

Chapter 11

Ecological Speciation: When and How Variation Among Environments Can Drive Population Divergence



Pim Edelaar

Abstract Speciation is a complex process, in part because it can be caused by a multitude of different mechanisms. One aspect of speciation that has received much attention lately is the importance that variation among environments may play in driving speciation, i.e., ecological speciation. However, attention has been largely limited to the role of divergent natural selection as a consequence of such variation. Nonetheless, variation among environment may also result in flexible individual responses: phenotypic plasticity, adjustment of the environment, and selection of the environment (incl. habitat choice). Here I discuss and give examples of how these other consequences of variation among environments can generate ecology-driven speciation, including when they are interacting with each other or with natural selection. I propose that such a bottom-up approach to speciation may help us uncover neglected aspects of the speciation process, including when speciation may not occur.

Keywords Ecological speciation · Ecological performance · Local adaptation · Population divergence · Phenotypic plasticity · Habitat selection · Selection of the environment · Adjustment of the environment

11.1 Approaches Toward the Study of Speciation

The process of speciation is beautiful and awe inspiring. But it can also be bewildering and sometimes frustratingly complex. This is because speciation happens via many different routes. It can be the outcome of many different events and mechanisms that may play larger or smaller roles (see other chapters in this book), that may interact with one another in various ways, and all of this dynamically varying in space and time during the course of speciation. To some extent, speciation is

P. Edelaar (✉)
University Pablo de Olavide, Seville, Spain
e-mail: edelaar@upo.es

inevitable, and any given species will give rise to other species sooner or later in one way or another, unless it goes extinct before this happens.

In order to try to make some sense of this rather chaotic process, several means by which to categorize the diversity in speciation have been proposed. An important dimension that has been used a lot is that of geography, so classifying to what extent speciation happened in isolated distribution ranges or not (see chapter: Bird distributions and their evolution). Another important dimension to classify speciation events has been that of biological mechanism: natural selection (on ecological characters), sexual selection (on mating characters), and genetic drift (neutral divergence in ecological and/or mating characters) (Schluter 2000; Dieckmann et al. 2004; Nosil 2012). The relative importance of natural selection, sexual selection, or neutral events in driving speciation remains an active area of research.

Nonetheless, the emphasis has shifted more recently to yet another way to subdivide the drivers of speciation, restoring the historical focus on the interaction between the organism and its environment (Sobel et al. 2010). For example, a mating trait may diverge between speciating populations so sexual selection is involved. But is perhaps the divergence in the mating trait still caused by adaptation to the environment, similar to the case for naturally selected ecological traits? An example of this could be when a population lives in an environment with a different predator community, and therefore it evolves a sexual ornament that is rather inconspicuous toward their local predators yet still attractive to potential mates. In that case, the sexual ornament may become so different from other populations that individuals from our population are now unable to attract individuals from other populations as mates and speciation occurred. Hence, even though speciation was driven by sexual selection, the adaptation of the sexual ornament to the local environment is also an underlying component. In order to highlight this aspect, much recent research is addressing whether speciation is driven by ecology (adaptation to the environment) or not.

The importance of ecology for speciation, in birds or otherwise, has been recognized since the beginning of the study of speciation (reviewed in Nosil 2012; Sobel et al. 2010). It is probably involved in most cases of speciation one way or another (Sobel et al. 2010). Nonetheless, the term “ecological speciation” has been developed and proven useful in order to provide specific focus on the role of ecology in speciation. In his book on ecological speciation, Nosil (2012) defines ecological speciation as “the process, by which barriers to gene flow evolve between populations as a result of ecologically based divergent selection between environments.” In this chapter, I will broaden this term a bit, for reasons that I will explain below. I will consider speciation to be ecological, if variation among environments induces divergent selective pressures on populations which somehow results into reproductive barriers.

But before going into detail, we first need to consider another aspect of the speciation process, because this is relevant to how I will approach the topic. I already addressed that speciation is complex and potentially driven by many different elements in variable ways. However, it usually also takes relatively much time, so it is exceptional (and unheard of in birds) to witness it from start to finish.

(Independent of the difficulty of defining when it has finished, see chapter on species definitions.) This is why we often resort to dynamical interpretations of static patterns: “What mechanism and situation has likely caused this outcome?” Next, we do this for a number of populations at different stages along the speciation events and extrapolate these insights in order to recreate a continuum: “How does each stage likely combine into a full speciation event?” This creates a methodological/philosophical weakness in the study of speciation of birds: There has never been an application of the experimental approach to investigate speciation from beginning to end. Nonetheless, by comparing across many different systems and stages along the speciation process, progress has been made. For example, certain routes toward speciation can be judged to be unimportant in birds: Unlike in plants, speciation by hybridization or by genome duplication is rare if not absent in birds.

However, relying on this interpolating comparative approach also comes with risks. If we use patterns to infer processes, then we are using prior knowledge and beliefs to analyze and interpret the data at hand. This may cause us to see what we expect to see and to overlook certain alternative interpretations. Likewise, if we want to study particular elements of the speciation process, then we may pick study systems that a priori seem more suitable for this or that are more likely to include these elements. And this may cause us to confirm our initial knowledge or beliefs, and to overlook systems, in which completely different mechanisms are operating.

In this chapter, I will therefore continue the tradition of subdividing the speciation process into discrete categories, in this case applied only to ecological speciation. But I hope to do it in such a way that it promotes attention for drivers that are typically not taken into account when interpreting patterns or when selecting research questions/hypotheses and study systems, be it birds or other organisms. In a way, by approaching the topic of how birds interact with their environments (which could lead to speciation) in a logical manner and from the bottom up, the relevant research questions arise almost by themselves.

11.2 Four Ways to Increase Ecological Performance: Which May Each Drive Speciation

How well organisms interact with their environment is perhaps the most important aspect of life itself. Even if it is not the most poetic way of viewing things, most of what we see a bird doing in its everyday life ultimately serves only a single purpose: to leave as many descendants (including other relatives) as possible at the end of its life. For this, birds need to be good at what they do, for example, finding food or attracting mates. However, since the environment is not the same everywhere or all the time and there are so many other species with whom to interact (as food items, predators, diseases, etc.), there is no single constant solution to the challenge of being best in leaving descendants. Different environments require different

solutions. This is one of the reasons of why new bird species arise and therefore why there are so many of them.

So what types of solutions are open to birds in order to be as good as possible at what they do? One useful way of thinking about this is to realize that when a population with certain characteristics is faced with a certain set of environments (including other species), there are *only four distinct ways by which ecological performance may increase* (Edelaar et al. 2017) and therefore by which reproductive success may increase. The first and most well-known mechanism is *natural selection*, meaning that individuals with unfavorable characteristics have a larger probability to die and a smaller probability to reproduce. (I therefore include sexual selection—competition over fertilizations—under this mechanism, which is not unusual: Sexual selection is often seen as a subset of natural selection.) If the favored characteristics have a heritable basis, then natural selection is a great way to adapt populations to their local environments (e.g., next generations of a bird evolving a denser plumage in colder environments).

However, natural selection cannot improve the performance of locally maladapted individuals directly. Therefore, three other ways to improve performance may evolve to help such maladapted individuals, as individually flexible responses. While these other three ways have evolved due to past natural selection, it seems useful to distinguish them from natural selection, because the way they operate is completely different and their effects (once evolved) are independent of current natural selection. The first one is *phenotypic plasticity*, whereby individuals change their characteristics such that they have a better match to the local environment (e.g., if the environment is too cold, fluff up your feathers or grow a denser plumage). However, given that ecological performance depends on the interaction between individual traits and environmental characteristics, alternatively individuals *may also change their environment such that this provides a better match to their phenotype*. This can be done by actively *adjusting the local environment*, i.e., manipulating and improving aspects of the current environment (e.g., building a warmer nest in a colder environment). Finally, individuals could *select environments* that have a better match to their phenotype (e.g., an individual with a thinner plumage feeds in sunnier places or at lower latitudes or altitudes). As far as I can tell, these are the only four ways by which ecological performance can increase: Either the phenotype or the environment is adjusted and this happens either via selection or via some sort of development (of the phenotype or of the environment), yielding four combinations.

The next question (and the topic of this chapter) is then, if these four distinct ways of improving ecological performance might promote the evolution of new bird species? To address this question, I will discuss them one by one. I will not perform an exhaustive review of all the relevant literature (partly because I believe it to be incomplete and potentially biased); instead, I will just use some examples that serve to illustrate the points made.

11.3 Ecological Speciation Driven by Natural Selection

There are many ways by which natural (incl. sexual) selection can cause ecological speciation. Adapting to specific aspects of one environment (e.g., food resources) may change traits (morphology, physiology, behavior, and life history) of a local population. This can influence how successful individuals are, if they happen to move into the environment of another population: such immigrants may simply have a lower probability to survive. This is known as ecologically based selection against immigrants (Nosil 2012). Alternatively, if they do manage to survive and reproduce with a member of the other population, they may produce offspring which have traits with intermediate values which are not adjusted to any of the available environments. Such mixed-pair offspring may then also have a lower probability to survive or reproduce, i.e., ecologically based selection against hybrids. In either case, there is a certain barrier to the reproductive mixing of populations adapted to different environments, and this can initiate, drive, or complete the speciation process. Such naturally selected differences between populations are likely to evolve when inhabiting different geographic ranges (i.e., in allopatry) but can also evolve within a single range (i.e., in sympatry), e.g., when specializing on different food items.

A good, if not the best, example of the link between divergent natural selection and speciation in birds are Darwin's finches. One group of these, called the ground finches (genus *Geospiza*), mainly feed on seeds. These seeds have strong seed coats that need to be cracked with their bills. Since small bills are not strong enough to crack large seeds, but large bills are too clumsy to handle small seeds, natural selection has been found to act against individuals that have bills which are not suitable for the type of seeds on offer. These finches live on the Galápagos Islands, and, on some islands, certain types of seeds (e.g., larger ones) are more common, and, on other islands, other types (e.g., smaller ones) are more available (Schluter and Grant 1984). Hence, populations of the same species living on different islands sometimes have evolved different bill sizes, adjusted to the local seed types.

But how is this morphological, naturally selected divergence related to speciation? There are several ways how morphological divergence is implicated in preventing homogenization of populations. First, any immigrant with a bill type that doesn't fit the local food resources has a lower survival. But on several islands, there are actually multiple types of seeds available and therefore multiple populations of distinct ground finches that are specialized on each type. How do these populations keep apart? One important aspect is that the finches seem to distinguish individuals as being from one population or the other by their morphology and prefer to mate with individuals that are of the same population (Fig. 11.1, Grant and Grant 2008). This was shown in an experiment where stuffed birds were used to measure the reaction of live individuals. It turned out that the sizes of the body, head, and bill affect whether an individual is recognized as belonging to the



Fig. 11.1 Medium Ground Finches (*G. fortis*) on Daphne Island. (a) An offspring of large-billed immigrants that mated with each other and (b) a typical smaller-billed resident (adult male) that doesn't mate with large-billed immigrants (Photos by B. R. Grant, adapted from Grant and Grant (2008), by permission from the Royal Society)

same population, both for territorial and mating interactions (Ratcliffe and Grant 1983). Most likely this is because chicks imprint on the morphology of their parents and later in life prefer to interact and mate with individuals that resemble their parents (Grant and Grant 2008). This imprinting behavior can be a strong facilitator of reproductive barriers among populations with different morphologies. Imprinting also occurs for male song: sons copy their father's song and daughters prefer a father-like song (see chapter on Song learning). While songs may diverge little by little among isolated populations on different islands just by chance (neutral evolution), the production of sounds also seems to be related to bill traits. For example, a large and heavy bill is not able to produce a rapid trill (Podos 2001). This means that when natural selection causes a divergence in bill size between populations living on distinct islands, then songs will change as well and, if birds from these populations meet again, they may avoid mating with each other, because their songs have become too different. And finally, if in spite of these barriers they do happen to mate and produce offspring, such offspring will have bills with intermediate sizes for which few seeds are available and almost certainly they will not obtain enough food for survival and reproduction. Hence, natural selection is involved in ecologically based selection against immigrants and hybrids but also in the change of mating traits, both directly (size) and indirectly (song production). Without divergent natural selection, most of these reproductive barriers would not exist, and only slow and accidental song divergence in allopatric populations would remain. Moreover, if allopatric populations that were not exposed to divergent natural selection came into secondary contact, they would be ecologically identical and therefore unlikely to coexist for a long time. Therefore, if it weren't for ecological speciation caused by natural selection, the total number of Darwin's finches on the Galápagos Islands as a whole and on any island in particular would be much reduced. Environmental variation drives biodiversity.

Above I discussed how natural selection may act against immigrants and hybrids directly and how it may influence mating traits. But we should also consider how

ecology and selective pressures could affect the *expression* of mating traits. Many mating traits are not fixed (unlike Darwin finch size or song type) but depend on the ability of an individual to develop or maintain these traits. For example, individuals that have problems obtaining enough food may not be able to grow large or colorful plumage ornaments or produce a lot of song or the more difficult song notes. They may be more likely to lose fights when competing over matings or unable to impress their potential mates with behavioral displays or courtship feeding. Basically, their sexually selected traits are of lower quality. Hence, an immigrant or hybrid that is not adapted to the local environment could easily have a lower or even no reproductive success due to low-quality sexual traits and hence low sexual attractiveness, and in that way divergent selection leading to divergence in local ecological performance could further initiate, promote, or finalize the reproductive isolation among populations. This is because sexual selection and natural selection are acting in synergy and the total strength of divergent selection is increased, facilitating speciation (Van Doorn et al. 2009). Here, sexual selection is acting on mating traits, but these mating traits are actually representations of the degree of local adaptation of ecological traits. Indeed, mate preferences and condition-dependent sexual signals can even evolve because of their utility in avoiding mating with locally maladapted individuals, which would otherwise result in poorly adapted offspring, so sexual selection may arise, because it allows for adaptive ecological speciation (Van Doorn et al. 2009).

11.4 Ecological Speciation Driven by Phenotypic Plasticity

When individuals can adaptively change their phenotype, then to some extent, this may prevent natural selection from acting. This is because when locally maladapted individuals improve their ecological performance, natural selection has less variation in performance to act upon. And by reducing natural selection from acting, plasticity reduces the scope for genetic changes to build up between populations. If so, then while plasticity increases local ecological performance, it may decrease the probability of genetic population divergence and perhaps speciation (Price 2006).

Could plasticity also cause speciation? Let's do a thought experiment. Imagine a bird with an allopatric distribution, for example, with populations on a continent and on an isolated island and these populations look and behave very differently. They might therefore upon first sight be considered to be two different species. However, what if we were to translocate eggs from the island to the continent and vice versa and the chicks grew up to completely resemble their foster parent "species"? Would you still call them two species, if their difference completely depended on the environmental conditions during growth? And what if migrants would be so different that they would not succeed in mating? (I'll come back to those questions later.) There is not too much evidence that such a strong degree of plasticity is present in birds (in contrast to, e.g., plants or other sessile organisms), but it is possible that part

of the divergence we see, especially for subspecies or locally adapted populations, is actually due to adaptive phenotypic plasticity.

There is actually a very nice example of how phenotypic plasticity can drive speciation: the African indigobirds (genus *Vidua*). These small passerines are brood parasites that lay their eggs in the nests of several estrildid species (waxbills, munias, and allies), but each species of indigobird uses a different host species (Sorenson et al. 2003). Similar to other brood parasites like cuckoos (family Cuculidae) or cowbirds (genus *Molothrus*), chicks are reared by foster parents of another species. This presents an interesting problem: How do the chicks know later on in life with whom to mate? In most brood parasites, species recognition is a hard-wired genetic trait. So whichever host rears it, a Common Cuckoo (*Cuculus canorus*) recognizes another Common Cuckoo for what it is. But in the indigobirds, chicks imprint upon their foster species. This means that males, when adult, will sing songs like their foster species (see also chapter on song learning). And that females, when adult, prefer males that sing songs like their foster species as well as look for nests of this foster species to parasitize. Although it is rare, sometimes females lay eggs in the nest of another host species, perhaps as a mistake or because they can't find a suitable nest of their host species in time. But this rare event has very interesting consequences. Chicks that are reared by this atypical host will now sing like (males) and prefer songs of (females) their alternate host. This means that such wrongly placed chicks will now seek each other out for mating, i.e., mating is assortative for the species of host parent. This then implies that, if eggs are placed in several nests of a new host that wasn't used by indigobirds yet, then all of the resulting indigobird chicks will form a reproductively isolated population or in fact a new species.

Sounds farfetched? Actually, the data supports this scenario for speciation in indigobirds (Sorenson et al. 2003). Imprinting on the host species appears to be a relatively new trait in this genus, and once it evolved, it resulted in more than ten largely sympatric species (Fig. 11.2). The rate of speciation in this group is also much higher than that in their hosts, strongly suggesting that the imprinting is a driver of speciation. In fact, we could see this as an example of adaptive radiation

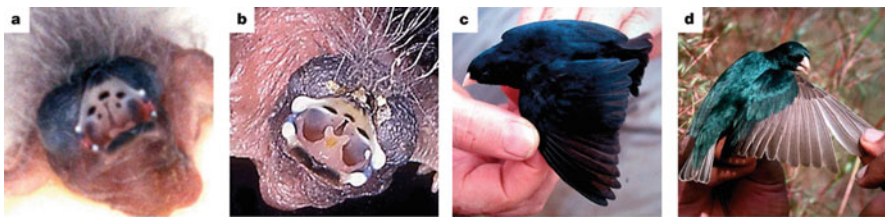


Fig. 11.2 The nestling mouth markings differ between (a) Cameroon Indigobird *Vidua camerunensis* and (b) Village Indigobird *V. chalybeata* to better mimic the young of their firefinch hosts, Black-bellied Firefinch *Lagonosticta rara* and Red-billed Firefinch *L. senegala*, respectively. Small differences between adult male (c) Village Indigobird *V. chalybeata* with dark plumage and wing and (d) Jambandu Indigobird *V. raricola* with greenish plumage and pale wing (Figure adapted from Sorenson et al. (2003), by permission from Nature Publishing Group)

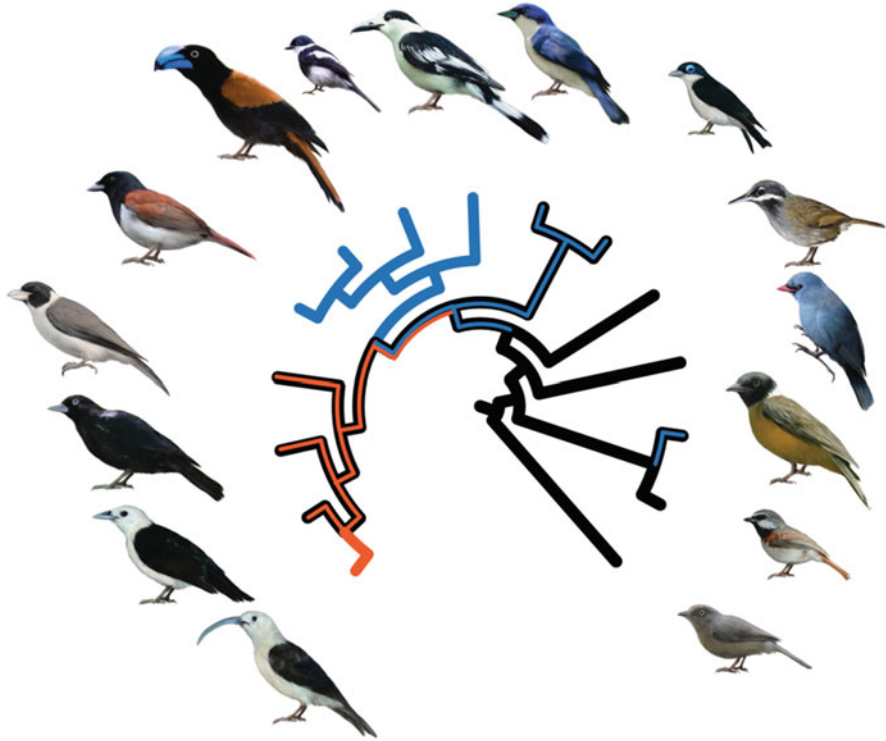


Fig. 11.3 Adaptive radiation is the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage (Schluter 2000). Depicted here are the Malagasy vangas (family Vangidae), their phylogenetic relations, and their foraging behavior (black gleaning, blue sallying, red probing). The vangas showed an explosive burst of speciation soon after colonization of Madagascar together with diversification into novel niches and the evolution of extraordinary ecomorphological diversity. However, over time the net rate of speciation declined, probably as the ecological opportunities became saturated. Adaptive radiations such as these show that the ecological conditions have a large effect on the final pattern of speciation. However, without additional information, it is not certain to what extent speciation is actually driven by ecology or whether ecological opportunity simply reduces the rate of extinction of species that evolved by other means. Other famous adaptive radiations in birds include the Darwin's finches from the Galápagos Islands, the honeycreepers from Hawaii, the crossbills from the northern hemisphere, or in fact the entire songbird clade after they managed to leave their area of origin, Australia (Figure from Reddy et al. 2012, by permission of the Royal Society)

(Fig. 11.3, Malagasy birds), where the key innovation of imprinting on the host allowed a rapid diversification to utilize a range of available resources (the different host species). While imprinting changes the phenotypes (male song as well as female host and song preferences) almost instantaneously via plasticity, adaptation via natural selection also does occur, because the indigobird chicks are reared alongside the chicks of the host and need to resemble host chicks in the markings of their mouth in order to be fed (Fig. 11.2). Hence, the assortative mating isn't just a by-product of imprinting: It actually is beneficial for females to prefer a male that

sings the song of the same host as the one she was reared by, because it means that both male and female were accepted by the same host and therefore had correct mouth markings and, assuming that this trait is heritable, these markings are then passed on to their offspring and increases the survival of their offspring.

If there exists an unutilized host species and we would experimentally place a large number of indigobird eggs in their nests, we could create a new species of indigobird within the time span of one generation (!). Nonetheless, this new species would be indistinguishable from the original species in morphological traits as well as genetically. Indeed, indigobird species are very similar to each other, since there is little need to look different (Fig. 11.2). Nonetheless, over time neutral genetic differences will build up gradually, and indeed the different indigobirds are genetically differentiated, even when sympatric, confirming the presence of reproductive isolation among them. Do you remember my hypothetical example presented earlier of two allopatric populations looking like different species due to plasticity only, yet that would not interbreed? Did you consider those to be different species? Well, one could argue that here we indeed have a case where reproductive isolation is greatly if not fully determined by phenotypic plasticity, if we consider that the host species is the environment with which the developing indigobird chick interacts in such a way that it changes its phenotype (the male songs and female preferences), yet where the different populations are formally considered to be distinct species (Sorenson et al. 2003).

The different host species are the different environments that cause phenotypic divergence and are the different resources that indigobird species specialize upon and allow them to coexist. So ecology is key in mechanistically driving speciation, even if divergent natural selection plays virtually no role, in support of my broader treatment of ecological speciation. However, not all cases of reproductive isolation between populations living in different environments that are due to plastic traits are support for this. The learning of song or the development of sexual preferences (song, morphology) and habitat preferences or other behaviors via imprinting is quite common among birds (see chapter Song and the example above on ecological speciation due to natural selection in Darwin's finches involving imprinting). Such learned differences in signals, preferences, and behaviors are often important reproductive barriers. But the important distinction to be made is why these learned traits have diverged between populations. In many cases, this may just be coincidental, neutral change, also known as cultural drift (similar to genetic drift), which would therefore not qualify as ecological speciation. In other cases, these learned traits may have been selected to enhance performance in local environmental settings, which would be ecological speciation due to natural selection (but acting on a nongenetically inherited trait). Only when individuals develop traits in response to their local environment which cause reproductive isolation could we think about ecological speciation driven by plasticity. Additional ways how plasticity may initiate speciation are discussed in more detail toward the end of this chapter in the section on feedbacks.

11.5 Ecological Speciation Driven by Adjustment of the Environment

Another way that birds could improve their local performance is by making adjustments to the local environment such that it matches better with their individual phenotypic characteristics. When confronted with ecologically divergent environments, this could result in divergence in the adjustments to the environment, and hypothetically this could lead to reproductive isolation among individuals making these adjustments. For example, if environmental aspects of male territories are adaptively adjusted to the specific phenotype of each male individual, then it is likely that females would prefer to settle and mate with males that have phenotypes similar to their own because of the favorable aspects of those males' territories, thereby creating positive assortative mating for phenotype.

However, as far as I know, it seems that adjusting the local environment is not a driver of speciation in birds. While it is possible that we just haven't recognized this route toward speciation for neglect of the mechanism, there may also be good reasons why this isn't the case (which then still helps us to understand nature). First, birds are among the most mobile of animals, and therefore any mismatch between phenotypes and environments is more likely to be resolved via selection of the environment (see next section) than via adjustment of the environment. The same is to some extent also true for phenotypic plasticity, which is much more pronounced in organisms with low mobility that are forced to deal with the local environment as it is. Second, environmental variation is often spatial, so if the individual that made the change to its local environment moves to another environment (e.g., an immigrant into an allopatric population), it is unable to take the adjustment with it and therefore the adjustment itself cannot play much of a role in reproductive isolation. This is in contrast to plasticity, where the change in the phenotype is much more likely to move and remain as a fixed part of the individual.

Even though birds are not expected to make many adjustments to their local environment, a conspicuous exception is the construction of nests, probably because eggs and altricial chicks do not move as easily as adult birds, yet are in need of a specific environment. However, I know of no data that show that the nest is adapted to (within-species) individual characteristics, e.g., that individuals with a lower capacity to brood chicks will build a warmer nest. Also, I know of no evidence that variation among nests (i.e., divergence in adjusted environments) causes reproductive isolation. This may be because it is unlikely that nest characteristics are going to affect the viability or reproductive success of immigrant individuals or their hybrid offspring. (Note that the decorated, sexually selected nest-like bowers of bowerbirds (family Ptilonorhynchidae) are not ways to increase ecological performance, so these are not relevant for our discussion on ecological speciation, but they do show that adjustment of the environment can matter for speciation.)

In conclusion, there is no evidence to date that adjusting the local environment in order to increase ecological performance plays a role in speciation in birds. It is possible that this is because of the specifics of the biology of birds. But in theory it could work, so keeping this possibility in mind might help us to uncover such cases.

11.6 Ecological Speciation Driven by Selection of the Environment

A particularly efficient and in fact ubiquitous way to increase ecological performance is to select the environment in which a phenotype has to perform: If an individual selects an environment that combines well with the phenotypic characters it already has (and cannot change via plasticity), then this improved phenotype-environment match can increase survival and/or reproduction (Edelaar et al. 2008, 2017), e.g., due to greater food uptake. Selection of the environment can vary from very small temporal and spatial scales to large ones. In the context of speciation, the largest effects are probably going to come from larger scale selection of the environment, since this provides longer-term, more consistent effects. Large-scale selection of the environment is better known as habitat choice, and this is rampant among birds: Any species of bird typically uses only a subset of the habitats available within its reach. For example, a swallow may be hawking for insects over forest canopy or a pond but will never be found searching the forest floor or dive to the bottom of the pond to look for insects. This is not because there are no insects to be found there—other birds do utilize this resource. It is in part because its phenotype (e.g., type of wings, legs, and bill) simply is not suitable to move around and capture prey in those habitats, even if it would try. Likewise, forest skulkers or diving birds also stick to their own habitats, because alternative habitats just do not combine well with their phenotypes. This habitat segregation reduces competition over the same resources and thereby allows for more species to occur in a certain area, i.e., species coexistence. Indeed, habitat is the commonest ecological difference between sympatric sister species in birds (Schluter 2000). Habitat segregation is one reason why structurally more diverse environments have a greater biodiversity, because one species cannot dominate all the resources available. But could habitat choice also drive speciation? For this we need to know when habitat selection evolves and to what extent it may create reproductive barriers.

Let us look at the last topic first. Two aspects of habitat choice seem to be important here: Being in different environments reduces the probability of simply meeting one another, and being in different environments may change how natural selection acts (on which traits and its strength and direction). The power of this first aspect should not be underestimated: If you never meet a potential partner, it will never become an actual partner. This is why allopatry can be such a powerful setting for speciation, because it already avoids the creation of mixed pairs just because of spatial constraints. But such spatial constraints can also be self-imposed, by habitat selection.

A good example of the capacity of habitat choice to drive speciation is found in the Red Crossbill *Loxia curvirostra*, a fascinating songbird occurring in many coniferous forests across the northern hemisphere. Perhaps the most striking aspect about this bird is that the tips of its mandibles are crossing (Fig. 11.4), which allows it to separate the scales of closed cones of coniferous trees and thereby to obtain the now unprotected seeds (Benkman and Lindholm 1991). However, depending on the species or variety of conifer, sizes and shapes of cones come in many ways, cone

scales may be thick and woody or thin and more paperlike, and even the sizes of seeds vary (Fig. 11.4). And this means that a single type of bill is simply not able to optimally exploit all this variation in this food resource. For example, a crossbill with a small and thin bill might be very efficient in prying out the small seeds from between the thin and weak scales of a small cone type but might be unable to separate the strong scales of a large cone with thick woody scales. In return, such a strong cone could be handled by a crossbill with a large and thick bill, but such a large bill would be quite clumsy and inefficient when dealing with small cones with thin scales and small seeds (Fig. 11.4). One might therefore expect that crossbills specialize even more, to feed on the seeds of only specific types of cones. And indeed, in those times of the year when food is scarce and foraging efficiency matters most, this is what happens (Benkman 1993). In North America, there are a number of conifers that hold their seeds in closed cones during the time of the year when food is scarce, and each of these conifers is used by crossbills which not only have the right bill size and shape to deal with these cones but also the appropriate internal bill structure to remove the cover from the seeds, given the size of the seeds (Fig. 11.4). This use of a particular conifer is a kind of selection of the environment, matching the type of cone to interact with the bill a crossbill has and cannot change (there is no plasticity in most bill traits). Of course, the resulting degree of phenotype-environment (bill-cone and seed) match will still affect food intake and therefore survival, i.e., natural selection is still expected to act. Indeed, in a resident population of crossbills where only a single type of conifer was available, it was found that natural selection acted on bill traits: Birds with bill traits that made them to obtain their food slower (known from observations in captivity) also had a lower survival rate in the wild (Benkman 2003).

This means that each type of cone will select for a specific type of crossbill that is able to feed on it. And this would easily lead to divergence among crossbills, if these conifers occurred in an allopatric setting, just as in the example with Darwin's finches on different islands. However, this is not quite the case—several different suitable conifers can be found in close vicinity of each other, including on the same mountain range (north and south slopes or at different altitudes) or even in large tracts of mixed forest. Moreover, since many conifers produce poor cone crops over large areas in some years, crossbills are highly mobile and may wander hundreds and even thousands of kilometers in search of suitable feeding areas, which brings them into contact with many different conifers. This means that the scope for mixing among diverging crossbill populations is very large. In such a setting, it seems unlikely that strong natural selection on bill traits could create divergence and speciation by itself. However, it would be naïve to assume that a crossbill would choose a type of conifer to feed upon randomly and that subsequently food intake affects survival (i.e., that natural selection acts). Of course we should consider that a crossbill can assess its food intake upon a particular cone type and, if it scores low, that the crossbill will move on in search of a better one. Several studies have shown that this occurs at a small scale: Predation on seeds of individual trees by crossbills is selective, and trees with “easy” cones are attacked most heavily (Benkman and Parchman 2009). However, it almost certainly also occurs at a large scale: The

different specialist crossbill populations are typically found in association with only a subset of conifers, including the type they specialize upon (Benkman 1993). And it must be very easy, and highly rewarding, for a crossbill in search of food to not stop and sample at every tree it encounters, but to recognize the species of conifer from kilometers away when flying above the forest canopy and to skip over patches of the type of conifers that it knows to be unsuitable from previous experience.

The best example of how such habitat choice drives speciation probably comes from a small area in the south of Idaho (Cassia County, USA). Here, on two nearby mountain tops, a resident population of crossbills is locally adapted to the local conifer: The crossbills have a larger bill in order to deal with the larger and more strongly defended cones (Fig. 11.4). However, the two mountains are part of the Rocky Mountains complex which also holds various other populations of crossbills (Fig. 11.4). And these other types of crossbills, when in search of food, do arrive in the area regularly and sometimes in large numbers. Therefore, mixed resident-immigrant breeding pairs could easily arise and erase the adaptive divergence in crossbills. Nonetheless, these mixed pairs are extremely rare, because when the breeding season starts, the immigrants have disappeared. Where have they gone? Have they all died? Indeed, it is known that the immigrant crossbills have bills that are not very suitable for feeding on the local cones (Fig. 11.4). However, given what I wrote above about choosing certain conifers and given the distances that these immigrant crossbills clearly can move, it seems likely that instead of accepting this low food intake rate as a given fact and let natural selection act on them (i.e., most immigrants will not reproduce or even starve to death), they instead choose to move on again and emigrate to other areas: selection of the environment acts. Although actual movements are very hard to quantify in this small bird, this inference is supported by the observation that, if the disappearance of immigrants was only due to selective mortality, it would be due to one of the strongest natural selection pressures measured to date (Benkman 2017). Hence, the more likely explanation, which corresponds with all we know about the biology and behavior of crossbills mentioned above, is that large-scale habitat choice is the main factor reducing the inflow of immigrant crossbills into this locally adapted crossbill population, as a kind of self-imposed allopatric setting (Edelaar and Bolnick 2012). The resulting reproductive isolation is so strong that the crossbills are not only morphologically diverged but also vocally and genetically distinct, and therefore this population has recently been described and accepted as a new species, the Cassia Crossbill *Loxia sinesciuris*.

In crossbills, large-scale selection of the environment therefore seems to be a strong contributor to speciation (see also Edelaar et al. 2012). However, selection of the environment can operate in multiple ways. For example, for the indigobird were I discussed plasticity as a driver for speciation, selection of the environment is also involved: Each species of indigobird chooses the nest of a different estrildid species for its chicks to grow up into, and this can be seen as a matching of the environment (the host type during rearing) to the phenotype (the pattern of mouth markings in chicks). Another way by which selection of the environment can drive speciation is by choosing not where but *when* to breed. Even when individuals occur and breed in

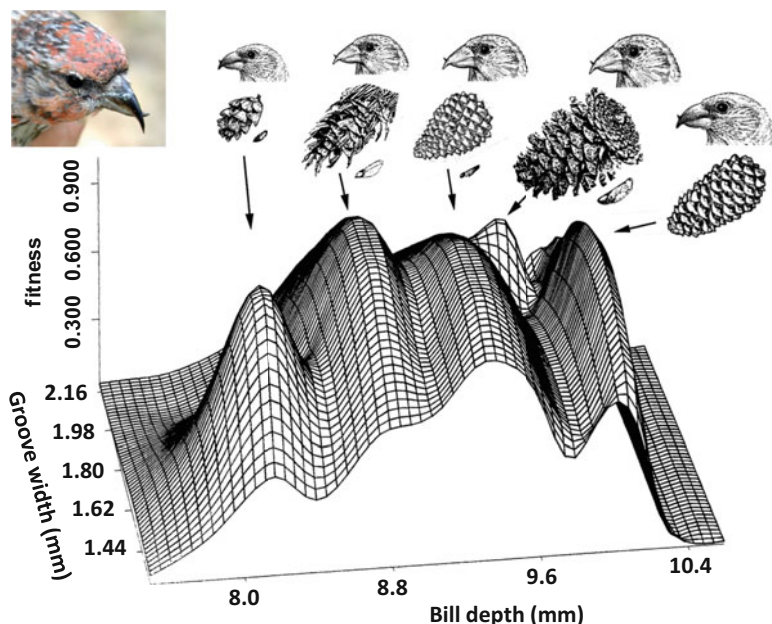


Fig. 11.4 The top-left panel shows a young male Red Crossbill *Loxia curvirostra* with his crossing bill tips—an apparent maldeformation which in fact greatly increases his ability to separate the scales of conifer cones, giving access to its seeds. The main panel shows for five different types of conifers (cones and seeds depicted) how only specific combinations of bill traits (bill depth and groove width) give a high feeding success (here expressed as relative fitness). A deeper bill increases biting force but requires more energy and reduces handling ability of small seeds, whereas the width of the husking groove inside the bill must match with the size of the seed, in order to facilitate removal of the protective seed coat. Each type of conifer is therefore utilized by a specialized crossbill population which differs in bill traits and overall size from other crossbill populations (note the marked increase in size from left to right and the more subtle variation in bill shape). At times, these different crossbills can be found in the same areas (e.g., the Rocky Mountains), but the largest crossbill on the right is restricted to just two mountain tops in the south of Idaho, because only there the specific conifer it specializes upon occurs (Figure adapted from Benkman 2003, by permission from John Wiley and Sons)

the same area, if they are reproductively active at different times, then mating will be greatly reduced. A good example of this is storm petrels of genus *Oceanodroma*. It was known that on a few islands on the Madeiran archipelago in the Atlantic, storm petrels bred twice a year: once during the hot season and once during the cool season. Only recently (Friesen et al. 2007) was it determined that these are actually not the same individuals: One petrel always breeds at the same time of the year and its chicks also breed at that time. In fact, it turned out that the timing is so conservative, that morphological and genetic differences are apparent between the two populations, and that they behave as two reproductively isolated species, resulting in the description of Monteiro's Storm Petrel (*O. monteiroi*). This new species overlaps fully in geographic distribution with the previously known Band-

rumped Storm Petrel (*O. castro*) but differs in its selection of the time of year when to breed. This selection of time is probably not a neutral trait, since the species differ in size (including the bill) and appear to have different diets even when co-occurring (Bolton et al. 2008), so presumably Monteiro's Storm Petrel has a higher performance when breeding during the hot season and selection of the breeding period is likely adaptive.

In general, when individuals are confronted with a variety of environments, preferring some environments over others can give important benefits. Selection of the environment (incl. habitat choice) is therefore expected to evolve easily and to be common. There are various ways by which this can lead to reproductive isolation, as illustrated above. Yet it is insufficiently recognized that individual flexibility in selection of the environment can be an independent contributor to speciation. This is especially true for allopatric populations living in different environments, where it is unclear how members of each population would respond to alternate environments (Sobel et al. 2010). Where and when to become reproductively active are among the first steps in the chain of reproductive events, prior to mate choice or hybrid performance. It is thus likely that individual-level selection of the environment in space and time could contribute a lot to reproductive isolation (in the past or currently) and more attention should be paid to this.

11.7 Feedbacks Between Plasticity, Adjusting the Environment, Selection of the Environment, and Natural Selection

In the introduction, I already highlighted the often complex nature of speciation and that it can be the outcome of many different events and mechanisms that may interact with one another in various ways in space and time. Indeed, while above I discussed how the three different types of individual flexible responses to environmental variation could directly affect reproductive isolation, these responses often do not operate independently of each other. Nor do they operate independently of natural selection. On the one hand, they have evolved due to prior natural selection, which favored the evolution of solutions for locally maladapted individuals which allowed them to increase their ecological performance and thereby avoid natural selection. But on the other hand, these individual responses influence the continued operation of natural selection.

I already mentioned that plasticity can reduce natural selection, since maladaptation is reduced by plasticity. The same is of course also true for the other two individual responses (adjustment of the environment and selection of the environment). This individual flexibility to enhance ecological performance could reduce or even remove natural selection and thereby prevent adaptive genetic divergence of

populations, which could reduce the probability of speciation. But this flexibility should also increase the probability to survive in a new environment. It may therefore increase the probability that a population manages to establish and survive when exposed to a new environment, e.g., after a natural range expansion, when accidentally blown to an oceanic island, when introduced by humans to a new geographical range (biological invasion), after dramatic change in the landscape (e.g., natural disasters, urbanization), and so on. In such populations that are exposed to a different environment and initially survive due to flexible individual responses, subsequent heritable changes due to natural selection could still occur. This then could cause populations to further diverge and potentially speciate. If so, then one could argue that it was the individual ability to change phenotypes or environments which allowed populations to speciate and therefore that this has been a key element of the final outcome.

These subsequent heritable changes that increase reproductive isolation could act on the same traits as the individual flexible response. For example, plasticity or habitat choice might become genetically fixed (genetic accommodation) and even evolve to values beyond those reached by individual flexibility. Upon secondary contact, such large and fixed differences between population might then be sufficient to keep them reproductively isolated, e.g., because one population occurs in the tree tops of coniferous forest and the other in the undergrowth of deciduous forest. But the heritable changes may also involve other traits, whose selective regimes have changed, because the individual flexible responses have changed the selective settings. For example, a population that shifted to use the caterpillars found in the tree tops of coniferous forest may subsequently evolve a range of additional traits that further increase ecological performance: shorter legs with stronger feet, long bills to probe between needles, improved physiology to digest caterpillars and to neutralize chemicals produced by conifers, breeding later in the year when caterpillars are most abundant, and so on. This is not only expected based on logic: Of course we have many examples of coadapted traits in birds. For example, woodpeckers have strong feet with curved nails to cling to bark, strong tail feathers to lean against trunks, a pointy bill to hammer into wood, a specialized skull that absorbs the hard blows which would cause brain damage in any other bird, an extra-long tongue with a harpoon-like tip to extract larvae from their tunnels and they climb along tree trunks and thick branches, hammer dead or damaged wood, hammer nesting cavities inside tree trunks, and so on. These morphological and behavioral traits work well together but would work poorly when combined with traits of other species (e.g., duck-like feet on a woodpecker). Therefore, any individual flexible response in a trait, be it via plasticity or environmental changes, could trigger the evolutionary change in other morphological, physiological or behavioral traits that on the one hand further increase ecological performance but on the other hand might also increase reproductive isolation from other populations. Indeed, the more traits that are different between populations, the greater the probability of a single or combined effect of traits on preventing hybridization (Nosil 2012).

In that context, and given their importance for reproductive isolation, it is worth stressing that mating traits might also secondarily change in response to the change

in a first trait. This is because mating traits by definition always involve the interaction between at least two individuals and therefore they do not operate in isolation: There is a signaler and a receiver. We could divide this interaction into three steps: The expression (emission) of mating traits depends on the phenotype of the signaler, the transmission of mating traits may depend on the environment of the signaler and the receiver, and the reception depends again on the phenotype of the receiver. Therefore any change in phenotype or environment could influence the success of a mating trait. Assuming that mating traits are generally initially successful, these changes probably cause a decrease in reproductive success, and therefore sexual selection will favor traits that respond appropriately to these changes in phenotype or environment, independent of whether they were caused by plasticity, adjustment of the environment, selection of the environment, or natural selection.

There are several examples of how mating traits are influenced by phenotypic or environmental variation, which could cause reproductive isolation. Starting from the emitting individual's perspective, I already discussed how bill size might affect the ability of Darwin's finches to produce certain vocalizations. This is also found in other bird groups, e.g., antbirds (family *Thamnophilidae*; Seddon 2005) and woodcreepers (in family *Furnariidae*; Palacios and Tubaro 2000). The same is true for body size: Just like humans or musical instruments, smaller birds generally produce higher-pitched vocalizations (Seddon 2005). So two populations that evolved different body or bill sizes may subsequently produce songs that are so different that they are not recognized anymore by the other population. Such changes in song might also evolve due to differences in environments, affecting transmission. Sound travels differently through open space than through densely vegetated areas, e.g., low-frequency sounds travel best through dense foliage, and songs containing short notes repeated at longer intervals are less affected by reverberations caused by leaves. In order to have a song reach the intended audience, birds may therefore change the volume of their song, the pitch of their notes, the degree of modulation (pitch variation) within each note, the spacing between notes, and so on depending on their habitat. Therefore, a shift in habitat choice could result in a shift in song characteristics, as, for example, observed in antbirds living at different heights above the ground in the forest (Seddon 2005) or in a set of bird species from the Amazon that are specialized in bamboo patches (Tobias et al. 2010). This change in song can be a flexible response at the individual level. For example, birds that live in noisy places like cities are known to change their songs such that they can still be heard by others. But it can also be a trait that is fixed in the population as in the antbirds (Seddon 2005). A shift in habitat can also be important for plumage characteristics (or any sexually selected trait). Sexual selection on plumage traits normally operates on the showy aspect: larger color patches, brighter colors, larger feathers, and so on. However, survival selection often operates against the expression of sexual ornaments, because they may attract predators or because they are very costly to produce or maintain, resulting in sexual ornamentation that is a balance between the two selective forces. Hence, depending on the color of the background and the amount and color of ambient light (e.g., open sky versus filtered light reaching the forest floor), selection may favor more or larger patches, at different positions, of

different colors, and so on. In leaf warblers (Phylloscopidae), species that live in darker forests generally have more pale patches in their plumage (Marchetti 1993). And a comparison across 20 pairs of closely related bird species found that species from more closed habitats (forests, etc.) generally had more orange and red colors in their plumage, because this is more visible in those habitats (McNaught and Owens 2002). Depending on the abundance of predators, food, or crucial nutrients, sexual ornaments may also change. For example, female House Finches *Haemorhous mexicanus* prefer intense red patches in males, but males need to be able to extract enough carotenoids from their food to produce such red feathers. Hence, when the environment is poorer in carotenoids, House Finch males concentrate their carotenoids into smaller intense red patches, instead of producing large but pale red patches. Environmental variation could even result in a shift in relative importance between plumage, vocalizations, or behavioral displays as sexual signals, which could cause diverged populations to not mate with each other anymore. For example, in finches, the more colorful species tend to sing less elaborate (Badyaev et al. 2002), and in general, nocturnal owls are very vocal but do not make much use of plumage or display behavior to attract the other sex or repel same-sex individuals. Finally, the traits of the receiver may also affect the evolution of sexual signals. For example, some families of birds (e.g., songbirds, parrots, and gulls) have evolved the capacity to see ultraviolet radiation (Horth 2007). Only in these groups would we expect to find sexual signals that involve the ability to reflect or absorb UV.

Overall then, the presence of feedbacks, especially toward natural selection, can magnify the impacts of initial flexible individual responses which increase ecological performance on population divergence and speciation. However, these flexible responses are expected to occur mainly initially during population divergence as they already operate at the individual level. If subsequently feedback into natural selection increases population divergence in the same and other (including mating) traits, then these initial changes due to flexible responses most likely leave little-to-no signature after the process. Hence, when we look at pairs of birds that have completed the speciation process, we may see large and fixed genetic difference between them (at the phenotypic level or at the genomic level) which strongly influence reproductive isolation. However, these final differences may cause us to overlook the initial differences that initiated the speciation process, and in some cases, these initial steps may simply not be visible anymore, e.g., due to genetic accommodation (i.e., the pattern misrepresents the process, as I suggested in the introduction). Hence, the capacity of individuals to flexibly and adaptively change their appearance or their local environment in response to local ecological settings may play a much more important role in the divergence and speciation of birds than we currently realize. However, it remains a methodological challenge to show this convincingly. But perhaps we should also be more receptive to the evidence when it presents itself. To a large extent, it is not sufficiently recognized that and how these individual flexible responses can drive speciation, so we may not even think about these alternative mechanisms when we look at a pattern (i.e., data from a certain study). By drawing attention to the existence of these flexible individual response to

improve ecological performance and their distinction from one another and from natural selection and by presenting real and hypothetical examples of how they may drive speciation, I hope that future studies will be in a better position to interpret patterns or to test specifically for their operation and their importance in the speciation process. Hopefully this makes the process of speciation less bewildering and complex but no less beautiful and awe inspiring.

References

- Badyaev AV, Hill GE, Weckworth BV (2002) Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in Finches. *Evolution* 56:412–419
- Benkman CW (1993) Adaptation to single resources and the evolution of Crossbill (*Loxia*) diversity. *Ecol Monogr* 63:305–325
- Benkman CW (2003) Divergent selection drives the adaptive radiation of Crossbills. *Evolution* 57:1176–1181
- Benkman CW (2017) Matching habitat choice in nomadic Crossbills appears most pronounced when food is most limiting. *Evolution* 71:778–785
- Benkman CW, Lindholm AK (1991) An experimental analysis of the advantages and evolution of a morphological novelty. *Nature* 349:519–520
- Benkman CW, Parchman TL (2009) Coevolution between Crossbills and black pine: the importance of competitors, forest area and resource stability. *J Evol Biol* 22:942–953
- Bolton M, Smith AL, Gomez-Diaz E, Friesen VL, Medeiros R, Bried J, Roscales JL, Furness RW (2008) Monteiro's Storm Petrel *Oceanodroma monteiroi*: a new species from the Azores. *Ibis* 150:717–727
- Dieckmann U, Doebeli M, Metz JAJ, Tautz D (2004) Adaptive speciation. Cambridge University Press, Cambridge
- Edelaar P, Bolnick DI (2012) Non-random gene flow: an underappreciated force in ecology and evolution. *Trends Ecol Evol* 27:659–665
- Edelaar P, Siepielski AM, Clobert J (2008) Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* 62:2462–2472
- Edelaar P, Alonso D, Lagerveld S, Senar JC, Björklund M (2012) Population differentiation and restricted gene flow in Spanish Crossbills: not isolation-by-distance but isolation-by-ecology. *J Evol Biol* 25:417–430
- Edelaar P, Jovani R, Gomez-Mestre I (2017) Should I change or should I go? Phenotypic plasticity and matching habitat choice in the adaptation to environmental heterogeneity. *Am Nat* 190:506–520
- Friesen VL, Smith AL, Gomez-Diaz E, Bolton M, Furness RW, Gonzalez-Solis J, Monteiro LR (2007) Sympatric speciation by allochrony in a seabird. *PNAS* 104(47):18589–18594
- Grant PR, Grant BR (2008) Pedigrees, assortative mating and speciation in Darwin's Finches. *Proc R Soc B* 275(1635):661–668
- Horth L (2007) Sensory genes and mate choice: evidence that duplications, mutations, and adaptive evolution alter variation in mating cue genes and their receptors. *Genomics* 90:159–175
- Marchetti K (1993) Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 362:149–152
- McNaught MK, Owens IPF (2002) Interspecific variation in plumage colour among birds: species recognition or light environment? *J Evol Biol* 15:505–514
- Nosil P (2012) Ecological speciation. Oxford University Press, Oxford

- Palacios MG, Tubaro PL (2000) Does beak size affect acoustic frequencies in woodcreepers? *Condor* 102:553–560
- Podos J (2001) Correlated evolution of morphology and vocal signal structure in Darwin's Finches. *Nature* 409:185–188
- Price TD (2006) Phenotypic plasticity, sexual selection and the evolution of colour patterns. *J Exp Biol* 209:2368–2376
- Ratcliffe LM, Grant PR (1983) Species recognition by Darwin's Finches (*Geospiza*, Gould). I. Discrimination by morphological cues. *Anim Behav* 31:1139–1153
- Reddy S, Driskell A, Rabosky DL, Hackett SJ, Schulenberg TS (2012) Diversification and the adaptive radiation of the vangas of Madagascar. *Proc R Soc B* 279:2062–2071
- Schluter D (2000) The ecology of adaptive radiation. Oxford University Press, Oxford
- Schluter D, Grant PR (1984) Determinants of morphological patterns in communities of Darwin's Finches. *Am Nat* 123:175–196
- Seddon N (2005) Ecological adaptation and species recognition drives vocal evolution in Neotropical suboscine birds. *Evolution* 59:200–215
- Sobel JM et al (2010) The biology of speciation. *Evolution* 64:295–315
- Sorenson MD, Sefc KM, Payne RB (2003) Speciation by host switch in brood parasitic Indigobirds. *Nature* 424:928–931
- Tobias JA, Aben J, Brumfield RT, Derryberry EP, Halfwerk W, Slabbekoorn H, Seddon N (2010) Song divergence by sensory drive in Amazonian birds. *Evolution* 64:2820–2839
- Van Doorn GS, Edelaar P, Weissing FJ (2009) On the origin of species by natural and sexual selection. *Science* 326:1704–1707

Open Access This chapter is licensed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license and indicate if changes were made.

The images or other third party material in this chapter are included in the chapter's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the chapter's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

