Freeman & Herron
pp 380-391

# EVOLUTIONARY ANALYSIS

FOURTH EDITION

Scott Freeman
*University of Washington*

Jon C. Herron
*University of Washington*


Upper Saddle River, NJ 07458

## Box 10.2 | Calculating phylogenetically independent contrasts

Here we use an example from Garland and Adoph (1994) to illustrate the calculation of independent contrasts from a phylogeny (see also: Felsenstein 1985; Martins and Garland 1991; Garland et al. 1999; Garland et al. 2005). Figure 10.16 shows the phylogeny we will use. It shows the relationships among polar bears, grizzly bears, and black bears, and gives the body mass and home range of each. We will calculate independent contrasts for both traits among the bears. The steps are as follows:

1. Calculate the contrasts for pairs of sibling species at the tips of the phylogeny. In our three-species tree, there is just one pair of sibling species in which both species reside at the tips: polar bears and grizzly bears. The polar bear–grizzly bear contrast for body mass is:

$$265 - 251 = 14$$

The polar bear–grizzly bear contrast for home range is:

$$116 - 83 = 33$$

2. Prune each contrasted pair from the tree, and estimate the trait values for their common ancestor by taking the weighted average of the descendants' phenotypes. When calculating the weighted average, weight each species by the reciprocal of the branch length leading to it from the common ancestor. In our example, we are pruning polar bears and grizzlies from the tree and estimating the body mass and home range of their common ancestor A. The branch lengths from A to its descendants are both two units long. Thus, the weighted average for body mass is:

$$\text{Body mass of species A} = \frac{\left(\frac{1}{2}\right)265 + \left(\frac{1}{2}\right)251}{\left(\frac{1}{2}\right) + \left(\frac{1}{2}\right)} = 258$$

The weighted average for home range is:

$$\text{Home range of species A} = \frac{\left(\frac{1}{2}\right)116 + \left(\frac{1}{2}\right)83}{\left(\frac{1}{2}\right) + \left(\frac{1}{2}\right)} = 99.5$$

3. Lengthen the branch leading to the common ancestor of each pruned pair by adding to it the product of the branch lengths from the common ancestor to its descendants, divided by their sum. In our example, we are lengthening the branch leading to species A. The new branch length is:

$$3 + \frac{2 \times 2}{2 + 2} = 4$$

## 10.5 Phenotypic Plasticity

Throughout much of this book, we treat phenotypes as though they were determined solely and immutably by genotypes. We know, however, that phenotypes are often strongly influenced by the environment as well. Chapter 9 included a section on estimating how much of the phenotypic variation among individuals is due to variation in genotypes and how much is due to variation in environments. Here, we focus on the interplay between genotype, environment, and phenotype.

Another way to say that an individual's phenotype is influenced by its environment is to say that its phenotype is plastic. When phenotypes are plastic, individuals with identical genotypes may have different phenotypes if they live in different environments. Phenotypic plasticity is itself a trait that can evolve, and it may or may not be adaptive. As with the other traits we have discussed, to demonstrate that an example of phenotypic plasticity is adaptive, we must first determine what it is for, then show that individuals who have it achieve higher fitness than individuals who lack it.

4. Continue down the tree calculating contrasts, estimating the phenotypes of the common ancestors, and lengthening the branches leading to the common ancestors. In our example, the only remaining contrast is between species A and black bears. We do not need to estimate the phenotype of species B, or lengthen the branch leading to it, because species B is at the root of our tree. The species A–black bear contrast for body mass is:

$$258 - 93 = 165$$

The species A–black bear contrast for home range is:

$$99.5 - 57 = 42.5$$

5. Divide each contrast by its standard deviation to yield the standardized contrasts. The standard deviation for a contrast is the square root of the sum of its (adjusted) branch lengths. The standard deviation for the polar bear–grizzly bear contrast is:

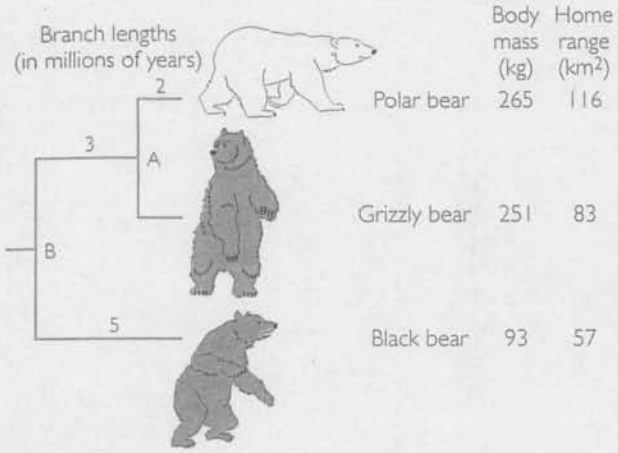
$$\sqrt{2 + 2} = 2$$

The standard deviation for the species A–black bear contrast is:

$$\sqrt{4 + 5} = 3$$

The standardized contrasts for our example are given in Figure 10.16.

Once we have calculated the standardized contrasts, we can use them to prepare a scatterplot and to perform traditional statistical tests.




| Contrast | Value for body mass | Standard deviation | Standardized contrast |
|---|---|---|---|
| Polar – Grizzly | 265 – 251 = 14 | 2 | 7 |
| A – Black bear | 258 – 93 = 165 | 3 | 55 |

| Contrast | Value for home range | Standard deviation | Standardized contrast |
|---|---|---|---|
| Polar – Grizzly | 116 – 83 = 33 | 2 | 16.5 |
| A – Black bear | 99.5 – 57 = 42.5 | 3 | 14.17 |

**Figure 10.16 An example showing how the data are adjusted when calculating phylogenetically independent contrasts** From Garland and Adolph (1994).

## Phenotypic Plasticity in the Behavior of Water Fleas

To illustrate phenotypic plasticity, we present the water flea, *Daphnia magna*. *Daphnia magna* is a tiny filter-feeding crustacean that lives in freshwater lakes (Figure 10.17). Conveniently for evolutionary biologists, *Daphnia* reproduce asexually most of the time. In other words, *Daphnia* clone themselves. This makes them ideal for studies of phenotypic plasticity, because researchers can grow genetically identical individuals in different environments and compare their phenotypes.

Luc De Meester (1996) studied phenotypic plasticity in *D. magna*'s phototactic behavior. An individual is positively phototactic if it swims toward light and negatively phototactic if it swims away from light. De Meester measured the phototactic behavior typical of different genotypes of *D. magna*. In each single test, De Meester placed 10 genetically identical individuals in a graduated cylinder, illuminated them from above, gave them time to adjust to the change in environment, then watched to see where in the column they swam. De Meester summarized the results by calculating an index of phototactic behavior. The

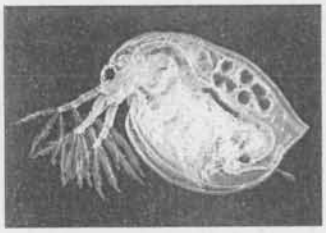


**Figure 10.17 A water flea, *Daphnia magna*** The branched appendages are antennae; the water flea uses them like oars for swimming. The dark object nearby is an eyespot. Also visible through the transparent carapace are the intestine and other internal organs. Enlarged about 10X.

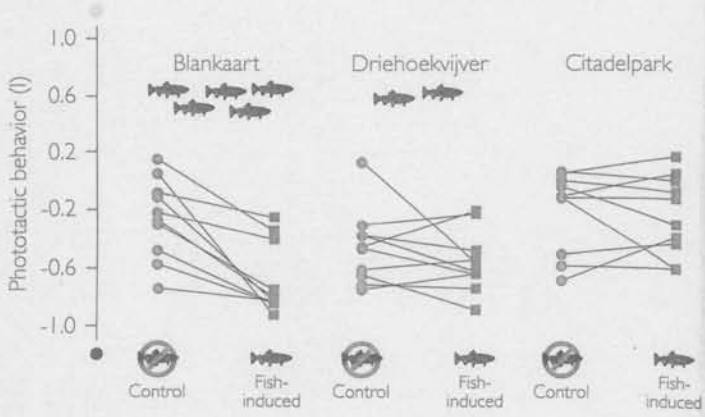



**Figure 10.18** **Variation in phototactic behavior in *Daphnia magna*** Blankaart, Driehoekvijver, and Citadelpark are three lakes in Belgium. Each red dot represents the average result from three to five tests of the phototactic behavior of a single genotype (described in main text). The connected blue square represents the average result from three or four tests of the phototactic behavior of the same genotype. The difference is that this time the *Daphnia* were tested in water that had previously been occupied by fish. Lake Blankaart is home to many fish; Lake Driehoekvijver has few fish; Lake Citadelpark has no fish. Redrawn from De Meester (1996).

index can range in value from −1 to +1. A value of −1 means that all the *Daphnia* in the test swam to the bottom of the column, away from the light. A value of +1 means that all the *Daphnia* in the test swam to the top of the column, toward the light. An intermediate value indicates a mixed result.

De Meester measured the phototactic behavior of 10 *Daphnia* genotypes (also called clones) from each of three lakes. The results, indicated by the red dots in Figure 10.18, show that most *Daphnia* tend somewhat to avoid light. They also show that each lake harbors considerable genetic variation in phototactic behavior.

*Genetically identical individuals reared in different environments may be different in form, physiology, or behavior. Such individuals demonstrate phenotypic plasticity.*

De Meester also measured the phototactic behavior of the same 30 *Daphnia* genotypes in water that had been previously occupied by fish. The results are indicated by the blue squares in Figure 10.18. The red dot and blue square for each genotype are connected by a line. These lines are called **reaction norms**; they show a genotype's change in phenotype across a range of environments. *Daphnia magna*'s phototactic behavior is phenotypically plastic. In Lake Blankaart, in particular, most *Daphnia* genotypes score considerably lower on the phototactic index when tested in the presence of chemicals released by fish.

Finally, and most importantly, De Meester's results demonstrate that phenotypic plasticity is a trait that can evolve. Recall that a trait can evolve in a population only if the population contains genetic variation for the trait. Each of the *Daphnia* populations De Meester studied contains genetic variation for phenotypic plasticity. That is, some genotypes in each population alter their behavior more than others in the presence versus the absence of fish (Figure 10.18). Genetic variation for phenotypic plasticity is called **genotype-by-environment interaction**.

Has phenotypic plasticity evolved in the *Daphnia* populations De Meester studied? It apparently has. The average genotype in Lake Blankaart shows considerably more phenotypic plasticity than the average genotype in either of the other lakes. Blankaart is the only one of the lakes with a sizeable population of fish. Fish are visual predators, and they eat *Daphnia*. A reasonable interpretation is that predation by fish selects in favor of *Daphnia* that avoid well-lit areas when fish are present.

Christophe Cousyn, De Meester, and colleagues (2001) tested this hypothesis by taking advantage of the fact that *Daphnia* produce resting eggs that remain viable even after being buried in sediment for decades. The researchers took sediment cores from Oud Heverlee Pond, a small man-made lake constructed in 1970. From sediments of three different depths, representing distinct episodes in the history of the pond, the researchers hatched *Daphnia* clones. Each set of clones is a sample from the population's past. The researchers measured the phototactic behavior of the reawakened genotypes in the presence and absence of chemicals released by fish.

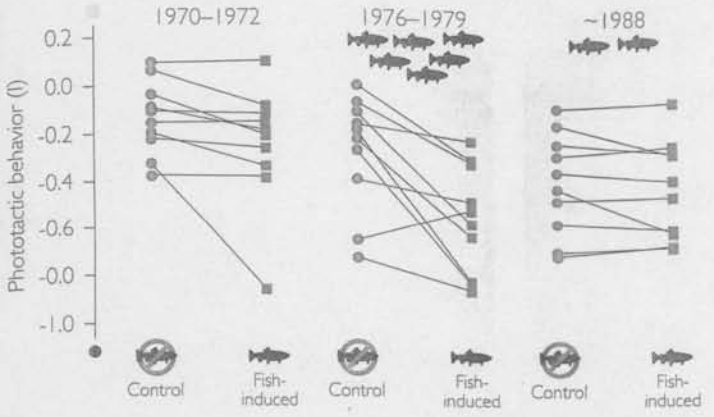



**Figure 10.19 Evolution of phototactic behavior in *Daphnia magna*** As in Figure 10.18, each pair of symbols connected by a line represents the phototactic behavior of a single genotype in the absence versus presence of chemicals released by fish. The three sets of genotypes come from samples of resting eggs produced during distinct episodes in the history of Oud Heverlee Pond. The earliest sample is from before the pond was stocked with plankivorous fish. The middle sample is from the period of heavy stocking. The last sample is from a period of reduced stocking. The degree of phenotypic plasticity shown by the population changed over time. Clones from the period of heavy stocking stay out of the light when they smell fish. Redrawn from Cousyn et al. (2001).

The people who built Oud Heverlee Pond began stocking it with planktivorous fish in 1973. They stocked it heavily until the mid-1980s, then less heavily through the late-1980s. Cousyn, De Meester, and colleagues predicted that the *Daphnia* population in the pond would have evolved in response to fish predation, and that genotypes preserved in resting resting eggs from the period of heavy stocking would show greater phenotypic plasticity in phototactic behavior than earlier or later genotypes.

The results appear in Figure 10.19. As predicted, the water flea population in Oud Heverlee changed over time. Clones from the period of heaviest fish stocking show the greatest shift in behavior in across environments. They stay out of the light when they smell predators.

Phenotypic plasticity is widespread, and perhaps underapprectiated as an adaptation. As Theodosius Dobzhansky pointed out in 1937 (page 170), "Selection deals not with the genotype as such, but with its dynamic properties, its reaction norm, which is the sole criterion of fitness in the struggle for existence."

*When there is genetic variation for the degree or pattern of phenotypic plasticity, plasticity itself can evolve. Plasticity is adaptive when it allows individuals to adjust their phenotype so as to increase their fitness in the particular environment in which they find themselves.*

## 10.6 Trade-Offs and Constraints

It is impossible for any population of organisms to evolve optimal solutions to all selective challenges at once. We have mentioned examples of trade-offs in passing. In Section 10.4, for example, we noted that large testes help bats win at sperm competition but appear to impose metabolic costs that lead to the evolution of smaller and less energetically demanding brains. In Chapter 3, page 92, we lamented the mosquito fish whose large gonopodium entices mates but slows his escape from predators. In this section, we explore additional factors that limit adaptive evolution. These include trade-offs, functional constraints, and lack of genetic variation.

*It is impossible to build a perfect organism. Organismal design reflects a compromise among competing demands.*

### Female Flower Size in a Begonia: A Trade-Off

The tropical plant *Begonia involucrata* is **monoecious**—that is, there are separate male and female flowers on the same plant. The flowers are pollinated by bees. As the bees travel among male flowers gathering pollen, they sometimes also transfer pollen from male flowers to female flowers. The male flowers offer the bees a reward, in the form of the pollen itself. The female flowers offer nothing; instead they get pollinated by deceit (Ågren and Schemske 1991). Not surprisingly, bees make more and longer visits to male flowers than to female flowers.

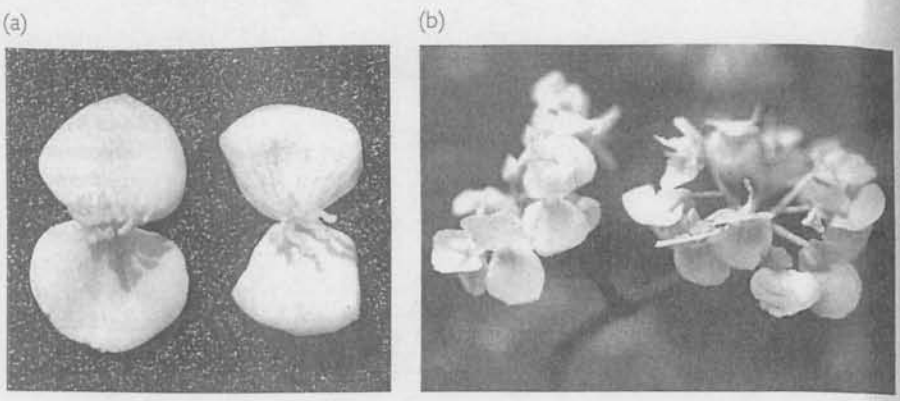



Figure 10.20 *Begonia involucrata* (a) Male (left) and female (right) flowers. The flowers lack true petals. Instead, each has a pair of petaloid sepals. The sepals are white or pinkish. In the center of each flower is a cluster of yellow anthers or stigmas. The stigmas of female flowers resemble the anthers of males. (b) An inflorescence, or stalk bearing many flowers. Each inflorescence makes both male and female flowers. Typically, the male flowers open first, and the female flowers open later. The inflorescence shown is unusual in having flowers of both sexes open at once.

The female flowers resemble the male flowers in color, shape, and size (Figure 10.20a). This resemblance is presumably adaptive. Given that bees avoid female flowers in favor of male flowers, the rate at which female flowers are visited should depend on how closely they mimic male flowers. The ability to attract pollinators should, in turn, influence fitness through female function, because seed set is limited by pollen availability. Presumption is not evidence, however. There are other possibilities. Doug Schemske and Jon Ågren (1995) sought to distinguish between two hypotheses about how bees might select on female flower size:

**Hypothesis 1:** The more closely female flowers mimic typical male flowers, the more often they will trick bees into visiting. Selection on female flowers is stabilizing, with best phenotype for females identical to the mean phenotype of males (Figure 10.21a, left).

**Hypothesis 2:** The more closely female flowers mimic the most rewarding male flowers, the more often they will succeed in duping bees. If larger male flowers offer bigger rewards, then selection on female flowers is directional, with bigger flowers always favored over smaller flowers (Figure 10.21a, right).

Schemske and Ågren made artificial flowers of three different sizes (Figure 10.21b), arrayed equal numbers of each in the forest, and watched to see how often bees approached and visited them. The results were clear: The larger the flower, the more bee approaches and visits it attracted (Figure 10.21c). Selection by bees on female flowers is strongly directional.

Taken at face value, Schemske and Ågren's results suggest that female flower size in *Begonia involucrata* is maladaptive. Selection by bees favors larger flowers, yet female flowers are no bigger than male flowers. Why are female flowers not huge? One solution to this paradox is that *B. involucrata* simply lacks genetic variation for female flowers that are substantially larger than male flowers. Schemske and Ågren have no direct evidence on this suggestion; *B. involucrata* is a perennial that takes a long time to reach sexual maturity, so quantitative genetic experiments are difficult to do.

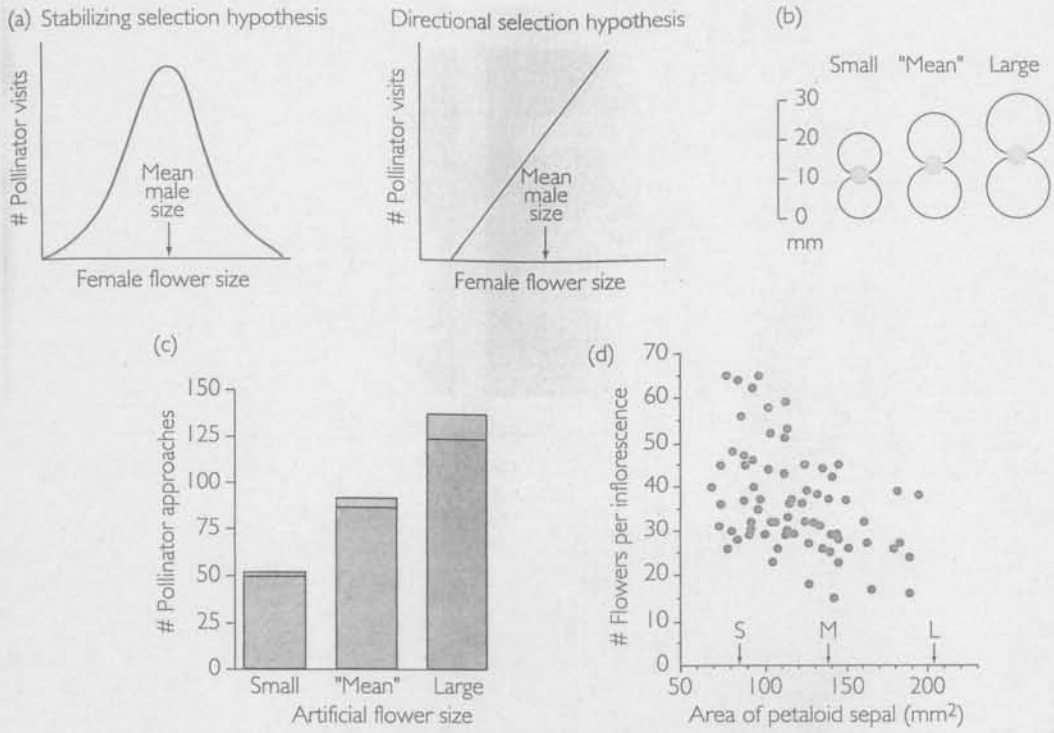



**Figure 10.21 An analysis of selection on female flower size in *Begonia involucrata*** (a) The two hypotheses investigated by Schemske and Ågren (1995). See text for more details. (b) Schemske and Ågren's three size classes of artificial flowers. The "mean" size class is the same size as the mean size of natural male flowers. (c) Pollinator preference as a function of flower size. The blue bars represent the number of bees that approached the artificial flowers; the brown bars represent the number of pollinators that actually visited the artificial flowers. Schemske and Ågren placed equal numbers of each size flower in the forest, but larger flowers attracted significantly more approaches and significantly more visits from bees. (d) Number of female flowers per inflorescence as a function of flower size. There is a statistically significant trade-off between flower size and flower number. From Schemske and Ågren (1995).

*Resources devoted to one body part or function may be resources stolen from another part or function.*

Another solution to the paradox is that focusing on individual female flowers gives us too narrow a view of selection. Schemske and Ågren expanded their focus from individual flowers to inflorescences (Figure 10.20b). The researchers measured the size and number of the female flowers on 74 inflorescences. They discovered a trade-off: The larger the female flowers on an inflorescence, the fewer flowers there are (Figure 10.21d). Such a trade-off makes intuitive sense. If an individual plant has a finite supply of energy and nutrients to invest in flowers, it can slice this pie into a few large pieces or many small pieces but not into many large pieces. Inflorescences with more flowers may be favored by selection for two reasons. First, bees may be more attracted to inflorescences with more flowers. Second, more female flowers mean greater potential seed production. Schemske and Ågren hypothesize that female flower size in *B. involucrata* has been determined, at least in part, by two opposing factors: directional selection for larger flower and the trade-off between flower size and number.

## Flower Color Change in a Fuchsia: A Constraint

*Fuchsia excorticata,* also known as the Kotukutuku, is a bird-pollinated tree endemic to New Zealand (Delph and Lively 1989). Its flowers hang downward like

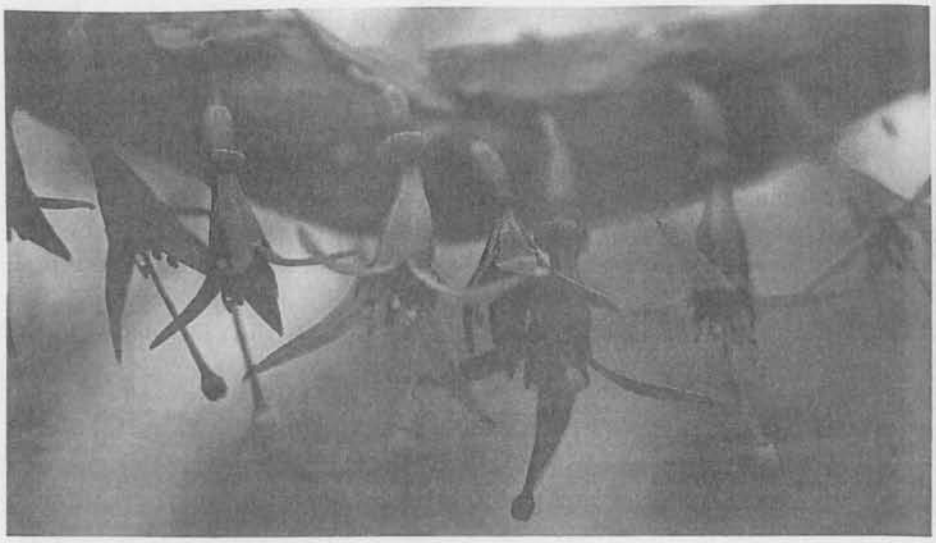


Figure 10.22 *Fuchsia excorticata* This bird-pollinated tree is native to New Zealand. Why do its flowers change color?

bells (Figure 10.22). The ovary is at the top (10.23a). The body of the bell consists of the hypanthium, or floral tube, and the sepals. The style resembles an elongated clapper. It is surrounded by shorter stamens and a set of reduced petals.

The hypanthium and sepals are the most conspicuously showy parts of the flower. They remain green for about 5.5 days after the flower opens, then begin to turn red (Figure 10.23b). The transition from green to red lasts about 1.5 days, at the end of which the hypanthium and sepals are fully red. The red flowers remain on the tree for about five days. The red flowers then separate from the ovary at the abscission zone and drop from the tree.

Pollination occurs during the green phase and into the intermediate phase, but it is complete by the time the flowers are fully red. The flowers produce nectar on days 1 through 7 (Figure 10.23b). Most flowers have exported more than 90% of their pollen by the end of that time. The stigmas are receptive to pollen at least until the second day of the fully red phase, but rarely does pollen arriving after the first day of the red phase actually fertilize eggs. Not surprisingly, bellbirds and other avian pollinators strongly prefer green flowers and virtually ignore nectarless red flowers (Delph and Lively 1985).

Why do the flowers of this tree change color? A general answer, supported by research in a variety of plants, is that color change serves as a cue to pollinators,

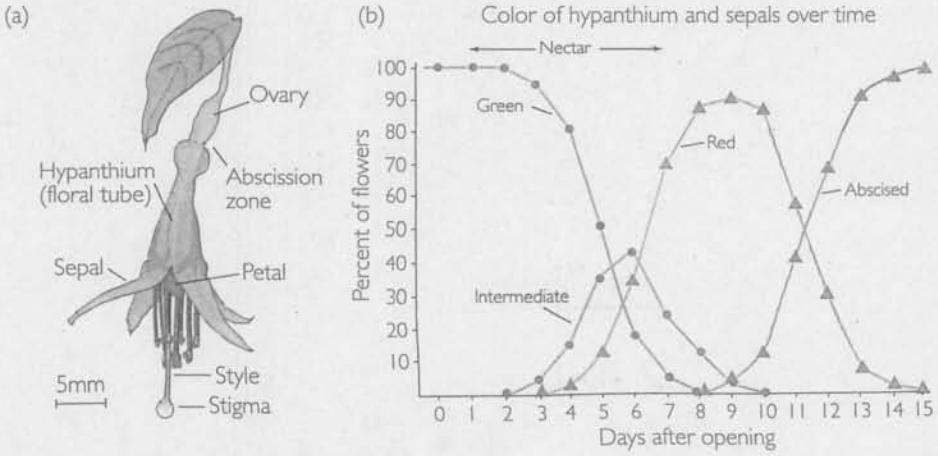



Figure 10.23 **Flower color change in *Fuchsia excorticata*** (a) A *Fuchsia excorticata* flower. (b) The horizontal axis shows flower age, in days after opening. The vertical axis and graph lines show the percentage of flowers that are in each color phase at each age. From Delph and Lively (1989).

alerting them that the flowers are no longer offering a reward (for a review see Delph and Lively 1989). By paying attention to this cue, pollinators can increase their foraging efficiency; they do not waste time looking for nonexistent rewards. Individual plants benefit in return, because when pollinators forage efficiently they also transfer pollen efficiently. They do not deposit viable pollen on unreceptive stigmas, and they do not deposit nonviable pollen on receptive stigmas.

This answer is only partially satisfying, however. Why does *F. excorticata* not just drop its flowers immediately after pollination is complete? Dropping the flowers would give an unambiguous signal to pollinators that a reward is no longer being offered, and it would be metabolically much cheaper than maintaining the red flowers for several days. Retention of the flowers beyond the time of pollination seems maladaptive.

Lynda Delph and Curtis Lively (1989) consider two hypotheses for why *F. excorticata* keeps its flowers (and changes them to red) instead of just dropping them. The first is that red flowers may still attract pollinators to the tree displaying them, if not to the red flowers themselves. Once drawn to the tree, pollinators could then forage on the green flowers still present. Thus, retention of the red flowers could increase the overall pollination efficiency of the individual tree retaining them. If this hypothesis is correct, then green flowers surrounded by red flowers should receive more pollen than green flowers not surrounded. Delph and Lively tested this prediction by removing red flowers from some trees but not from others, and from some branches within trees but not from others. The researchers then compared the amount of pollen deposited on green flowers in red-free trees and branches versus red-retaining trees and branches. They found no significant differences. The pollinator-attraction hypothesis does not explain the retention of the red flowers in *F. excorticata*.

The second hypothesis Delph and Lively consider is that a physiological constraint prevents *F. excorticata* from dropping its flowers any sooner than it does. This physiological constraint is the growth of pollen tubes. After a pollen grain lands on a stigma, the pollen germinates. The germinated pollen grain grows a tube down through the style to the ovary. The pollen grain's two sperm travel through this tube to the ovary, where one of the sperm fertilizes an egg. The growth of pollen tubes takes time, especially in a plant like *F. excorticata*, which has long styles. If the plant were to drop its flowers before the pollen tubes had time to reach the ovaries, the result would be the same as if the flowers had never been pollinated at all. Delph and Lively pollinated 40 flowers by hand. After 24 hours, they plucked 10 of the flowers, dissected them, and examined them under a microscope to see whether the pollen tubes had reached the ovary. After 48 hours, they plucked and dissected 10 more flowers, and so on. The results appear in Table 10.2. It takes about 3 days for the pollen tubes to reach the ovary.

*Traits or behaviors that would appear to be adaptive may, in fact, be physiologically or mechanically problematic.*

This result is consistent with the physiological constraint hypothesis. *F. excorticata* cannot start the process of dropping a flower until about 3 days after the flower is finished receiving pollen. Dropping a flower involves forming a structure called an abscission zone between the ovary and the flower (Figure 10.23a).

Table 10.2 Pollen tube growth in *Fuchsia excorticata*

| Days since pollination | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Percentage of 10 flowers with pollen tubes in ovary | **0** | **20%** | **100%** | **100%** |

*Source*: After Delph and Lively (1989).

The abscission zone consists of several layers of cells that form a division between the ovary and the flower. In *F. excorticata,* the growth of the abscission layer takes at least 1.5 days. The plant is therefore constrained to retain its flowers for at least 4.5 days after pollination ends. In fact, the plant retains its flowers for about 5 days. Delph and Lively suggest that flower color change in *F. excorticata* is an adaptation that evolved to compensate for the physiological constraints that necessitate flower retention. Given that the plant had to retain its flowers, selection favored individuals offering cues that allow their pollinators to distinguish the receptive versus unreceptive flowers on their branches. The pollinators deposit the incoming pollen onto receptive stigmas only, and they carry away only outgoing pollen that is viable.

## Host Shifts in an Herbivorous Beetle: Constrained by Lack of Genetic Variation?

In several previous chapters, we have made the point that genetic variation is the raw material for evolution by natural selection. Because natural selection is the process that produces adaptations, genetic variation is also the raw material from which adaptations are molded. Conversely, populations of organisms may be prevented from evolving particular adaptations simply because they lack the necessary genetic variation to do so.

Here is an extreme example: Pigs have not evolved the ability to fly. We can imagine that flying might well be adaptive for pigs. It would enable them to escape from predators and to travel farther in search of their favorite foods. Pigs do not fly, however, because the vertebrate developmental program lacks genetic variation for the growth of both a trotter and a wing from the same shoulder. Other vertebrates have evolved the ability to fly, of course. But in bats and in birds, the developmental program has been modified to convert the entire forelimb from a leg to a wing; in neither group does an entirely new limb sprout from the body. Too bad for pigs.

Pig flight makes a vivid example, but in the end it is a trivial one. The wished-for adaptation is too unrealistic. Douglas Futuyma and colleagues have sought to determine whether lack of genetic variation has constrained adaptation in a more realistic and meaningful example (Funk et al. 1995; Futuyma et al. 1995; references therein). Futuyma and colleagues studied host plant use by herbivorous leaf beetles in the genus *Ophraella*. Among these small beetles, each species feeds, as larvae and adults, on the leaves of one or a few closely related species of composites (plants in the sunflower family, the Asteraceae). Each species of host plant makes a unique mixture of toxic chemicals that serve as defenses against herbivores. For the beetles, the ability to live on a particular species of host plant is a complex adaptation that includes the ability to recognize the plant as an appropriate place to feed and lay eggs, as well as the ability to detoxify the plant's chemical defenses.

An estimate of the phylogeny for 12 species of leaf beetle appears in Figure 10.24. The figure also lists the host plant for each beetle species. The evolutionary history of the beetle genus has included several shifts from one host plant to another. Four of the host shifts were among relatively distantly related plant species: They involved switches from a plant in one tribe of the Asteraceae to a plant in another tribe. These shifts are indicated in the figure by changes in the shading of the phylogeny. Other shifts involved movement to a new host in the same genus as the ancestral host, or in a genus closely related to that of the ancestral host.

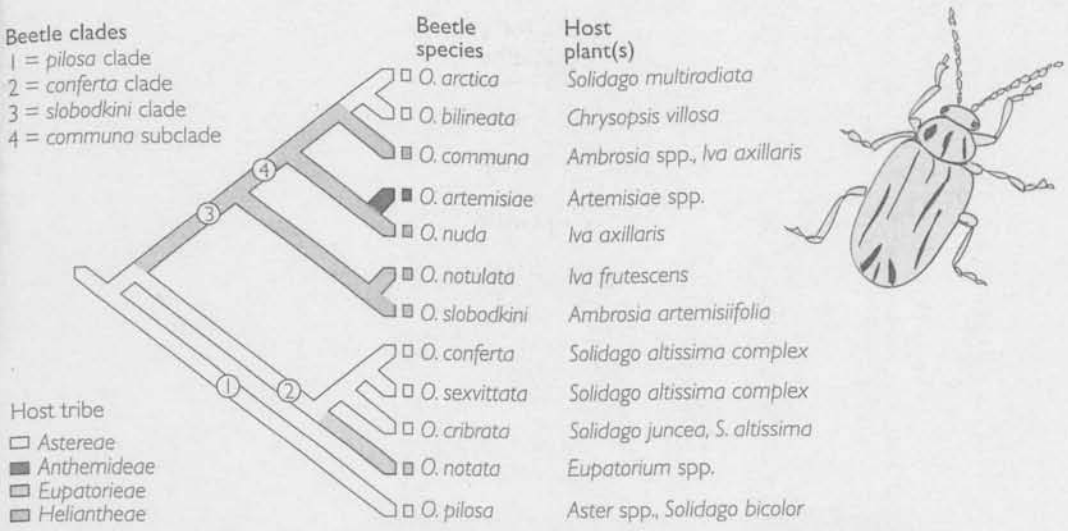



**Figure 10.24 Phylogeny of the leaf beetles, genus *Ophraella*** The numbers on the tree define the major branches (clades) of beetles. The shading of branches indicates the tribes of host species. The evolutionary history of the beetle genus has included four host shifts across tribes. From Futuyma et al. (1995).

Each combination of a beetle species and the host plant used by one of its relatives represents a plausible evolutionary scenario for a host shift that might have happened, but did not. For example, the beetle *Ophraella arctica* might have switched to the host *Iva axillaris*. Futuyma and colleagues have attempted to elucidate why some host shifts have actually happened while others have remained hypothetical. Here are two hypotheses:

**Hypothesis 1:** All host shifts are genetically possible. That is, every beetle species harbors sufficient genetic variation in its feeding and detoxifying mechanisms to allow at least some individuals to feed and survive on every potential host species. If a few individuals can feed and survive, they can be the founders for a new population of beetles that will evolve to become well-adapted to the new host. Because all host shifts are genetically possible, the pattern of actual host shifts has been determined by ecological factors and by chance. Ecological factors might include the abundance of the various host species within the geographic ranges of the beetle species, and the predators and competitors associated with each host species.

**Hypothesis 2:** Most host shifts are genetically impossible. That is, most beetle species lack sufficient genetic variation in their feeding and detoxifying mechanisms to allow any individuals to feed and survive on any but a few of the potential host species. The pattern of actual host shifts has been largely determined by what was genetically possible. Genetically possible host shifts have happened; genetically impossible host shifts have not.

We have presented these hypotheses as mutually exclusive. In fact, the truth is almost certainly that the actual pattern of host shifts has resulted from a mixture of genetic constraints, ecological factors, and chance. What Futuyma and colleagues were looking for was concrete evidence that genetic constraints have been at least part of the picture.

Futuyma and colleagues used a quantitative genetic approach (see Chapter 9) to determine how much genetic variation the beetles harbor for feeding and surviving on other potential hosts. The researchers examined various combinations

**Table 10.3** Summary of tests for genetic variation in larval or adult feeding on potential host plants

*(a) Tests for genetic variation in larval or adult feeding, by relationship among host plants*

| | Genetic variation? | |
|---|---|---|
| **Beetle tested for feeding on a plant that is . . .** | **Yes** | **No** |
| . . . in the same tribe as the beetle's actual host | 7 | 1 |
| . . . in a different tribe than the beetle's actual host | 14 | 17 |

Conclusion: Genetic variation for feeding is more likely to be found when a beetle is tested on a potential host that is closely related to its actual host.

*(b) Tests for genetic variation in larval or adult feeding, by relationship among beetles*

| | Genetic variation? | |
|---|---|---|
| **Beetle tested for feeding on a plant that is . . .** | **Yes** | **No** |
| . . . the host of a beetle in the same major clade | 12 | 4 |
| . . . the host of a beetle in a different major clade | 9 | 14 |

Conclusion: Genetic variation for feeding is more likely to be found when a beetle is tested on a potential host that is the actual host of a closely related beetle.

*Source*: From Table 7 in Futuyma et al. (1995).

of four of the beetle species listed in Figure 10.24 with six of the host plants. Their tests revealed that there is little genetic variation in most beetle species for feeding and surviving on most potential host species. In 18 of 39 tests of whether larvae or adults of a beetle species would recognize and feed on a potential host plant, the researchers found no evidence of genetic variation for feeding. In 14 of 16 tests of whether larvae could survive on a potential host plant, the researchers found no evidence of genetic variation for survival.

*Populations sometimes lack the genetic variation that would provide the raw material to evolve particular adaptations.*

These results suggest that hypothesis 2 is at least partially correct. Many otherwise-plausible host shifts appear to be genetically impossible. Futuyma and colleagues performed an additional test of hypothesis 2 by looking for patterns in their data on genetic variation for larval and adult feeding. If hypothesis 2 is correct, then a beetle species is more likely to show genetic variation for feeding on a potential new host if the new host is a close relative of the beetle's present host. Futuyma et al.'s data confirm this prediction (Table 10.3a). Likewise, if hypothesis 2 is correct, then a beetle species is more likely to show genetic variation for feeding on a potential new host if the new host is the actual host of one of the beetles' close relatives. Futuyma et al.'s data also confirm this prediction (Table 10.3b). Futuyma and colleagues conclude that hypothesis 2 is at least partially correct. The history of host shifts in the beetle genus *Ophraella* has been constrained by the availability of genetic variation for evolutionary change.

## Host Shifts in Feather Lice: Constrained by Dispersal Ability?

In the study we have just discussed, Futuyma and colleagues sought to show that host shifts are at least sometimes constrained by lack of genetic variation. The alternative explanations for why some host shifts have happened and others have not are ecological factors and chance. Dale Clayton and Kevin Johnson (2003) have identified a case in which host shifts appear to be constrained by an ecological factor.

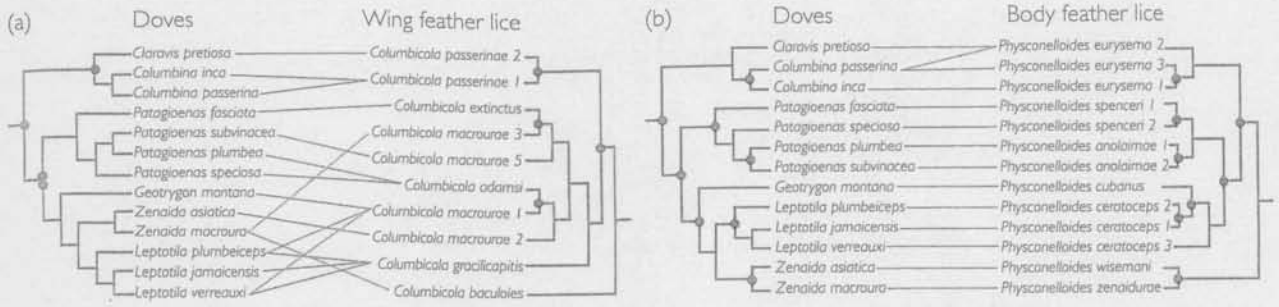



**Figure 10.25 Phylogenetic congruence and discord for doves and their feather lice** (a) The tree on the left is doves; the tree on the right is for their wing feather lice (genus *Columbicola*). Lines connect the parasite species to the bird species they infect. The many crossing lines indicate frequent host shifts in the evolutionary history of the lice. (b) The tree on the left is for doves; the tree on the right is for their body feather lice (genus *Physconelloides*). Lines connect the parasite species to the bird species they infect. The absence of crossing lines indicates that the lice have not changed hosts. Instead, they have gone along for the ride, splitting into new lineages when their hosts have. Redrawn from Clayton and Johnson (2003).

Clayton and Johnson analyzed the history of host shifts in the feather lice that infest doves. These ectoparasites include lice that live on wing feathers (genus *Columbicola*) and lice that live on body feathers (genus *Physconelloides*). Figure 10.25a compares the evolutionary trees for several dove species versus their wing feather lice. The phylogenies are not congruent, indicating that body feather lice have switched host species frequently. Figure 10.25b compares the evolutionary trees for the same dove species versus their body feather lice. This time the phylogenies are highly congruent, indicating that body feather lice have not switched host species. Instead, they have simply gone along for the ride, speciating only when their hosts have speciated.

Why have wing feather lice switched host species often while body feather lice have not? Experiments in which Clayton and colleagues (2003) transferred feather lice to novel hosts suggest that many host switches are genetically possible. Transplanted lice attach and feed on novel hosts. They can also evade the host's preening as long as their new host is similar in body size to their native host. Instead of being constrained by lack of variation for the ability to survive on novel hosts, Clayton and Johnson think that body feather lice simply have fewer chances to switch host species. This is because body feather lice disperse among individual hosts less readily than wing feather lice do. Field observations by Noah Whiteman and colleagues (2004) support this contention. These researchers looked for wing and body lice from Galápagos doves on Galápagos hawks. The two parasite species are equally common on doves, their native host, but on hawks dove wing lice are much more common than dove body lice.

One way feather lice move from one host to another is via direct bodily contact between the two birds. Another way is by hitching a ride on the legs of a parasitic hippoboscid fly, as shown in Figure 10.26. The flies are less host-specific than lice, so a stowaway louse may find itself deposited on a novel host. Published records suggest that wing feather lice hitch rides on flies much more often than body feather lice. Apparently the reason body feather lice have so rarely switched host species is that they could not get a lift.

In this section and the previous one we have examined complications of organismal form and function that must be taken into account when studying adaptation. In the next section, we consider another kind of complication that must sometimes be taken into account—a complication in the action of natural selection itself.

**Figure 10.26 Dispersal via a lousy fly** This drawing, based on a live example, shows three wing feather lice hitching a ride on the legs of a parasitic fly. After Clayton et al. (2004).