most biologists is that tradeoffs present limits to adaptation (Futuyma and Moreno 1988). As the above quotations from *The Origin of Species* show, Darwin anticipated this argument as well as two concepts that are still prominent today. He clearly understood that: (1) genetic correlations (a term he did not use) are common and can cause evolutionary responses in traits not under direct selection and (2) correlations can be caused by resource allocation tradeoffs.

One profound biological consequence of tradeoffs involves their role in biodiversity. First, there is heritable genetic variation for most traits of organisms, ranging from morphology to life history. What maintains this genetic diversity within species? A leading hypothesis is that tradeoffs in fitness-enhancing traits, including tradeoffs across environments, maintain genetic diversity. Second, species diversity is likely maintained by tradeoffs in species' traits (Clark et al. 2007; see Losos and Mahler, Chapter 15). Analogous to the process operating within species, tradeoffs across environments limit the niche breadth and geographical range of a species, thus generating and maintaining species diversity.

Two kinds of tradeoffs are distinguished, based on whether they involve one or multiple traits (Box 10.1). A one-trait tradeoff occurs when there is opposing selection on a single trait by different selective agents (including different environments) or through different components of fitness (Figure 10.1A). Most examples of stabilizing selection are due to one-trait tradeoffs. In humans, higher birth weight increases postpartum infant survival, while babies that are too large are more likely to die during childbirth (Karn and Penrose 1951). The ovipositors of parasitoid wasps cannot reach flies in larger galls produced by larvae of the goldenrod gall fly, but these larger galls are found and attacked more frequently by birds (Weis and Gorman 1990). Mauricio and Rausher (1997) demonstrated stabilizing selection on glucosinolate concentration in *Arabidopsis thaliana*, resulting from a balance between selection for increased defense in the presence of herbivores and the cost of glucosinolate production (see Berenbaum and Schuler, Chapter 11). Additionally, polymorphisms are often maintained by opposing selection in two

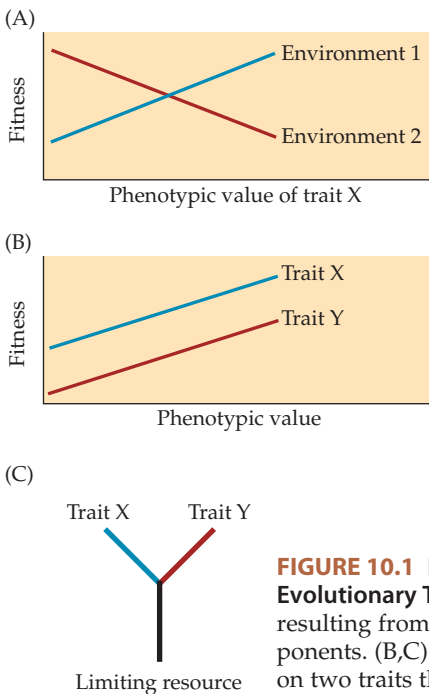


FIGURE 10.1 Depictions of Natural Selection Scenarios that Result in an Evolutionary Tradeoff (A) A one-trait tradeoff caused by opposing selection resulting from different environments, selective agents, and/or fitness components. (B,C) A two-trait tradeoff caused by consistent directional selection on two traits that share a limiting resource.

BOX 10.1**DEFINITIONS OF TERMS AND CONCEPTS RELATING TO TRADEOFFS AND ADAPTIVE CORRELATIONS**

Definitions of key terms used in this chapter are provided in this box. Because some of these terms have a wide range of usage in the literature, definitions supplied are as specific as possible to reduce confusion.

Adaptive negative correlation: A negative correlation (within or among species) that is generated by fitness benefits of not expressing two traits simultaneously. For example, traits that are each costly but functionally redundant may show adaptive negative correlations. The signature of an adaptive negative correlation is negative correlational selection on the two traits that interact to determine fitness.

Correlated evolution: Repeated (parallel or convergent) evolution of an association between two traits across species; it is typically tested by a phylogenetically independent contrast or the generalized least squares equivalent method (Pagel 1999).

Genetic correlation: A measure of the degree to which two traits are affected by the same locus or loci as a result of pleiotropy or linkage disequilibrium. Selection on one trait produces an evolutionary change in all traits that have an

additive genetic correlation with the selected trait (Conner and Hartl 2004).

Tradeoff: Any case in which fitness cannot be maximized because of competing demands on the organism, which can take the form of opposing selection on one trait (i.e., one-trait tradeoff) or of selection to increase two or more traits that share a limiting resource (i.e., multiple-trait tradeoff). A one-trait tradeoff may or may not arise due to the allocation of a limiting resource.

Trait hierarchy: Phenotypic traits can be defined at a number of hierarchical levels—each level dependent on a number of traits at lower levels. For example, the form of an enzyme encoded by a gene is a phenotype, as is a physiological function like metabolic rate that depends on a number of enzymes. A number of different physiological functions affect morphological traits like height, and physiology and morphology together can affect behavioral phenotypes such as courtship. Finally, all these lower level traits can affect high-level life history traits like survival and reproduction, which determine the ultimate trait of individual fitness (Conner and Hartl 2004).

environments, indicative of one-trait tradeoffs (Futuyma 1997). Although studies employing reciprocal transplants that find local adaptation imply a tradeoff, the traits under selection are often not identified and so the nature of the tradeoff is unknown.

A multiple-trait tradeoff occurs when two or more traits (including fitness components), which are both under directional selection to increase, share a limiting resource (Figure 10.1B,C). In other words, a tradeoff occurs when multiple traits that compete for resources are favored by natural selection. Examples of multiple-trait tradeoffs include flower size versus number (Worley and Barrett 2000), offspring size versus number (Mesina and Fox 2001), and levels of different defensive chemicals that share a common precursor (Berenbaum et al. 1986). One-trait and multiple-trait tradeoffs are fundamentally different, because in a one-trait tradeoff there

is opposing selection, while in a multiple-trait tradeoff selection acts to increase allocation to all traits. Both types of tradeoffs are also sometimes referred to as costs (Futuyma 1997).

There are many uses of the term tradeoff in the literature. In this chapter, attention is focused on tradeoffs that take one of three forms: (1) costs of functional traits, such as defense against enemies; (2) life-history tradeoffs within environments; and (3) adaptation to alternative environments (including the evolution of specialization, niche breadth, and range limits).

Life history tradeoffs typically involve multiple traits, while costs of functional traits and adaptation to alternative environments can occur through either one or multiple traits. Much of the work on adaptation to alternative environments does not examine specific traits, but rather it measures fitness or a high-level trait (e.g., damage by herbivores) in each environment (see “trait hierarchy” in Box 10.1). For example, Fry (1996) has defined a tradeoff as any case in which traits that increase fitness on one host are detrimental on others (i.e., phenotypic focus) or any case for which there is no (homozygous) genotype with maximal fitness in both environments (i.e., genotypic focus) (Fry 2003). These fitness tradeoffs could be caused by opposing selection on a single trait in the two environments or by two traits that share a limiting resource and are both selected in the same direction in the two environments. An example of a one-trait tradeoff across environments is coat color in mice: darker colors are favored in woodlands and lighter colors in open beach habitats (Hoekstra et al. 2004).

An example of a multiple-trait tradeoff in adaptation to alternative environments comes from work by Charles Fox and colleagues on seed beetle (*Stator limbatus*) life histories. Increased egg size and number are presumably both favored in all environments but are negatively genetically correlated (Fox et al. 1997). Larger egg size is under stronger positive selection on more resistant host plants (*Cercidium floridum*) compared to less resistant plants (*C. microphyllum* or *Acacia greggii*) (Fox and Mousseau 1996). Thus, adaptation to alternative host plants is mediated by a genetic tradeoff between egg size and number (Fox et al. 1997). Ultimately, beetles collected from *C. floridum* populations lay fewer and larger eggs than beetles collected from susceptible plant populations (Fox and Mousseau 1998). Remarkably, in addition to the genetic differentiation between populations of beetles, an adaptive maternal effect has evolved such that individual beetles alter egg size (and number) appropriately on hosts of varying resistance (Fox et al. 1997).

Many hypotheses in evolutionary ecology assume that natural selection influences organisms' allocation of limiting resources to fitness components and fitness-enhancing traits (Figure 10.2). It may very well be that life history traits, which typically use a large fraction of the total resources available, must trade off. Nonetheless, much work on tradeoffs examines the relationship between low-level traits, requiring few resources, and high-level traits, contributing to fitness (see Figure 10.2). Demonstrating that tradeoffs are a source of constraint is exceedingly challenging, for a number of reasons that are detailed in the following sections.

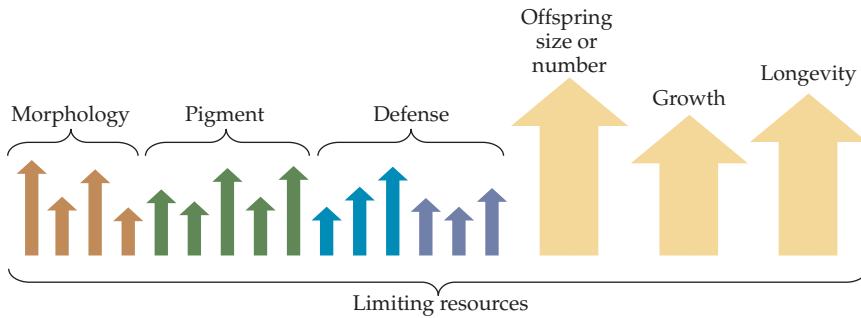


FIGURE 10.2 A Model of Resource Allocation Arrows represent different traits, with their width signifying the amount of the organism's resource budget used and height indicating relative link to fitness. Larger arrows are typically higher-level traits comprised of many lower-level traits (see Box 10.1). Colors represent classes or types of traits (e.g., yellow indicates life history traits, while blues represent defensive traits).

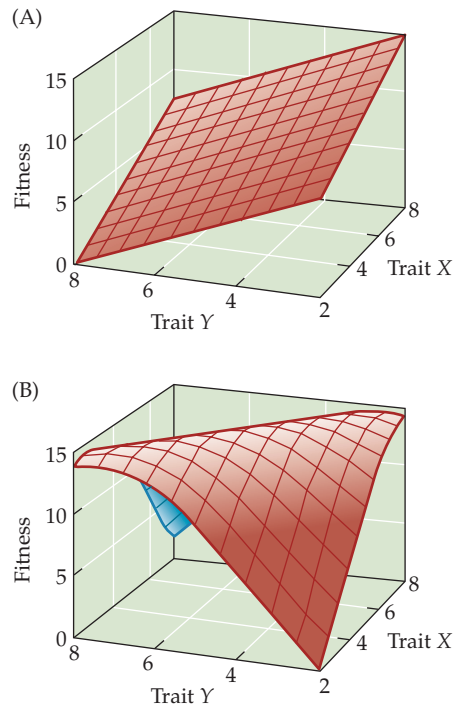
Interpreting Correlations

Although it is intuitive that tradeoffs must exist (allocation of limiting resources, fitness cannot be infinite), it has been surprisingly difficult to obtain strong evidence for tradeoffs within species, where they are actually operating (van Noordwijk and de Jong 1986; Fry 2003). We have compelling evidence for life history tradeoffs (Rose and Charlesworth 1981; Schluter et al. 1991; Stearns 1992; Messina and Fox 2001; Roff 2002) but perhaps less for adaptations to different environments or for specific functional traits such as morphology. We emphasize that strong evidence for a negative correlation between traits, even two traits that are both under positive directional selection, does not necessarily indicate a tradeoff, because negative correlations could also be caused by developmental or physiological linkages that are not due to adaptation or shared limiting resources or by adaptation, specifically natural selection favoring a negative correlation (i.e., adaptive negative correlation, see following).

A very popular evolutionary ecological shorthand has been to study the correlations (phenotypic, genetic, or species correlations) between two traits presumed both to be positively associated with fitness. Such correlations are interpreted in three main ways: adaptive, constraining, or as evidence of a tradeoff. In many cases, these interpretations have little or no support beyond the presence of the correlation itself. This finding is particularly true for positive correlations with size-related traits, because genes that increase size through any number of actions (e.g., resource accrual, rates of cell growth and division, physiological processes) will pleiotropically affect the dimensions and numbers of myriad traits in an organism. Given recent examples of rapid, independent evolution of pairs of traits that are positively genetically correlated, such as Beldade et al. (2002) and others to be discussed in this chapter, one should not assume that a correlation

FIGURE 10.3 Hypothetical Depictions of Directional Selection and Negative Correlational Selection on a Pair of Traits

In both cases there are two traits X and Y, with the smallest values of each in the lower right corner. Fitness is on the vertical axis, and the fitness surface is depicted in red. (A) The two traits are under independent directional selection in opposite directions, resulting in the evolution of the means of the two traits in opposite directions (i.e., not a negative genetic correlation between the traits). The lines on the fitness surface parallel to each trait axis are all parallel to each other, showing that there is no interaction between the traits in determining fitness and, thus, no correlational selection. The elevation and intercept are altered by changes in the other trait, but the selection gradient (slope) that measures the strength of selection does not. (B) Negative correlational selection, in which the two traits interact to determine fitness. The fitness surface is a ridge, with equally high fitness stemming from larger values of one trait associated with smaller values of the other. Valleys of low fitness occur when both traits have low (front, right) or high (back, left) values. Note that the lines on the surface parallel to each trait axis change as the value of the other trait changes, depicting a true interaction between the traits in determining fitness.



causes a meaningful constraint (although this has not been adequately tested with negative correlations). The presence of a negative genetic correlation between two traits that both are reasonably assumed to be under positive directional selection (e.g., fitness components) can be reasonably interpreted as a tradeoff, but this interpretation is strengthened by actual evidence for selection and evidence of a shared limiting resource.

The type of selection that will lead to adaptive correlations is called correlational selection, which is fundamentally distinct from directional selection on the individual traits (Figure 10.3). In correlational selection, there is a ridge in the fitness surface, so that several different combinations of the two traits lead to high fitness (along the ridge), while at least two combinations lead to low fitness (see Figure 10.3B). In directional selection, only one combination leads to the highest fitness and one combination leads to the lowest fitness (e.g., low values of one trait and high values of the other and vice versa; see Figure 10.3A). The key point is that with correlational selection there is no consistent pattern of selection on each trait individually; selection on the one trait depends on the value of the other trait and vice versa. Correlational selection is estimated by a significant cross-product (interaction) term between two traits in a Lande–Arnold (1983) selection gradient analysis (i.e., multiple regression) (see Figures 10.3 and 10.4).

As a potential example of an adaptive negative correlation, van der Meijden et al. (1988) argued that resistance to and tolerance of herbivory were alternative strategies. Plant species that are able to resist herbivory (i.e., are not attacked) do not experience strong selection to tolerate herbivory (i.e., have little fitness impact from damage); and vice versa, species that are tolerant are not expected to experience strong selection for resistance. This pattern has been borne out for genotypes within plant species (Fineblum and Rausher 1995; Stowe 1998; Pilson 2000; Fornoni et al. 2003) as well as animal genotypes (Raberg et al. 2007), although it is certainly not universal (Núñez-Farfán et al. 2007). Resistance and tolerance to other forms of stress (e.g., frost, herbicide application) have similarly shown evidence of selection for a negative correlation between the two as a result of alternative fitness peaks favoring high resistance and low tolerance or low resistance and high tolerance (Agrawal et al. 2004; Baucom and Mauricio 2008) (Figure 10.4). This effect is probably because the traits are both redundant and costly, resulting in selection for a negative correlation between the two.

It is currently unclear whether or not adaptive correlations and correlational selection are common. Alternative organismal strategies may result

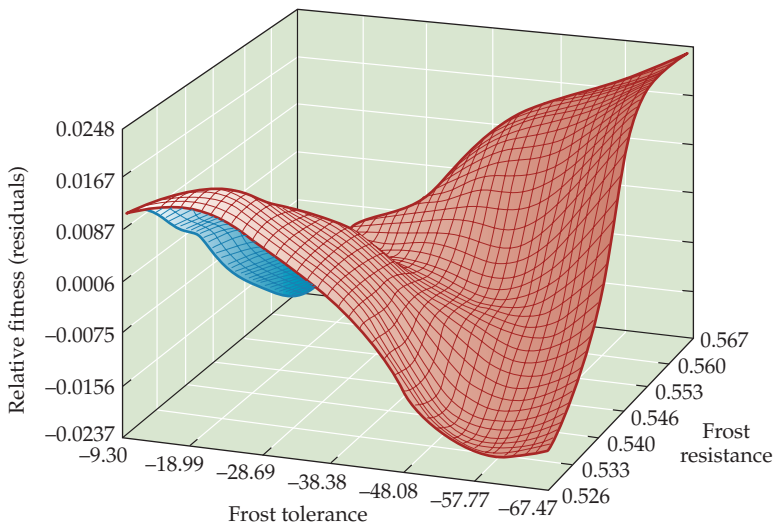


FIGURE 10.4 Fitness Surface Depicting Negative Correlational Selection on Resistance and Tolerance to Frost Damage in Wild Radish (*Raphanus raphanistrum*) Data were taken from a field experiment on 75 paternal half-sibling families subjected to a natural, catastrophic hard frost late in the spring. The two fitness peaks occur at high frost tolerance and low resistance (near left corner) and high resistance and low tolerance (far right); note that lowest tolerance is on the right. Intermediate values of both traits led to intermediate levels of fitness (the “saddle” in the center of the figure). (Adapted from Agrawal et al. 2004.)

from adaptive correlations (i.e., costly redundant traits) or from fundamental tradeoffs (see previous discussion of Fox's beetles). Distinguishing adaptive negative genetic correlations from tradeoffs is straightforward if data on selection are available, but this is not the case for most examples in the literature.

Detecting Tradeoffs: Great Successes and Hurdles

Perhaps the modern version of tradeoffs in life history theory stems from Lack's (1947) study of clutch size in altricial birds, in which he hypothesized that stabilizing selection results from decreased survival of offspring in larger clutches under resource-limiting conditions (a one-trait tradeoff; see Figure 10.1). This work laid the foundation for many studies, for example by Ricklefs (1977) that employed a comparative analysis to examine costs of reproduction associated with clutch size. Major reviews on the topic include Stearns (1992) and Roff (2002). Over a century before Lack, in *The Origin of Species*, Darwin (1859: 148) summarized the view that most adaptations are costly: "If under changed conditions of life a structure before useful becomes less useful, any diminution, however slight, in its development, will be seized on by natural selection, for it will profit the individual not to have its nutriment wasted in building up an useless structure." Costs are defined in terms of fitness, and thus, Darwin's conceptualization can be thought of in the context of the one-trait tradeoff (see Figure 10.1A). The multiple-trait tradeoffs are also based on costs, in that limiting resources cannot be allocated simultaneously to two fitness-enhancing traits (see Figure 10.1C).

In the study of plant resistance to insect herbivores, costs of resistance traits have long been invoked to explain two interrelated issues: (1) why completely resistant plants have not evolved and taken over, and (2) why genetic variation for resistance traits is maintained in natural populations (Whittaker and Feeny 1971). Pioneering work by May Berenbaum, Ellen Simms, and colleagues used quantitative genetic approaches to estimate costs of resistance (Berenbaum et al. 1986; Simms and Rausher 1987, 1989). Using monocarpic plants, they predicted that in the absence of herbivores, the genotypes that invested the most in resistance traits would have the lowest lifetime reproduction. In at least a few cases, opposing natural selection on the same trait was demonstrated by growing plants in environments with herbivores versus without herbivores (Berenbaum et al. 1986; Mauricio and Rausher 1997; Shonle and Bergelson 2000). However, many other studies failed to find costs (Simms 1992; Bergelson and Purrington 1996; Strauss et al. 2002). The emerging paradigm is that costs are often dependent on the environment in two ways, which have been referred to as ecological costs (Strauss et al. 2002). First, costs are likely to be most detectable under competitive or otherwise stressful conditions in which resources

become especially limiting. Many experiments designed to detect costs are conducted under benign conditions and thus, may underestimate costs. Second, even if a trait is not a significant energetic drain on the organism, it may reduce fitness-enhancing interactions. For example, highly defended plants may have reduced visitation by pollinators (Strauss et al. 1999).

Another success story in the detection of costs has been the tradeoff between investment in flight muscles and fecundity in insects (Zera and Harshman 2001). Many insect species are naturally polymorphic, with macropterous (normal winged) and micropterous (reduced wings and/or flight muscles) forms—a polymorphism that is thought to have evolved because flight muscles are costly and the benefit of flight is low in some environments (e.g., high, local resource availability and low predation). Studies have consistently shown phenotypic and genetic negative correlations between flight structures and fecundity, indicative of a tradeoff, because these traits are not redundant.

Evolution of Insect Host Range

One of the great challenges in the study of plant–animal interactions has been the question of host specialization in herbivorous insects, an example of the broader problem of ecological specialization (Futuyma and Moreno 1988; Fry 2003). Well over 50% of herbivorous insects feed on plants in a single genus, a highly restricted subset of the available host species (Schoonhoven et al. 2005). Tradeoffs have been the long-held explanation for host restriction, on the supposition that adaptations to the defenses of one host species detract from the ability to cope with defenses of other hosts. A jack-of-all-trades is master of none.

Somewhat counterintuitively, researchers have often used generalist herbivores to test for tradeoffs in host use—possibly because it is difficult to force specialists to feed on non-hosts. Mackenzie (1996) reported that among 77 clones of the black bean aphid (*Aphis fabae*), a tradeoff in fecundity was found on one out of three pairwise combinations of the three hosts. Three independent selection experiments with two-spotted spider mites (*Tetranychus urticae*) found that lines adapted to novel and somewhat toxic hosts showed a tradeoff in fitness on the original host (Gould 1979; Fry 1996; Agrawal 2000), although this was detectable only by the loss of adaptation to the novel host when the adapted mites were reverted onto the original host for several generations. In a fourth study of these mites, Yano et al. (2001), like previous authors, found no reduction of fecundity on the original host but reported that adaptation to the novel host was associated with reduced male ability to compete for mates.

Specialization and tradeoffs have also been studied in oligophages (e.g., herbivores restricted to one plant family). Evidence comes from the oligophagous pea aphid (*Acyrtosiphon pisum*), for which Via and Hawthorne

(2002) have identified the genetic basis of a tradeoff in performance on two legume hosts. Nonetheless, many other systems have failed to find evidence for tradeoffs (James et al. 1988; Forister et al. 2007; Futuyma 2008). For example, Ueno et al. (1995) used specialist *Epilachna spp.* beetles to test hypotheses about the evolution of host shifts and specialization. They employed the approach of assessing genetic variation for performance on the typical host plant and the host plants of close beetle relatives. Where heritable variation was found, there was essentially no evidence for tradeoffs in the use of alternative hosts.

Difficulties in Detecting Multiple-Trait Tradeoffs within Species

Because a multiple-trait tradeoff is likely to be reflected in a negative correlation between traits at some level in the trait hierarchy, much effort, mainly in the 1980s, was directed towards discovering negative genetic correlations, especially in the study of host use by herbivorous insects (Futuyma and Moreno 1988). Many of these studies failed to find negative correlations (Rausher 1984; Futuyma and Philippi 1987; James et al. 1988; Karowe 1990; Fox 1993; Forister et al. 2007; Ferrari et al. 2008; Agosta and Klemens 2009). However, a negative correlation between two traits might not be found even when there is some underlying, fundamental tradeoff between these traits.

The basic idea is that stronger positive relationships can mask underlying tradeoffs. This point was first made for phenotypic relationships by van Noordwijk and de Jong (1986), who showed graphically how variation in resource acquisition could create a positive correlation between two traits, even when there is a tradeoff in the allocation of that resource between the traits (Figure 10.5). Houle (1991) extended this general concept to genetic correlations, showing theoretically that if there were more loci involved in resource acquisition than in allocation of that resource, the genetic correlation could be positive in spite of a fundamental allocation tradeoff.

If negative phenotypic or genetic correlations among traits that are both positively related to fitness are found, it is excellent evidence for a multiple-trait tradeoff. In many cases in the literature, the traits are fitness components such as survival or fecundity, so the relationship to fitness is clear, but in other cases the positive relationship of the traits to fitness should be demonstrated empirically, ideally using Lande–Arnold selection gradients (Lande and Arnold 1983) and/or experimental manipulation (Conner and Hartl 2004). What about the cases in which positive phenotypic correlations are found between traits that are expected to trade off, based on knowledge of their biology? The first step is to estimate the genetic correlations, as these are not affected by the environmental correlations (van Noordwijk and de Jong 1986). This approach could be implemented using sibling analysis, but a more reliable method of testing for genetic correlation is

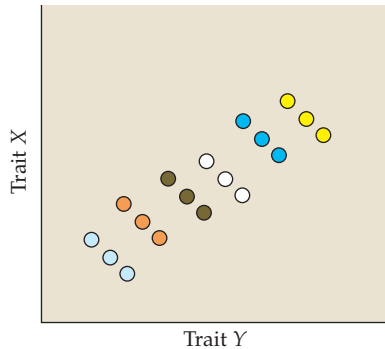


FIGURE 10.5 How a Tradeoff in the Allocation of Resources to Two Traits Can Be Masked across Scales Within each color, a tradeoff is represented, which could be within a genotype or across genotypes within a species. Different colors represent alternative scales (e.g., resource environments, genotypes with altered resource acquisition, or different species). Three scenarios discussed in this chapter could fit the pattern. First, van Noordwijk and de Jong (1986) proposed that a strong positive environmental correlation caused by variation in resource acquisition could create a positive phenotypic correlation between two traits, even when there is a tradeoff between the two traits. For example, in resource rich environments, egg size and number may increase, even though the two traits show a negative correlation within a resource environment. Houle (1991) extended this concept to genetic correlations, showing that if there is more genetic variation in resource acquisition than allocation, the genetic correlation could also be positive in spite of a tradeoff. We add to these scales by suggesting that positive species correlation may occur if species vary in their total acquisition despite genetic tradeoffs that occur within species (see Figure 10.8).

artificial selection (Bell and Koufopanou 1986; Conner 2003; Fry 2003). We suggest imposing artificial selection on one of the traits and testing for an evolutionary response in the opposite direction in the other trait. Ideally, this evaluation would be conducted in all four treatment combinations (i.e., selection for increased and decreased values of each trait individually) with replication. However, if there were more genetic variation for resource acquisition than for allocation, then the correlated responses would still be expected to be positive. In this case, one could attempt to control resource acquisition, if this can be measured.

A study of the expected tradeoff between flower size and number in water hyacinth (*Eichhornia paniculata*) serves as a good illustration for both this approach and the often equivocal case of tradeoffs (Worley and Barrett 2000). Using a maximum-likelihood pedigree analysis on the base population, the genetic correlation between flower size and number was estimated as weakly but significantly *positive* (0.18) and was nonsignificantly negative after leaf area and flowering time were included in the model, in an attempt to reduce variance in resource acquisition; thus, there was no initial

evidence for a tradeoff. The authors then selected for increased flower number and both increased and decreased flower size for two generations, with two replicate lines of each of the three treatments. The predicted correlated responses to selection, if a tradeoff exists, were found in half of the six selection lines; that is, in both of the replicates selected for decreased flower size and in one of the replicates selected for increased flower number. The response to selection in the other three lines was not significant. Thus, the evidence for a tradeoff between flower size and number is equivocal.

If the evidence for negative genetic correlations between two traits that are expected to trade off is absent or equivocal, the next step in testing for tradeoffs is to dissect the traits more finely, both phenotypically and genetically. One possibility is to examine traits at a lower level in the trait hierarchy (see Box 10.1), because high-level traits, such as fitness components, plant damage by herbivores, or insect performance on a given host plant, are affected by more gene loci, thus increasing the probability that resource acquisition loci mask the postulated allocation tradeoff. For example, the genetic correlations among the physiological and/or morphological traits that determine fitness components, herbivore resistance, or host use could be examined with artificial selection. Selection experiments on lower-level traits that provide herbivore resistance have often successfully demonstrated tradeoffs (Ågren and Schemske 1993; Zangerl and Berenbaum 1997; Siemens and Mitchell-Olds 1998; Stowe 1998; Marak et al. 2003). For a more complete understanding of any tradeoff, it is necessary to uncover the gene loci underlying the complex traits. From there, it is possible to determine whether there are negatively pleiotropic resource allocation loci, and if so, how they function and how large their effects are on higher-level phenotypic traits, relative to acquisition loci. Although these kinds of studies are still very difficult even in genetic model organisms, they are becoming more feasible with rapid advances in sequencing and other molecular genetic technologies. One example of this general approach is a quantitative trait loci (QTL) analysis of fitness components in a cross between two ecotypes of wild barley (Verhoeven et al. 2004); the investigators found QTL for fitness traits in each environment, but no case in which different alleles at these QTL were favored in the two environments. In other words, there was a lack of evidence for tradeoffs at the level of small sections of chromosomes. Even here, it may be that tradeoffs might be found at the level of individual genes, or for lower-level traits, as all the traits examined in this study were high-level components of fitness.

Evidence that Genetic Correlations Cause Evolutionary Constraint

Even if a negative genetic correlation between two fitness-enhancing traits exists, it is unclear how strong an evolutionary constraint it would cause. For a pair of traits, only a genetic correlation coefficient of -1 would prevent

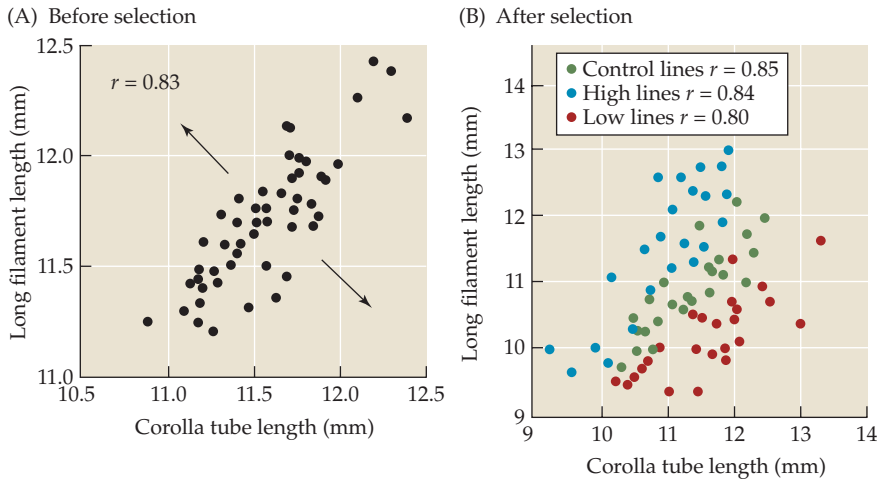


FIGURE 10.6 Artificial Selection Perpendicular to the Major Axis of the Correlation Between Filament and Corolla Tube Lengths in Wild Radish (*Raphanus raphanistrum*) (A) The genetic correlation in the original population. The arrows show the direction of selection in the high and low anther exertion lines; note that these are in the direction of least variation in bivariate space. Each point is the mean of all offspring of one sire from a nested half-sibling design (Conner and Via 1993). The correlation of these sire family means is an estimate of the additive genetic correlation. (B) Results after five or six generations of selection (Conner et al., unpublished). Selection has moved the elliptical cloud of points in the directions of the arrows in (A) without changing the shape of the ellipse, that is, the correlation within each group. Each point is the mean for a full-sibling family; the resulting correlations are broad-sense genetic correlations that include covariance due to dominance and maternal effects. The difference in estimation methods is responsible for the greater range of values in panel (B) than in panel (A). (Adapted from Conner 2003.)

evolution of larger values of both traits (Via and Lande 1985; Houle 1991). Genetic correlations greater than -1 would slow down, but not prevent, a response to selection, because there is at least some independent genetic variation for both traits (Figure 10.6A). This is a crucial point—if there is any genetic variation in the direction of selection, evolution *can* occur (although it may or may not occur over a timescale concordant with environmental change). There is also convincing evidence that positive genetic correlations may not even slow down response to strong selection, because when artificial selection is applied perpendicular to the major axis of the correlation, rapid evolution occurs. For example, artificial selection in *Bicyclus anynana* butterflies has produced independent evolution of a variety of positively correlated traits, including forewing versus hindwing-spot size (Beldade et al. 2002) and forewing area and body size (Frankino et al. 2005), although selection on wing-spot color composition failed to produce independent

evolution (Allen et al. 2008). Artificial selection on filament and corolla tube lengths in wild radish produced a response in just a few generations (Conner 2003; Conner et al., unpublished) again despite a strong positive genetic correlation between the traits caused by pleiotropy (Conner 2002) (Figure 10.6B).

While there is no theoretical quantitative genetic reason why selection perpendicular to the major axis of a negative genetic correlation should produce different results than the selection against a positive correlation (as in examples previously cited), we are not aware of any studies that have attempted to do so. Of most relevance and interest would be artificial selection to simultaneously increase two traits that are both known to be positively related to fitness in nature, are thought to compete for a limiting resource (and thus have a fundamental tradeoff between them), and are known to be negatively genetically correlated; to our knowledge, a study of this description has not been attempted. Life history traits are prime candidates for such experiments, and their close ties to fitness may make correlations between life history traits likely constraints.

The lack of constraint seen in artificial selection studies on pairs of traits that are positively correlated might also be explained if constraints are not pairwise, but fundamentally multivariate (Blows and Hoffmann 2005; Walsh and Blows 2009). The argument here is that while there is some genetic variation perpendicular to the major axis in most or all pairs of traits (i.e., the genetic correlation is not 1 or -1), there may be dimensions in multivariate space where genetic variation is completely lacking. Indeed, this may be the dimension in which there is directional or stabilizing selection that has depleted the available variation. While there is some laboratory evidence for selection on multivariate axes (Brooks et al. 2005; Van Homrigh et al. 2007), the examples to date are for complex traits (e.g., cuticular hydrocarbons in *Drosophila* spp., components of a cricket call) for which the direction of selection would be difficult to predict. In the cuticular hydrocarbon example, genetic variance is lacking along the multivariate axis upon which sexual selection is exerted by females (Van Homrigh et al. 2007), and artificial selection on male mating success for 10 generations failed to produce a response (McGuigan et al. 2008), as would be predicted if the hydrocarbons are the major determinant of male mating success. To our knowledge, artificial selection has not been applied directly to a multivariate axis.

In an analogous fashion, it is possible that tradeoffs are often not pairwise, but involve multiple traits simultaneously. Many key limiting resources (carbon, nitrogen, phosphorus, amino acids, water) are allocated among many traits simultaneously or sequentially in an organism. Thus, two traits that are relatively minor sinks for a resource might not tradeoff with each other, but might together tradeoff with a more major resource sink (see Figure 10.2). This is an area for future study.

Macroevolutionary Approaches to Studying Tradeoffs and Correlations

As defined here, the terms tradeoffs and adaptive correlations are microevolutionary phenomena (see Box 10.1). Nonetheless, tradeoffs and correlations within ancestral species may influence the patterns of divergence across closely related descendant species. Whereas an intraspecific pattern may reflect a tradeoff or adaptive correlation, interspecific patterns may represent different adaptive solutions to a tradeoff or be biased by genetic correlation. A pattern of tradeoffs may be more evident across species than within species, because there has been substantial time for selection to create larger relative differences in trait means—an extension of the fact that artificial selection may be a more powerful way to detect negative correlations than sibling analysis. An example may be *r*- versus *K*-life-history strategies in closely related species, for which there are many examples among plants and insects (Gadgil and Solbrig 1972; Stearns 1992; Roff 2002; Mooney et al. 2008).

One way that microevolutionary processes might determine macroevolutionary patterns across species is what Schluter called evolution along genetic lines of least resistance (Schluter 1996), whereby genetic correlations within ancestral species bias the phenotypic divergence of correlated traits among descendent species, so that species occupy a restricted area of bivariate space. A number of studies have now tested whether plant and animal species tend to diverge mainly along the trajectory predicted by genetic or phenotypic correlations within one of these species, and most studies find that this is the case, but that a few species do diverge substantially from this predicted trajectory (Schluter 1996; Hansen and Houle 2008; Marroig and Cheverud 2005; Hunt 2007; Conner 2006). For example, Schluter's original study (1996) showed that macroevolutionary patterns of morphological diversification in stickleback fish, birds, and mice conformed to patterns of within-species genetic correlations. Therefore, genetic correlations may bias the direction of macroevolutionary divergence, but this bias can be broken, presumably when selection or drift is strong enough.

A hypothesis in plant defense evolution has been that shared precursors limit the production of diverse types of beneficial defenses (i.e., an allocation tradeoff) (Berenbaum et al. 1986; Gershenzon and Croteau 1992; Agrawal et al. 2002). Alternatively, changes in the level of a common precursor may cause similar effects in the expression of multiple products by simply changing the overall flux through the pathway, causing the levels of the products to be positively correlated (Martens and Mithofer 2005), which is another example of variance in acquisition being greater than variance in allocation. Most research on this topic has been on model species in which the flow of specific compounds can be followed, or competition for a particular enzymatic precursor can be identified (Keinanen et al. 1999; Kao et

al. 2002; Laskar et al. 2006; Scalliet et al. 2006). However, an approach that considers patterns across species addresses a different question about the long-term persistence and convergent evolution of particular compounds or the associations between branches of biosynthetic pathways (Liscombe et al. 2005; Pelsler et al. 2005; Agrawal 2007). In other words, are physiological tradeoffs more or less evident as species diversify? Do associations between biosynthetic pathways persist over evolutionary time, or are they eroded by natural selection or nonadaptive processes that reduce their interdependence?

In a study of phenolics and cardenolides (two classes of plant defenses) across 35 species of milkweed, strong evidence was found for integration among phenolic classes and among flavonoids (a class of phenolics) and cardenolides (Agrawal et al. 2009b). Within the phenolics, caffeic acid derivatives and flavonoids share *p*-coumaric acid as a precursor, and there appears to be evolutionary competition for this precursor (i.e., species have evolved to different points along the tradeoff). In contrast, cardenolides and flavonoids, which are both constructed with products from the acetate–malonate pathway (Andersen et al. 2006), show positively correlated interspecific expression. This latter result suggests that milkweed species have evolved changes in the flux through the acetate–malonate pathway, resulting in concordant shifts in flavonoids and cardenolides. We do not interpret these results to mean there is no physiological competition for precursors, but rather that species are evolving to different levels of acquisition of the precursor (Houle 1991).

Another long-standing hypothesis in plant–herbivore interactions is that plants that possess one type of highly effective defense should lack others (i.e., an adaptive negative correlation based on costs and redundancy). Within a species, this outcome may result in an adaptive negative correlation as previously discussed. Nonetheless, intraspecific analyses rarely find significant genetic correlations between defensive traits (Koricheva et al. 2004). A comparative approach has been taken to examine the macroevolutionary correlations between putatively defensive traits, although very few have employed phylogenetically informed methods. Most of these studies do not support a negative correlation model (Steward and Keeler 1988; Twigg and Socha 1996; Heil et al. 2002; Rudgers et al. 2004; Agrawal and Fishbein 2006). In an example from our own research, two defensive traits of milkweeds show no genetic correlation within one species but are positively correlated across species (Figure 10.7). Thus, one can only conclude that the redundancy model of negative correlations between resistance traits is too simple, especially in the context of variable environments and multiple herbivores.

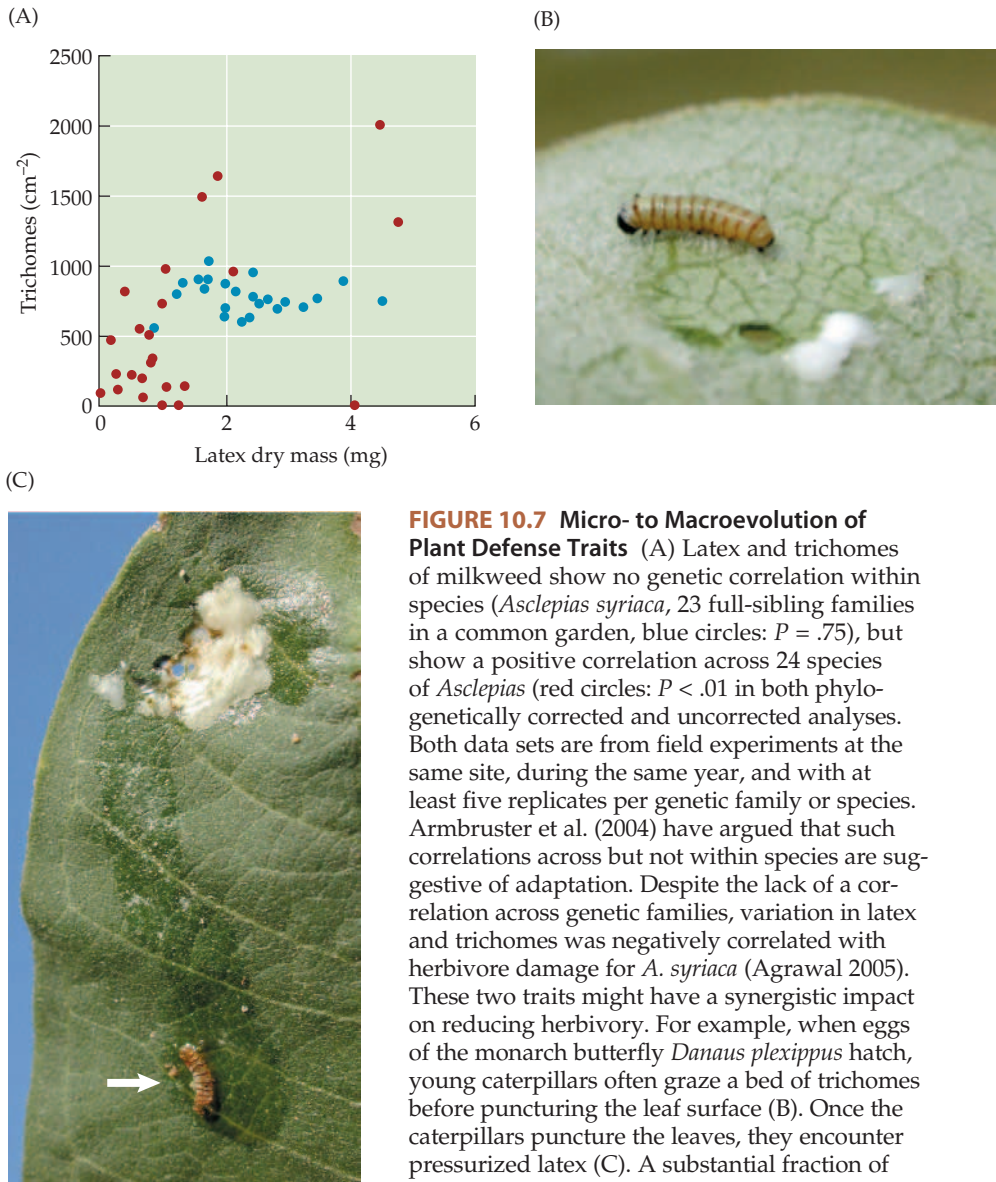


FIGURE 10.7 Micro- to Macroevolution of Plant Defense Traits

(A) Latex and trichomes of milkweed show no genetic correlation within species (*Asclepias syriaca*, 23 full-sibling families in a common garden, blue circles: $P = .75$), but show a positive correlation across 24 species of *Asclepias* (red circles: $P < .01$ in both phylogenetically corrected and uncorrected analyses). Both data sets are from field experiments at the same site, during the same year, and with at least five replicates per genetic family or species. Armbruster et al. (2004) have argued that such correlations across but not within species are suggestive of adaptation. Despite the lack of a correlation across genetic families, variation in latex and trichomes was negatively correlated with herbivore damage for *A. syriaca* (Agrawal 2005). These two traits might have a synergistic impact on reducing herbivory. For example, when eggs of the monarch butterfly *Danaus plexippus* hatch, young caterpillars often graze a bed of trichomes before puncturing the leaf surface (B). Once the caterpillars puncture the leaves, they encounter pressurized latex (C). A substantial fraction of monarch caterpillars die in latex (see arrow). (A, data from Agrawal 2005 and Agrawal and Fishbein 2006; adapted from Agrawal 2007; photos by Anurag Agrawal.)

Case Study of Adaptive Allocation to Plant Defense across Scales

As discussed throughout this chapter, allocation to plant defense has been one of the major areas of research on tradeoffs and adaptive correlations. One-trait tradeoffs (i.e., fitness costs of the trait in the absence of herbivores, but benefits in the presence of herbivores), two-trait tradeoffs (i.e., competition for a shared precursor between different beneficial defenses), and adaptive correlations between defense types (i.e., resistance versus tolerance) have all been proposed. One axis on which negative correlations have been predicted is in the expression strategy of single traits. For example, based in plant defense theory, constitutive and inducible resistance have long been predicted to show a pattern of negative correlation within and across species (Rhoades 1979; Brody and Karban 1992; Koricheva et al. 2004). The basis for this hypothesis is that plants investing in high levels of constitutive defense (i.e., traits that are always expressed) will experience minimal attack and need not be inducible following herbivory (Zangerl and Bazzaz 1992). Conversely, cases for which the probability of attack is unpredictable, plants may be expected to invest relatively little in constitutive defense but to show high levels of inducibility following attack.

The predicted negative correlation between constitutive and induced resistance could be adaptive if the traits are each beneficial, redundant, and costly. Despite some support for this negative genetic correlation (Koricheva et al. 2004), several statistical issues have plagued the accurate assessment of the relationship, which is typically estimated as a species- or family-mean correlation between investment in constitutive traits and inducibility and defined as the absolute increase in the same traits after herbivore damage (Morris et al. 2006).

We have been studying the relationship between constitutive and induced cardenolide production in milkweeds (*Asclepias* spp.) (Rasmann et al. 2009; Rasmann and Agrawal, unpublished data) (Figure 10.8). Cardenolides disrupt the sodium and potassium flux in animal cells, making them remarkably potent toxins, with no known primary function in plants (Malcolm 1991). In response to foliar herbivory by specialist monarch butterfly caterpillars, most species of *Asclepias* induce increases in cardenolide expression; similarly, root herbivory by larvae of specialist cerambycid beetles (*Tetraopes* spp.) typically increases cardenolide concentrations in roots. In both above- and below-ground tissues, we have now repeatedly found the striking pattern of a negative genetic correlation between constitutive and induced cardenolides within species and a positive association between constitutive cardenolides and induction across species (see Figure 10.8).

The intraspecific data could be interpreted in two ways. The negative genetic correlation between constitutive and induced cardenolides in *A. syriaca* could be an adaptive negative correlation. That is, constitutive and induced cardenolides may be redundant (because inducing higher levels of

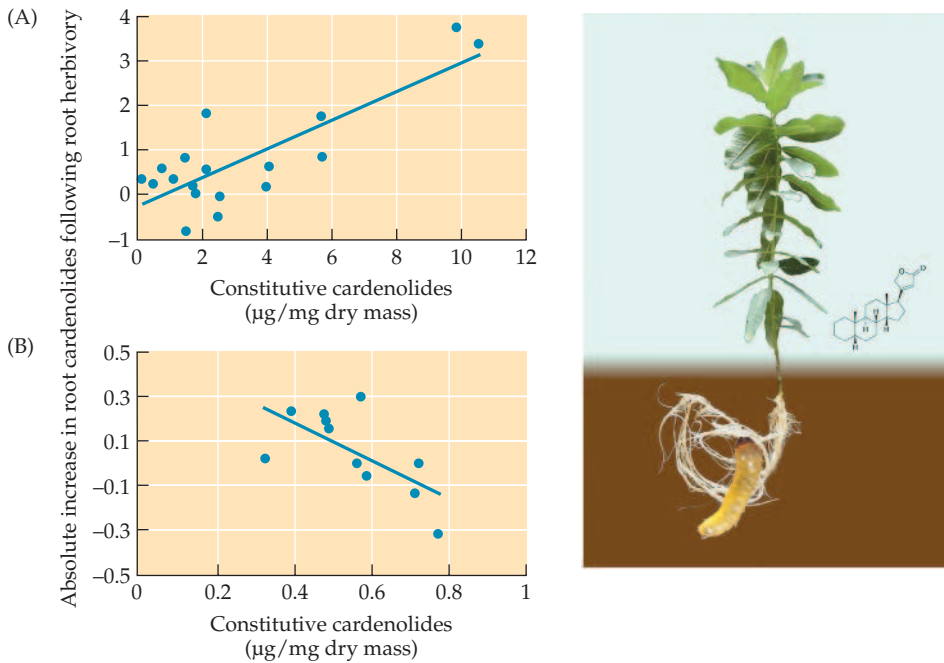


FIGURE 10.8 The Relationship between Constitutive and Induced Cardenolides in the Roots of Milkweeds The relationship is presented across (A) 18 species of *Asclepias* and (B) 11 full-sibling families of *Asclepias syriaca*. Slopes are significant after being corrected for various statistical biases (Morris et al. 2006), including phylogenetic nonindependence. Similarly, divergent relationships have been found for above-ground leaf cardenolide concentrations in response to monarch caterpillar herbivory. (From Rasmann et al. 2009; Rasmann and Agrawal, unpublished data; photo by Sergio Rasmann.)

cardenolides in high constitutive genotypes may provide little additional defense) and costly. We currently do not have data to address either of these suppositions. Alternatively, constitutive and induced cardenolides may exhibit a two-trait tradeoff. That is, the traits may not be redundant (i.e., both may be under positive selection), and limiting resources (i.e., the absolute total amount of cardenolides) prevent both high constitutive cardenolides and inducibility from being simultaneously attained. Indeed, in both the root data presented here (see Figure 10.8B) and in work on cardenolides in leaves (Bingham and Agrawal, submitted 2010), it does appear that *A. syriaca* genotypes produce a maximum level of cardenolides that is modulated by increasingly low levels following damage, maintaining intermediate levels following damage, or decreasing cardenolides after damage. The fact that the highest constitutive cardenolide genotypes decrease cardenolides following damage is surprising but has been consistently observed in our experiments.

This pattern of a negative correlation is not exhibited across species; in fact, it is reversed (see Figure 10.8), indicating that macroevolution has not proceeded along the lines of least resistance. On the contrary, it appears that species have evolved the ability to produce different amounts of cardenolides (Agrawal et al. 2009a; Agrawal et al. 2009b) and that as total cardenolide production has changed, so too has inducibility in a proportional manner. This pattern suggests that species variation in production of cardenolides is greater than variation in allocation patterns to constitutive and induced resistance. The logic here is exactly the same as that described by van Noordwijk and de Jong (1986), except that the positive association occurs across species. We note that the species differences in total cardenolide production may be due to either altered acquisition of the resources needed to produce cardenolides or to the altered allocation of the same set of resources to cardenolides (only in the latter case would one expect to find a negative correlation with some other traits). In either case, the countervailing micro- and macroevolutionary patterns reflect major shifts in total plant investment in defense across species.

Conclusion

We have emphasized several overarching themes in the study of tradeoffs. First, tradeoffs can either act through a single trait selected in opposite directions by different selective agents, fitness components, or environments, or they can act through multiple traits that compete for a shared limiting resource. Second, variation in acquisition of a limiting resource can be greater than variation in allocation of that resource, resulting in a positive, rather than negative, correlation between traits that actually trade off. This outcome can occur (1) at the phenotypic level within populations, if positive environmental correlations are greater than negative genetic correlations; (2) at the genetic level within populations, if genetic variation in acquisition is greater than genetic variation in allocation; or (3) at the macroevolutionary level, if interspecific variation in acquisition is stronger than negative genetic correlations within species. Third, negative correlations by themselves can be difficult to interpret, as they could either represent a tradeoff or an adaptation, with the latter being more likely in traits that are both redundant and costly. Finally, future work on tradeoffs should both move down lower and up higher in the trait hierarchy, by identifying individual gene loci and physiological processes directly involved in resource allocation and by determining the effects of these loci and processes on as comprehensive a fitness measure as possible.

Acknowledgments

We thank Doug Futuyma for stimulating us to think about tradeoffs and for detailed comments on the manuscript. We also thank Susan Cook, Alexis

Erwin, Monica Geber, Amy Hastings, Raffica La Rosa, Brian Lazzaro, Anne Royer, Mike Stastny, and Marjorie Weber for comments and discussion. During the writing of this chapter, we were supported by NSF DEB 0447550 and 0950231 to AAA, NSF DBI 0638591 and DEB-0919452 to JKC, and a postdoctoral fellowship from the Swiss National Science Foundation PA0033-121483 to SR.

Literature Cited

- Agosta, S. J. and J. A. Klemens. 2009. Resource specialization in a phytophagous insect: No evidence for genetically based performance trade-offs across hosts in the field or laboratory. *J. Evol. Biol.* 22: 907–912.
- Agrawal, A. A. 2000. Host range evolution: Adaptation of mites and trade-offs in fitness on alternate hosts. *Ecology* 81: 500–508.
- 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. A. 2007. Macroevolution of plant defense strategies. *Trends Ecol. Evol.* 22: 103–109.
- Agrawal, A. A. and M. Fishbein. 2006. Plant defense syndromes. *Ecology* 87: S132–S149.
- Agrawal, A. A., J. K. Conner, and J. R. Stinchcombe. 2004. Evolution of plant resistance and tolerance to frost damage. *Ecol. Lett.* 7: 1199–1208.
- Agrawal, A. A., M. Fishbein, R. Halitschke, and 3 others. 2009a. Evidence for adaptive radiation from a phylogenetic study of plant defenses. *Proc. Natl. Acad. Sci. USA* 106: 18067–18072.
- Agrawal, A. A., A. Janssen, J. Bruin, and 2 others. 2002. An ecological cost of plant defense: Attractiveness of bitter cucumber plants to natural enemies of herbivores. *Ecol. Lett.* 5: 377–385.
- Agrawal, A. A., J.-P. Salminen, and M. Fishbein. 2009b. Phylogenetic trends in phenolic metabolism of milkweeds (*Asclepias*): Evidence for escalation. *Evolution* 63: 663–673.
- Ågren, J., and D. W. Schemske. 1993. The cost of defense against herbivores: An experimental study of trichome production in *Brassica rapa*. *Am. Nat.* 141: 338–350.
- Allen, C. E., P. Beldade, B. J. Zwaan, and 1 other. 2008. Differences in the selection response of serially repeated color pattern characters: Standing variation, development, and evolution. *BMC Evol. Biol.* 8: 94.
- Andersen, Ø. M. and K. R. Markham (eds.). 2006. *Flavonoids: Chemistry, Biochemistry and Applications*. CRC Press/Taylor & Francis, Boca Raton.
- Armbruster, W. S., C. Pelabon, T. F. Hansen, and 1 other. 2004. Floral integration, modularity and accuracy: Distinguishing complex adaptations from genetic constraints. In M. Pigliucci and K. Preston (eds.), *Phenotypic Integration: Studying the Ecology and Evolution of Complex Phenotypes*, pp. 23–49. Oxford University Press, New York.
- Baldwin, I. T. and W. Hamilton. 2000. Jasmonate-induced responses of *Nicotiana sylvestris* results in fitness costs due to impaired competitive ability for nitrogen. *J. Chem. Ecol.* 26: 915–952.
- Baucom, R. S. and R. Mauricio. 2008. Constraints on the evolution of tolerance to herbicide in the common morning glory: Resistance and tolerance are mutually exclusive. *Evolution* 62: 2842–2854.

- Beldade, P., K. Koops, and P. M. Brakefield. 2002. Developmental constraints versus flexibility in morphological evolution. *Nature* 416: 844–847.
- Bell, G. and V. Koufopanou. 1986. The cost of reproduction. *Oxford Surveys Evol. Biol.* 3: 83–131.
- Berenbaum, M. R., A. R. Zangerl, and J. K. Nitao. 1986. Constraints on chemical coevolution: Wild parsnips and the parsnip webworm. *Evolution* 40: 1215–1228.
- Bergelson, J. and C. B. Purrington. 1996. Surveying patterns in the cost of resistance in plants. *Am. Nat.* 148: 536–558.
- Blows, M. W. and A. A. Hoffmann. 2005. A reassessment of genetic limits to evolutionary change. *Ecology* 86: 1371–1384.
- Brody, A. K. and R. Karban. 1992. Lack of a tradeoff between constitutive and induced defenses among varieties of cotton. *Oikos* 65: 301–306.
- Brooks, R., J. Hunt, M. W. Blows, and 3 others. 2005. Experimental evidence for multivariate stabilizing sexual selection. *Evolution* 59: 871–880.
- Clark, J. S., M. Dietze, S. Chakraborty, and 4 others. 2007. Resolving the biodiversity paradox. *Ecol. Lett.* 10: 647–659.
- Conner, J. and S. Via. 1993. Patterns of phenotypic and genetic correlations among morphological and life history traits in wild radish, *Raphanus raphanistrum*. *Evolution* 47: 704–711.
- Conner, J. K. 2002. Genetic mechanisms of floral trait correlations in a natural population. *Nature* 420: 407–410.
- Conner, J. K. 2003. Artificial selection: A powerful tool for ecologists. *Ecology* 84: 1650–1660.
- Conner, J. K. 2006. Ecological genetics of floral evolution. In L. D. Harder and S. C. H. Barrett (eds.), *The Ecology and Evolution of Flowers*, pp. 260–277. Oxford University Press, New York.
- Conner, J. K. and D. L. Hartl. 2004. *A Primer of Ecological Genetics*. Sinauer Associates, Sunderland, MA.
- Darwin, C. 1859. *On The Origin of Species By Means of Natural Selection, or The Preservation of Favoured Races in The Struggle for Life*. John Murray, London.
- Falconer, D. S. and T. F. C. Mackay. 1996. *Introduction to Quantitative Genetics*. Longman, Essex, England.
- Ferrari, J., S. Via, and H. C. J. Godfray. 2008. Population differentiation and genetic variation in performance on eight hosts in the pea aphid complex. *Evolution* 62: 2508–2524.
- Fineblum, W. L. and M. D. Rausher. 1995. Tradeoff between resistance and tolerance to herbivore damage in a morning glory. *Nature* 377: 517–520.
- Forister, M. L., A. G. Ehmer, and D. J. Futuyma. 2007. The genetic architecture of a niche: Variation and covariation in host use traits in the Colorado potato beetle. *J. Evol. Biol.* 20: 985–996.
- Fornoni, J., P. L. Valverde, and J. Nú ez-Farfán. 2003. Quantitative genetics of plant tolerance and resistance against natural enemies of two natural populations of *Datura stramonium*. *Evol. Ecol. Res.* 5: 1049–1065.
- Fox, C. W. 1993. A quantitative genetic analysis of oviposition preference and larval performance on two hosts in the bruchid beetle, *Callosobruchus maculatus*. *Evolution* 47: 166–175.
- Fox, C. W. and T. A. Mousseau. 1996. Larval host plant affects fitness consequences of egg size variation in the seed beetle *Stator limbatus*. *Oecologia* 107: 541–548.
- Fox, C. W. and T. A. Mousseau. 1998. Maternal effects as adaptations for trans-generational phenotypic plasticity in insects. In T. A. Mousseau and C. W. Fox (eds.), *Maternal Effects as Adaptations*, pp. 159–177. Oxford University Press, New York.

- Fox, C. W., M. S. Thakar, and T. A. Mousseau. 1997. Egg size plasticity in a seed beetle: An adaptive maternal effect. *Am. Nat.* 149: 149–163.
- Frankino, W. A., B. J. Zwaan, D. L. Stern, and 1 other. 2005. Natural selection and developmental constraints in the evolution of allometries. *Science* 307: 718–720.
- Fry, J. D. 1996. The evolution of host specialization: Are trade-offs overrated? *Am. Nat.* 148: S84–S107.
- Fry, J. D. 2003. Detecting ecological trade-offs using selection experiments. *Ecology* 84: 1672–1678.
- Futuyma, D. J. 1997. *Evolutionary Biology*, 3rd ed. Sinauer Associates, Sunderland MA.
- Futuyma, D. J. 2008. Specialization, speciation, and radiation. In K. Tilmon (ed.), *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects*, pp. 36–150. University of California Press, Berkeley.
- Futuyma, D. J. and G. Moreno. 1988. The evolution of ecological specialization. *Ann. Rev. Ecol. Syst.* 19: 207–234.
- Futuyma, D. J. and T. E. Philippi. 1987. Genetic variation and covariation in response to host plants by *Alsophila pometaria* (Lepidoptera: Geometridae). *Evolution* 41: 269–279.
- Gadgil, M. and O. T. Solbrig. 1972. Concept of *r*-selection and *k*-selection—evidence from wild flowers and some theoretical considerations. *Am. Nat.* 106: 14–31.
- Gershenzon, J. and R. Croteau. 1992. Terpenoids. In G. A. Rosenthal and M. R. Berenbaum (eds.), *Herbivores: Their Interactions With Secondary Plant Metabolites*, 2nd ed., Vol. I. *The Chemical Participants*, pp. 165–219. Academic Press, San Diego.
- Gould, F. 1979. Rapid host range evolution in a population of the phytophagous mite *Tetranychus urticae* Koch. *Evolution* 33: 791–802.
- Hansen, T. F. and D. Houle. 2008. Measuring and comparing evolvability and constraint in multivariate characters. *J. Evol. Biol.* 21: 1201–1219.
- Heil, M., T. Delsinne, A. Hilpert, and 5 others. 2002. Reduced chemical defence in ant-plants? A critical re-evaluation of a widely accepted hypothesis. *Oikos* 99: 457–468.
- Hoekstra, H. E., K. E. Drumm, and M. W. Nachman. 2004. Ecological genetics of adaptive color polymorphism in pocket mice: Geographic variation in selected and neutral genes. *Evolution* 58: 1329–1341.
- Houle, D. 1991. Genetic covariance of fitness correlates—what genetic correlations are made of and why it matters. *Evolution* 45: 630–648.
- Hunt, G. 2007. Evolutionary divergence in directions of high phenotypic variance in the ostracode genus *Poseidonamicus*. *Evolution* 61: 1560–1576.
- James, A. C., J. Jakubczak, M. P. Riley, and 1 other. 1988. On the causes of monophagy in *Drosophila quinaria*. *Evolution* 42: 626–630.
- Kao, Y. Y., S. A. Harding, and C. J. Tsai. 2002. Differential expression of two distinct phenylalanine ammonia-lyase genes in condensed tannin-accumulating and lignifying cells of quaking aspen. *Plant. Physiol.* 130: 796–807.
- Karn, M. N. and L. S. Penrose. 1951. Birth weight and gestation time in relation to maternal age, parity and infant survival. *Ann. Eugenetic.* 16: 147–164.
- Karowe, D. N. 1990. Predicting host range evolution—colonization of *Coronilla varia* by *Colias philodice* (Lepidoptera, Pieridae). *Evolution* 44: 1637–1647.
- Keinanen, M., R. Julkunen-Tiitto, P. Mutikainen, and 3 others. 1999. Trade-offs in phenolic metabolism of silver birch: Effects of fertilization, defoliation, and genotype. *Ecology* 80: 1970–1986.
- Koricheva, J., H. Nykanen, and E. Gianoli. 2004. Meta-analysis of trade-offs among plant antiherbivore defenses: Are plants jacks-of-all-trades, masters of all? *Am. Nat.* 163: E64–E75.

- Lack, D. 1947. The significance of clutch size. *Ibis* 89: 302–352.
- Lande, R. and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- Laskar, D. D., M. Jourdes, A. M. Patten, and 3 others. 2006. The *Arabidopsis* cinnamoyl CoA reductase *irx4* mutant has a delayed but coherent (normal) program of lignification. *Plant J.* 48: 674–686.
- Liscombe, D. K., B. P. MacLeod, N. Loukanina, and 2 others. 2005. Evidence for the monophyletic evolution of benzyloquinoline alkaloid biosynthesis in angiosperms. *Phytochemistry* 66: 1374–1393.
- MacKenzie, A. 1996. A trade-off for host plant utilization in the black bean aphid, *Aphis fabae*. *Evolution* 50: 155–162.
- Malcolm, S. B. 1991. Cardenolide-mediated interactions between plants and herbivores. In G. A. Rosenthal and M. R. Berenbaum (eds.), *Herbivores: Their Interactions With Secondary Plant Metabolites*, 2nd ed., Vol. I: *The Chemical Participants*, pp. 251–296. Academic Press, San Diego.
- Marak, H. B., A. Biere, and J. M. M. Van Damme. 2003. Fitness costs of chemical defense in *Plantago lanceolata* L.: Effects of nutrient and competition stress. *Evolution* 57: 2519–2530.
- Marroig, G. and J. M. Cheverud. 2005. Size as a line of least evolutionary resistance: Diet and adaptive morphological radiation in new world monkeys. *Evolution* 59: 1128–1142.
- Martens, S. and A. Mithofer. 2005. Flavones and flavone synthases. *Phytochemistry* 66: 2399–2407.
- Mauricio, R. and M. D. Rausher. 1997. Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. *Evolution* 51: 1435–1444.
- McGuigan, K., A. V. Homrigh, and M. W. Blows. 2008. An evolutionary limit to male mating success. *Evolution* 62: 1528–1537.
- Messina, F. J. and C. W. Fox. 2001. Offspring size and number. In C. W. Fox, D. A. Roff, and D. J. Fairbairn (eds.), *Evolutionary Ecology: Concepts and Case Studies*, pp. 113–127. Oxford University Press, New York.
- Mole, S. 1994. Trade-offs and constraints in plant-herbivore defense theory: A life-history perspective. *Oikos* 71: 3–12.
- Mole, S. and A. J. Zera. 1993. Differential allocation of resources underlies the dispersal-reproduction trade-off in the wing-dimorphic cricket, *Gryllus rubens*. *Oecologia* 93: 121–127.
- Mole, S. and A. J. Zera. 1994. Differential resource consumption obviates a potential flight fecundity trade-off in the sand cricket (*Gryllus firmus*). *Func. Ecol.* 8: 573–580.
- Mooney, K. A., P. Jones, and A. A. Agrawal. 2008. Coexisting congeners: Demography, competition, and interactions with cardenolides for two milkweed-feeding aphids. *Oikos* 117: 450–458.
- Morris, W. F., M. B. Traw, and J. Bergelson. 2006. On testing for a tradeoff between constitutive and induced resistance. *Oikos* 112: 102–110.
- Núñez-Farfán, J., J. Fornoni, and P. L. Valverde. 2007. The evolution of resistance and tolerance to herbivores. *Ann. Rev. Ecol. Evol. Syst.* 38: 541–566.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.
- Pelser, P. B., H. de Vos, C. Theuring, and 3 others. 2005. Frequent gain and loss of pyrrolizidine alkaloids in the evolution of *Senecio* section *Jacobaea* (Asteraceae). *Phytochemistry* 66: 1285–1295.

- Pilson, D. 2000. The evolution of plant response to herbivory: Simultaneously considering resistance and tolerance in *Brassica rapa*. *Evol. Ecol.* 14: 457–489.
- Raberg, L., D. Sim, and A. F. Read. 2007. Disentangling genetic variation for resistance and tolerance to infectious diseases in animals. *Science* 318: 812–814.
- Rasmann, S., A. A. Agrawal, A. C. Erwin, and 1 other. 2009. Cardenolides, induced responses, and interactions between above and belowground herbivores in the milkweeds (*Asclepias* spp). *Ecology* 90: 2393–2404.
- Rausher, M. D. 1984. Tradeoffs in performance on different hosts: Evidence from within- and between-site variation in the beetle *Deloyala guttata*. *Evolution* 38: 582–595.
- Rausher, M. D. 1992. Natural selection and the evolution of plant-insect interactions. In B. D. Roitberg and M. B. Isman (eds.), *Insect Chemical Ecology: An Evolutionary Approach*, pp. 20–88. Chapman & Hall, New York.
- Reznick, D. 1985. Costs of reproduction: An evaluation of the empirical evidence. *Oikos* 44: 257–267.
- Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. In G. A. Rosenthal and D. H. Janzen (eds.), *Herbivores: Their Interaction With Secondary Plant Metabolites*, pp. 3–54. Academic Press, New York.
- Ricklefs, R. E. 1977. Evolution of reproductive strategies in birds—reproductive effort. *Am. Nat.* 111: 453–478.
- Roff, D. A. 2002. *Life History Evolution*. Sinauer Associates, Sunderland, MA.
- Rose, M. R. and B. Charlesworth. 1981. Genetics of life-history in *Drosophila melanogaster*. II. Exploratory selection experiments. *Genetics* 97: 187–196.
- Rudgers, J. A., S. Y. Strauss, and J. F. Wendel. 2004. Trade-offs among anti-herbivore resistance traits: Insights from Gossypieae (Malvaceae). *Am. J. Bot.* 91: 871–880.
- Scalliet, G., C. Lionnet, M. Le Behec, and 10 others. 2006. Role of petal-specific orcinol O-methyltransferases in the evolution of rose scent. *Plant Physiol.* 140: 18–29.
- Schluter, D. 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50: 1766–1774.
- Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection pressures and life-history trade-offs. *Proc. Roy. Soc. Lond. B* 246: 11–17.
- Schoonhoven, L., J. van Loon, and M. Dicke. 2005. *Insect-Plant Biology*, 2nd ed. Oxford University Press, New York.
- Shonle, I. and J. Bergelson. 2000. Evolutionary ecology of the tropane alkaloids of *Datura stramonium* L. (Solanaceae). *Evolution* 54: 778–788.
- Siemens, D. H. and T. Mitchell-Olds. 1998. Evolution of pest-induced defenses in *Brassica* plants: Tests of theory. *Ecology* 79: 632–646.
- Simms, E. L. 1992. Costs of plant resistance to herbivores. In R. S. Fritz and E. L. Simms (eds.), *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*, pp. 392–425. University of Chicago Press, Chicago.
- Simms, E. L. and M. D. Rausher. 1987. Costs and benefits of plant resistance to herbivory. *Am. Nat.* 130: 570–581.
- Simms, E. L. and M. D. Rausher. 1989. The evolution of resistance to herbivory in *Ipomoea purpurea*. II. Natural selection by insects and costs of resistance. *Evolution* 43: 573–585.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Steward, J. L. and K. H. Keeler. 1988. Are there trade-offs among antiherbivore defenses in *Ipomoea* (Convolvulaceae)? *Oikos* 53: 79–86.

- Stowe, K. A. 1998. Experimental evolution of resistance in *Brassica rapa*: Correlated response of tolerance in lines selected for glucosinolate content. *Evolution* 52: 703–712.
- Strauss, S. Y., J. A. Rudgers, J. A. Lau, and 1 other. 2002. Direct and ecological costs of resistance to herbivory. *Trends Ecol. Evol.* 17: 278–285.
- Strauss, S. Y., D. H. Siemens, M. B. Decher, and 1 other. 1999. Ecological costs of plant resistance to herbivores in the currency of pollination. *Evolution* 53: 1105–1113.
- Twigg, L. E. and L. V. Socha. 1996. Physical versus chemical defense mechanisms in toxic *Gastrolabium*. *Oecologia* 108: 21–28.
- Ueno, H., N. Fujiyama, I. Yao, and 2 others. 2003. Genetic architecture for normal and novel host-plant use in two local populations of the herbivorous ladybird beetle, *Epilachna pustulosa*. *J. Evol. Biol.* 16: 883–895.
- van der Meijden, E., M. Wijn, and H. J. Verkaar. 1988. Defense and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51: 355–363.
- Van Homrigh, A., M. Higgie, K. McGuigan, and 1 other. 2007. The depletion of genetic variance by sexual selection. *Curr. Biol.* 17: 528–532.
- van Noordwijk, A. J. and G. de Jong. 1986. Acquisition and allocation of resources—their influence on variation in life-history tactics. *Am. Nat.* 128: 137–142.
- Verhoeven, K. J. F., T. K. Vanhala, A. Biere, and 2 others. 2004. The genetic basis of adaptive population differentiation: A quantitative trait locus analysis of fitness traits in two wild barley populations from contrasting habitats. *Evolution* 58: 270–283.
- Via, S. and D. J. Hawthorne. 2002. The genetic architecture of ecological specialization: Correlated gene effects on host use and habitat choice in pea aphids. *Am. Nat.* 159: S76–S88.
- Via, S. and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39: 505–522.
- Walsh, B. and M. W. Blows. 2009. Abundant genetic variation + strong selection = multivariate genetic constraints: A geometric view of adaptation. *Ann. Rev. Ecol. Evol. Sys.* 40: 41–59.
- Weis, A. E. and W. L. Gorman. 1990. Measuring selection on reaction norms—an exploration of the *Eurosta-Solidago* system. *Evolution* 44: 820–831.
- Whittaker, R. H. and P. P. Feeny. 1971. Allelochemicals: Chemical interactions between species. *Science* 171: 757–770.
- Worley, A. C. and S. C. H. Barrett. 2000. Evolution of floral display in *Eichhornia paniculata* (Pontederiaceae): Direct and correlated responses to selection on flower size and number. *Evolution* 54: 1533–1545.
- Yano, S., J. Takabayashi, and A. Takafuji. 2001. Trade-offs in performance on different plants may not restrict the host plant range of the phytophagous mite, *Tetranychus urticae*. *Exp. Appl. Acarol.* 25: 371–381.
- Zangerl, A. R. and F. A. Bazzaz. 1992. Theory and pattern in plant defense allocation. In R. S. Fritz and E. L. Simms (eds.), *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*, pp. 363–391. University of Chicago Press, Chicago.
- Zangerl, A. R. and M. R. Berenbaum. 1997. Cost of chemically defending seeds: Furanocoumarins and *Pastinaca sativa*. *Am. Nat.* 150: 491–504.
- Zera, A. J. and L. G. Harshman. 2001. The physiology of life history trade-offs in animals. *Ann. Rev. Ecol. Syst.* 32: 95–126.