Bird song, ecology and speciation

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The study of bird song dialects was once considered the most promising approach for investigating the role of behaviour in reproductive divergence and speciation. However, after a series of studies yielding conflicting results, research in the field slowed significantly. Recent findings, on how ecological factors may lead to divergence in both song and morphology, necessitate a re-examination. We focus primarily on species with learned song, examine conflicting results in the literature and propose some potential new directions for future studies. We believe an integrative approach, including an examination of the role of ecology in divergent selection, is essential for gaining insight into the role of song in the evolution of assortative mating. Habitat-dependent selection on both song and fitness-related characteristics can lead to parallel divergence in these traits. Song may, therefore, provide females with acoustic cues to find males that are most fit for a particular habitat. In analysing the role of song learning in reproductive divergence, we focus on post-dispersal plasticity in a conceptual framework. We argue that song learning may initially constrain reproductive divergence, while in the later stages of population divergence it may promote speciation.

Keywords: assortative mating; dialects; ecological speciation; habitat-dependent selection; song learning

1. INTRODUCTION

Species-specific song plays a prominent role in mate selection, and can be an important isolating mechanism among bird species (Marler 1957, 1960; Lanyon 1969; Gill & Murray 1972; Searcy *et al.* 1981; Becker 1982; Payne 1986; Catchpole 1987; Grant & Grant 1996). In many instances song differences probably prevent hybridization among species that are fully capable of producing viable and fertile offspring (Prager & Wilson 1975; Grant & Grant 1997*a*; Baker & Boylan 1999). In addition to the role of song in mate selection at the species level, female mate preferences may also be influenced by intraspecific variation in song (figure 1). It has long been suggested that preferences for a local dialect may lead to reproductive divergence and potentially speciation (Marler & Tamura 1962; Nottebohm 1969; Baker 1975; Baptista 1975; Baker & Mewaldt 1978). However, an extensive search for assortative mating based on intraspecific acoustic variation has led to a large number of studies with conflicting results. Therefore, the role of bird song in speciation has remained controversial (e.g. Baker & Cunningham 1985*a,b*; Baptista 1985; Petrinovich 1985; Zink 1985).

Despite the controversy, recent studies on brood-parasitic birds have clearly shown that acoustic variation can catalyse reproductive divergence, and that song, in combination with parental imprinting, can play a crucial role in speciation. Female indigobirds, *Vidua chalybeata*, some-times lay their eggs in the nest of a different species of host from the ones by which they were raised. Male offspring learn the song of the new host species, and females imprint on the song of the new host. This combination of factors may therefore lead to a new reproductively isolated subpopulation (Klein & Payne 1998; Payne *et al.* 1998, 2000; ten Cate 2000). Although brood-parasitic birds form a rather exceptional example, this study nevertheless emphasizes that intraspecific variation in song can lead to reproductive isolation.

We review how geographical variation in song may affect gene flow through its influence on the ability of males to attract females or to establish and maintain a territory (e.g. Kroodsma *et al.* 1984; Baker & Cunningham 1985*a*). We argue that determining the role of song in speciation is complicated by a dichotomy that exists among studies that focus solely on assortative mating, and others that focus on ecological divergence and habitat-dependent selection pressures. Furthermore, an important consideration in interpreting the results of studies on assortative mating is that song dialects are learned and species may adjust their song after dispersal to a new breeding neighbourhood (reviews in Krebs & Kroodsma 1980; Kroodsma 1982; Baptista & Gaunt 1997; Payne & Payne 1997). We present a conceptual framework for the role of song learning in reproductive divergence, which attempts to show how learned song may constrain or promote speciation. Throughout, we focus predominantly on species that learn their songs and form dialects, although theoretical considerations about the role of ecology may also apply to species that do not depend on learning for the development of adult song.

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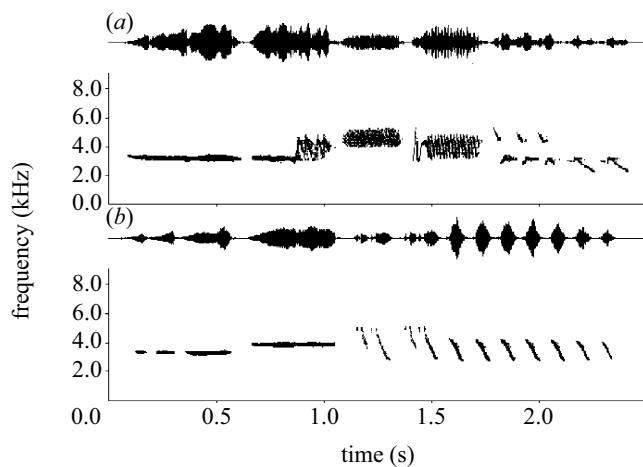493

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Figure 1. Acoustic divergence. Sonograms with amplitude–time wave form, illustrating an example of acoustic differences between male songs typical for two populations of white-crowned sparrows. These populations represent two different subspecies: (a) migratory *Zonotrichia leucophrys oriantha* (recorded in montane Colorado), and (b) sedentary *Z. l. nutalli* (recorded in coastal California).

2. SONG VARIATION AND GENE FLOW

(a) *Female preferences*

The impact of dialectal variation on female mate choice has been investigated using a wide variety of approaches. Mate preferences have been tested extensively in captivity by measuring the response of copulation–solicitation displays to standardized playback experiments. For example, in white-crowned sparrows, *Zonotrichia leucophrys*, females show stronger responses to local dialects (Baker *et al.* 1981; Baker 1982, 1983; Lampe & Baker 1994). However, other studies suggest that females that originate from a population in which available males sing a mixture of dialects (including song variation from different subspecies) show no consistent preferences. These results are interpreted to mean that females prefer familiar dialects, and consequently do not show a preference in a choice test if they have previous experience in the wild of both dialects (Chilton *et al.* 1990; Chilton & Lein 1996). Similarly, another study found that white-crowned sparrow females show a preference for the local dialect heard during their first year of life, but that this preference attenuates when exposed only to foreign dialect in their second year (MacDougall-Shackleton *et al.* 2001). Exposure to a mixture of dialects has not been tested in many species, but by using the female copulation–solicitation display, mate preferences for local dialect have been found for a few other species (e.g. yellowhammer, *Emberiza citrinella*: Baker *et al.* (1987); swamp sparrow, *Melospiza georgiana*: Balaban (1988*b*); song sparrow, *Melospiza melodia*: Searcy *et al.* (1997)).

A comparison of the songs of fathers and mates of females revealed no preferences for the father's dialect in corn buntings, *Miliaria calandra*. Here, females mated both within and outside their natal area (McGregor *et al.* 1988). However, in another study on the same species, females avoided males if they established a territory within a dialect area different from their own. Therefore, these males had a dramatically lower mating success compared

to their neighbours (Hegelbach 1986). In Darwin's finches, *Geopiza* spp., females tend to avoid choosing a mate of exactly the same song type as their father's, but they do prefer *similar* songs, which results in a preference for conspecific over heterospecific song (Millington & Price 1985; Grant & Grant 1996, 1997*b*).

Females can also be treated with testosterone to induce singing, which allows a comparison of their own song to the song of their mates. Tomback & Baker (1984) used this method to show that female white-crowned sparrows usually sang the same song as their mates. This suggests that females had mated assortatively, preferring male song that matched the song they had learned before meeting their mates. However, a number of other studies, using the same species and the same approach, found evidence for random mating, without consistent matching between females and mates (e.g. Petrinovich *et al.* 1981; Baptista & Morton 1982; Petrinovich & Baptista 1984).

(b) *Male responses to playback*

The response of territorial males to playback of dialectal variation has also been tested extensively. In general, territorial males respond most strongly to familiar dialects, followed by foreign dialects, and heterospecific song (e.g. white-crowned sparrow: Milligan & Verner (1971), Baker *et al.* (1981), Petrinovich & Patterson (1981); Darwin's finches: Ratcliffe & Grant (1985); swamp sparrow: Balaban (1988*b*); song sparrow: Searcy *et al.* (1997)). This may indicate that males may have more difficulty in establishing territories in areas with foreign dialects, thereby reducing gene flow among dialects (Baker *et al.* 1981; Baker 1982, 1983; Lampe & Baker 1994). Similarly, male song sparrows that share more songs with neighbours have been shown to be more successful in maintaining their territory (Beecher *et al.* 2000; Wilson *et al.* 2000).

An indirect method applied to investigate assortative mating is to analyse the geographical association of song with genetic characteristics. While some studies have found concordance in geographical patterns of acoustic and genetic variation (white-crowned sparrow: Baker (1982), Baker *et al.* (1982, 1984)), many others do not. In a variety of studies, dialects do not correspond with discrete genetic boundaries (rufous-collared sparrow, *Zonotrichia capensis*: Handford & Nottebohm (1976), Lougheed & Handford (1992), Lougheed *et al.* (1993); white-crowned sparrow: Zink & Barrowclough (1984), Hafner & Petersen (1985); brown-headed cowbird, *Molothrus ater*: Fleischer & Rothstein (1988); indigo bunting, *Passerina cyanea*: Payne & Westneat (1988); yellow-naped amazon, *Amazona auropalliata*: Wright & Wilkinson (2001)). In addition, one study found a correlation between song and genetic variation for some populations, but not for others (swamp sparrow; Balaban (1988*a*)).

The studies published after Baker and Cunningham's review in 1985 have not solved the controversy surrounding song and speciation. The search for assortative mating has led to conflicting results and limited new insights. Evidence for a link between acoustic variation and female preference varies with methodology and species. However, studies of male responses to acoustic variation give a more consistent picture, and suggest male exclusion may reduce gene flow. Studies that investigate geographical congru-

ence in acoustic and genetic variation yield some positive evidence, but seem to accumulate more negative results.

3. THE ROLE OF ECOLOGY

(a) *Divergence in song and morphology*

While the role of song in reproductive divergence remains controversial, relatively few species have been studied to date (cf. Slater 1985; West & King 1985), and still fewer examine how ecology and natural selection might be involved (cf. Nottebohm 1985). The latter is of particular importance for two reasons: (i) there is ample evidence for habitat-dependent selection leading to intraspecific divergence in vocalizations, and (ii) there is growing support for ecological gradients between different habitats being important in divergence and speciation (e.g. Endler 1977; Bush 1994; Smith *et al.* 1997; Orr & Smith 1998; Schluter 1998; Schilthuizen 2000).

We suggest that searching for assortative mating based on acoustic cues is far more likely to be successful if one includes populations that inhabit different habitats. Habitat-dependent selection potentially leads to predictable habitat-dependent acoustic characteristics and parallel divergence in song and habitat-dependent fitness. Habitats differ with respect to the density and type of vegetation, resulting in different selection pressures on acoustic signals as a consequence of the way in which sound attenuates and degrades as it penetrates the physical environment (e.g. Linskens *et al.* 1976; Marten & Marler 1977; Marten *et al.* 1977; Martens 1980; Endler 1992; Forrest 1994; Brown & Handford 1996, 2000). For example, lower frequencies transmit better in dense vegetation, which is associated with a lower average frequency used by forest species than species found in open habitats (Chappuis 1971; Morton 1975; Ryan & Brenowitz 1985). In addition, reflective layers in dense vegetation lead to reverberations, and, depending on the acoustic structure of a song, this may be detrimental (e.g. Richards & Wiley 1980; Wiley & Richards 1978, 1982; Wiley 1991; Dabelsteen *et al.* 1993; Holland *et al.* 1998) or beneficial to signal efficiency (Slabbekoorn *et al.* 2002). Yet, it is important to note that the function of a song should depend on reaching receivers over relatively long distances for sound transmission to play a role as a selection pressure. In addition to transmission differences, ambient noise levels and their spectral characteristics may show consistent differences among habitats (Slabbekoorn 2002). Consequently, different levels of competing noise may also lead to habitat-dependent divergent selection (Ryan & Brenowitz 1985; Slabbekoorn & Smith 2002).

Habitat-dependent selection on song characteristics may lead to acoustic similarity among populations living in the same habitat, and divergence among populations living in different habitats. Many studies on various species of birds have shown evidence for such intraspecific divergence correlated with the acoustic properties of the habitat (e.g. rufous-collared sparrow: Nottebohm (1975), Handford (1981, 1988), Handford & Lougheed (1991), Tubaro *et al.* (1993); white-throated sparrow, *Zonotrichia albicollis*: Wasserman (1979), Waas (1988); great tit, *Parus major*: Hunter & Krebs (1979); Carolina wren, *Thryothorus ludovicianus*: Gish & Morton (1981); summer tanager, *Piranga rubra*: Shy (1983); northern cardinal, *Cardinalis car-*

dinalis: Anderson & Conner (1985); song sparrow: Shy & Morton (1986); rufous-browed peppershrike, *Cyclarhis gujanensis*: Tubaro & Segura (1995); greenisch warbler, *Phylloscopus trochiloides*: Irwin (2000); blue tit, *Parus caeruleus*: Doutrelant & Lambrechts (2001), Doutrelant *et al.* (2001); little greenbul, *Andropadus virens*: Slabbekoorn & Smith (2002); but see Payne 1978; Williams & Slater 1992; Date & Lemon 1993; Doutrelant *et al.* 1999; Naguib *et al.* 2001). Furthermore, some interspecific studies have found evidence suggesting that closely related species have also diverged acoustically in a way that corresponds to the transmission properties of their respective habitats (*Acrocephalus* warblers: Jilka & Leisler (1974), Heuwinkel (1982); *Sylvia* warblers: Bergmann (1978); and Darwin's finches: Bowman (1979, 1983)).

The same habitats that drive song divergence, may also lead to divergence in morphological, life history, or behavioural traits (e.g. Endler 1977, 1986; Lougheed & Handford 1993; Smith *et al.* 1997; Lambrechts *et al.* 1997). If habitat-dependent selection is strong enough, divergence in a particular trait may evolve despite substantial gene flow (Slatkin 1987; Rice & Hostert 1993; Smith *et al.* 1997), and may affect male fitness depending on whether a male disperses within or between habitats. Habitat-dependent assortative mating based on song preferences may evolve due to female sexual imprinting on songs of her natal population (Laland 1994; Irwin & Price 1999; ten Cate & Vos 1999). Another mechanism that may promote assortative mating is the gain in fitness through female choice (Kirkpatrick 1985, 1996; Price *et al.* 1993; Price 1998); females could potentially exploit associations of habitat-dependent male fitness and habitat-dependent male song. Theoretical models suggest reproductive divergence may rapidly evolve in this scenario, with assortative mating based on a cue under divergent selection (Servedio & Kirkpatrick 1997; Servedio 2000).

(b) *Dialects and habitat-dependent selection*

Evidence for mate preference based on habitat-dependent song characteristics is scarce. Studies that focus on assortative mating and dialectal variation typically pay little attention to ecological factors, while studies that focus on song divergence related to habitat typically lack data on behavioural (or fitness) consequences. This dichotomy is further characterized by distinctive methodological approaches with respect to the measurement of acoustic characteristics. Studies investigating assortative mating and dialectal variation tend to examine song characteristics through visual inspection of sonograms, or more recently, on shape similarity using cross-correlation methods (e.g. Gaunt *et al.* 1994). This leads to acoustic characterization of songs with respect to features such as: syllable type, syllable or song type repertoire, and syntax (within or among song combinatorial variation). In contrast, studies examining habitat-dependent song divergence usually measure the acoustic structure of songs via a number of objective measurements. Typically, these involve spectral characteristics, such as maximum and minimum frequency, or the average frequency use; and temporal characteristics, such as the duration of the song, the number of sound units in the song (notes, elements, or syllables) or, derived from these, the delivery rate of sound units.
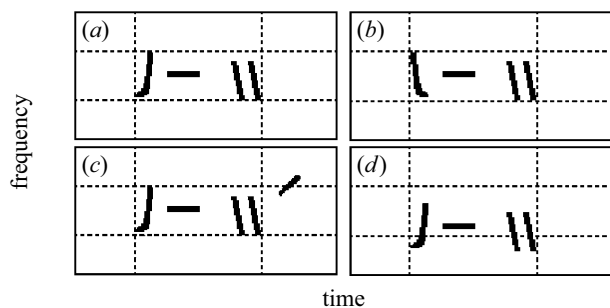
Figure 2. Dialects and acoustic variation. Each sonogram represents the song typically found in one population of a fictional bird species, and differences between two sonograms represent consistent differences between two populations. The vertical dashed lines indicate onset and offset of the song, and demarcate the song duration (DUR). The horizontal dashed lines indicate the maximum frequency (F_{max}) and the minimum frequency (F_{min}), demarcating the frequency range. The divergence between the population typically singing song (*a*) and the population typically singing song (*b*) concerns a divergence in dialect (different starting syllable), but not a divergence in temporal structure or frequency use. The divergence between (*a*) and (*c*) concerns dialectal divergence (additional new syllable), and divergence in the acoustic characteristics: DUR and F_{max}. Songs (*a*) and (*d*) do not show dialectal divergence, but do show divergence in the acoustic characteristics: F_{max} and F_{min}.

Few studies have simultaneously measured dialectal variation based on song type or syllable shape *and* spectral and temporal characteristics that may be affected by habitat-dependent selection. Baptista & Morton (1982) measured dialectal variation and a set of objective measurements on acoustic structure in their study of geographical variation in song of white-crowned sparrows. Their results showed significant differences between populations for both measures. Similarly, Anderson & Conner (1985) found differences in the two types of measurements among songs of different populations of the northern cardinal, both measurements showing a correlation with the vegetation type of the habitat. However, a different dialect does not automatically mean a difference in acoustic structure relevant in the context of habitat-dependent selection, and vice versa (figure 2). This is an important distinction. Many systems of dialects bear no relationship to the distribution of populations across different habitats. At the same time, populations may still show habitat-dependent divergence in acoustic structure (cf. Slabbekoorn & Smith 2002). Such habitat-dependent acoustic divergence may be minor compared to the overall pattern of acoustic variation among different dialects, but may provide an acoustic habitat-specific marker.

Irrespective of the measurements taken, most important is what is detected by the birds. The fact that females can perceive dialectal differences is clear, but are they also capable of perceiving subtle differences in frequency or delivery rate? Classic studies on species recognition, using male response in field playbacks, yield insight into a species' sensitivity to such acoustic variation (e.g. Falls 1963; Emlen 1972; Shiovitz & Lemon 1980; Nelson 1988). These studies show that modification of only one acoustic

parameter, such as a decrease in frequency to just outside the conspecific range, can lead to a significant decrease in response. Several other studies show that birds are remarkably sensitive to spectral and temporal detail in relatively complex song (e.g. Sinnott *et al.* 1980; Cynx *et al.* 1990; Hurly *et al.* 1992; Lohr & Dooling 1998). Artificial circumstances in tests with operant conditioning may overestimate sensitivity when findings are extrapolated to the field, but field playbacks also confirm that minute acoustic changes, close to the perceptual resolution of a species, may be meaningful to birds under natural conditions (Slabbekoorn & ten Cate 1998).

In an interesting study of acoustic features used for mate choice in captive zebra finches, *Taenopygia guttata*, Clayton (1990*a,b*) demonstrated that 'micro-structural' variation (i.e. syllable type) was most important for mate choice within subspecies, while 'macro-structural' variation (i.e. more general spectral and temporal characteristics) was most important for mate choice among subspecies. This study not only shows that females are able to perceive subtle differences in general acoustic characteristics, but also that they use it for discrimination. Furthermore, it suggests a hierarchical organization of acoustic cues, with divergence in general acoustic structure being more important than variation in, for example, actual syllable types in discriminating among males from reproductively isolated populations. Although in the wild the two zebra finch subspecies only occur in allopatry, this example clearly shows the importance of measuring the acoustic structure of different dialects in detail.

In sum, we believe that ecological studies are crucial for gaining insight into the role of song in divergence and speciation. In our view, future efforts should be directed toward investigations of song characteristics for which female choice has fitness consequences associated with ecological factors within the habitat. Therefore, analyses of geographical variation in song dialects should cover different habitat types, and should not be undertaken without investigation of those acoustic characteristics that may be affected by habitat-dependent selection.

4. SONG AND SPECIATION

(a) *Habitat, dispersal and song learning*

If populations of the same species occupy distinct habitats, parallel divergent selection may lead to concordance of acoustic, and other, traits. Because of such a parallel divergence, song may provide a habitat-dependent acoustic label and function as an indicator of fitness-related traits. For instance, populations of the little greenbul that inhabit dense rainforest in central Africa differ morphologically from populations that inhabit gallery forest in the ecotone bordering the rainforest (Smith *et al.* 1997). At the same time, these populations have distinctive song characteristics providing a habitat-dependent acoustic label that females could use in mate choice (Slabbekoorn & Smith 2002). However, many species of birds *learn* their song from nearby singing males during a sensitive phase early in life (e.g. Kroodsma 1982; Marler 1997). Therefore, one wonders whether males are still recognizable as being local or immigrant despite their developmental flexibility.

Learned song can be an indicator of a natal population

in several ways. An acoustic signature of the population may remain in the case of predispersal learning from father or neighbour, with either restricted or no learning later in life. Well-known examples of this type of learning are found in zebra finches (e.g. Clayton 1990*a*,*b*; Zann 1997) and Darwin's finches (e.g. Grant & Grant 1996; 1997*b*). However, many species are able to adjust their songs after dispersal (reviews in Krebs & Kroodsma 1980; Kroodsma 1982; Baptista & Gaunt 1997; Payne & Payne 1997). Although this may allow a male to partly converge to the songs of neighbours after dispersal, an acoustic signature of the natal population may still remain in at least two ways. First, post-dispersal adjustment to local song variants may take place via a process of selective attrition. In this process males learn a song repertoire before dispersal, from which they eventually select only the part that best matches the song of new neighbours (Marler & Peters 1982; Nelson 1992; Nelson *et al.* 1996*a*). Second, even if a male is able to learn completely new songs after dispersal, an acoustic signature of the natal population may remain when song plasticity is constrained by genetically determined components.

There is substantial evidence to suggest that components of highly plastic learned song may have a genetic basis. Despite intraspecific variation in learned song, species-specific characteristics such as duration, rhythm, frequency range, or tonal quality are typically heritable (Marler & Pickert 1984; Marler & Sherman 1985; Baptista 1996). Such heritable song characteristics are attributed to neural song templates or species-specific learning preferences with a genetic basis (Thorpe 1958; Marler & Peters 1977, 1988, 1989; Marler 1990, 1991; Kroodsma & Canady 1985; Eales 1987; Nelson & Marler 1993; Mundinger 1995; Braaten & Reynolds 1999; Soha & Marler 2000). Recently, Nelson (2000) showed that white-crowned sparrows not only inherently prefer learning from their own species, but even prefer their own subspecies' song. Acoustic variation may also have an indirect genetic basis, when song is affected by resonance characteristics inherently coupled to heritable variation in morphology (Slabbekoorn & Smith 2000). Acoustic characteristics have been shown to be correlated with body size (e.g. Wallschläger 1980; Tubaro & Mahler 1998), vocal tract length (e.g. Suthers 1994) and bill morphology (Palacios & Tubaro 2000; Podos 2001).

Although empirical evidence for a correlation between heritable characteristics of song and ecological variables is limited, a convincing example is found in migratory and sedentary subspecies of the white-crowned sparrow. Experiments in captivity showed that subspecies differ genetically in timing and flexibility of song learning. These differences are correlated to ecological aspects of their migratory mode and can be explained as adaptations to the length of the breeding season and the relative uncertainty over breeding location (Nelson *et al.* 1995, 1996*a*,*b*).

(b) *Acoustic and reproductive divergence*

Acoustic divergence may provide habitat-dependent acoustic labels, which females may use in mate choice. Assortative mating can then evolve through fitness benefits if females of a particular habitat choose males with song signalling high mate quality for that same habitat. Theor-etical studies support the view that assortative mating based on habitat-dependent cues is likely to lead to reproductive divergence and speciation, particularly in cases of large adjacent populations with ongoing reciprocal gene flow (Servedio & Kirkpatrick 1997; Servedio 2000; Gavrilets *et al.* 2000). However, a better understanding of the role of song learning, and the reliability of acoustic labels is required, in order to determine when assortative mating is likely to evolve.

The reliability of a habitat-associated population marker depends on both the relative developmental plasticity of individuals, which allows for post-dispersal song adjustment, and the acoustic variation present in populations. In the context of song learning and reproductive divergence, it is useful to refer to 'realized' and 'potential' acoustic variation. Realized acoustic variation is the range of song characteristics for all individuals of a population. Potential acoustic variation is the range of song characteristics these same individuals could produce after dispersal, given their morphology, capacity to learn, and all other genetic and environmental constraints. Thus, one can think of potential acoustic variation as the limits to the plasticity of learned song after a bird disperses to another population. We will first explain, with some examples, the concept of potential variation before coming back to realized variation and the possible role of population differences in the evolution of assortative mating.

Currently, there is little empirical data on the potential variation of any bird species. However, some insight into the plasticity limits of learned song can be gained by exposing individuals to extreme tutoring regimes in the laboratory. For example, experimental studies on swamp sparrows reveal great plasticity on the one hand—individuals are capable of very accurate heterospecific imitations (e.g. Marler 1991), but clear limits to the flexibility on the other hand—individuals fail to imitate artificially high song trill rates (Podos 1996; Podos *et al.* 1999). Such findings elucidate some, but not all, of the possible determinants of the potential acoustic variation in natural populations. Although heterospecific imitations occur in the field in some species (e.g. Baptista & Morton 1981; Baker & Boylan 1999), they have not been reported for swamp sparrows. In the field, heritable learning preferences, as discussed above, are likely to restrict heterospecific learning due to the natural presence of conspecific song tutors.

In the example of the swamp sparrow, it is clear that the limits to post-dispersal adjustment of learned song are determined by a complex interplay of genetic components and tutor experiences. Another example highlighting constraints to vocal plasticity is found in a comparative study on performance limits and song characteristics of Darwin's finches. Natural selection, associated with feeding efficiency on different food items, has led to a divergence in bill morphology among the various finch species leading, secondarily, to acoustic divergence in the species-specific songs (Podos 2001; but see Slabbekoorn & Smith 2000). This suggests that a difference in the shape or size of the bill alters vocal capacity and therefore affects potential variation.

In contrast to potential variation, realized variation between populations may easily diverge due to song learning processes (e.g. Thielcke 1973; Lemon 1975; Mund-
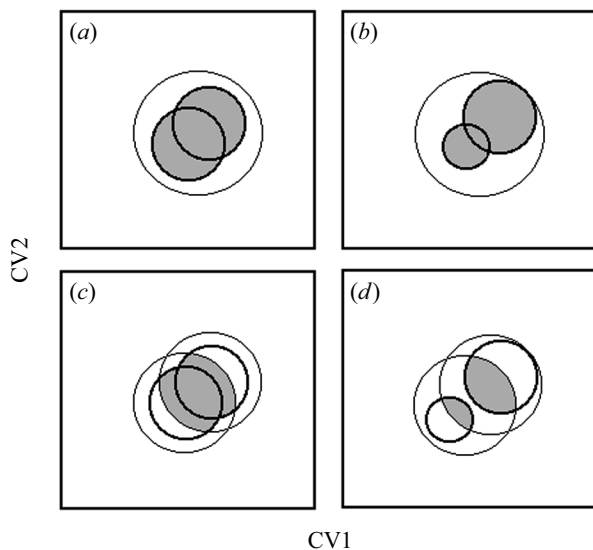
Figure 3. Acoustic divergence with song learning. Acoustic divergence between two populations of the same species is depicted in a multivariate space, with two canonical variates (CV1 and CV2) reflecting interpopulation differences based on a set of acoustic measurements. Four hypothetical stages of population divergence are illustrated. The circles with thick lines indicate the realized acoustic variation (R), the circles with a thin line indicate the potential acoustic variation (P). R is the range of song characteristics for all individuals of a population. P is what these same individuals could produce if dispersing to another population, given their morphology, capacity to learn, and all other genetic and environmental constraints. The mutual overlap of P with R is shaded. The shape and size of circles are a simplification of what may be found for acoustic measurements on real populations. (a) Divergence in R reflects phenotypic variation without any divergence in P. (b) Divergent selection may lead to differentiation between the two populations (e.g. by contraction in one population, and acoustic shift in the other). However, the divergence in R only reflects phenotypic variation without any divergence in P. (c) Divergence in R and P. The P of both populations still shows large mutual overlap with their respective R, which makes the divergence relatively unreliable as a population marker. (d) Divergence in R and P. Song learning in response to selection drives the R of one population to the edge of its P, while the other population is showing contraction of R. Both processes lead to a considerable reduction in the mutual overlap of P with the other population's R. In this way song learning increases the reliability of song as a population marker, without any further divergence in the P of both populations.

inger 1982; Slater 1989; Payne 1996; J. Ellers and H. Slabbekoorn, unpublished data). In the absence of very strong selection, such divergence in realized variation is not likely to be driven to the edges of potential variation (as shown in figure 3a). However, physical properties of the habitat may impose selection on acoustic variants, causing certain syllables with particular acoustic features to be heard more easily, and subsequently learned more readily (Hansen 1979; Morton *et al.* 1986). As a result, selective learning may lead to the contraction of realized variation, or drive realized variation to the edge of the potential (figure 3b). Both factors can result in acoustic

divergence between two populations living in different habitats and may lead to fixation of particular song characteristics without genotypic changes affecting potential variation.

Without a difference in potential variation, any individual dispersing between populations would be able to learn the song of the new population. Even if two populations show some divergence in potential variation (figure 3c), the mutual overlap with the other population's realized variation may still be too high for song to be a reliable cue to a male's origin. However, with some difference in potential variation, divergent selection on realized variation could reduce the overlap (figure 3d). This could lead to a dramatic increase in the reliability of song as an acoustic population marker without any further divergence in potential variation.

The consequences of song learning and post-dispersal plasticity in reproductive divergence may be summarized as follows. Initially, song learning may limit the potential for assortative mating by female choice because a lack of overlap in realized variation may not reflect a lack of overlap in potential variation. This may have been the case in some previous dialect studies if immigrating males were capable of learning the local dialect. Such circumstances would render a mate preference for local song useless in finding a male adapted to the local habitat, and could explain a lack of assortative mating based on song. However, if potential variation differs among populations, divergent selection on learned song components could reduce the mutual overlap of potential, and realized, variation and promote the reliability of song as an acoustic label. Under these circumstances, with a reliable label, reproductive divergence could be accelerated through female choice.

In general, phenotypic plasticity can soften the impact of natural selection on genetic variation, allowing individuals to persist in different environments by altering their phenotype (Via & Lande 1985; Sultan 1987; Cheplick 1991; Schlichting & Pigliucci 1998). The developmental plasticity of song due to learning processes may have the same effect, allowing individuals to switch habitats and adjust their song to locally appropriate acoustic characteristics. Nevertheless, after some initial genetic divergence, learned song may be an example of phenotypically plastic behaviour that varies geographically and can promote reproductive divergence and speciation (West-Eberhard 1989; Foster 1999). Future studies should address the relative plasticity in learned song to gain insight into the relationship between realized and potential variation of song characteristics. Investigation of the flexibility of immigrant males to blend with the local song dialect will probably lead to a better understanding of the role of song in reproductive divergence.

5. CONCLUSIONS

A review of the literature suggests that there are two main reasons for the large number of conflicting studies that try to link dialectal variation to assortative mating. First, many studies ignored the role of ecology, and have dealt with dialectal variation without examining fitness consequences for female mate preferences. Second, studies have often measured divergence in realized acoustic

variation between populations, without examining divergence in potential acoustic variation.

Baptista & Trail (1992) compared the rate of speciation among bird taxa with and without song learning. They found only a weak correlation between high species diversity and vocal learning, and suggested a limited role for song learning in promoting speciation. It seems probable that their results reflect the variability in the impact of learned song on reproductive divergence. The potential of song for promoting assortative mating depends on the relative plasticity of song allowing post-dispersal adjustment of acoustic characteristics. We clearly need more studies addressing the interrelationship between song divergence and learning. One promising approach may be to use simulation studies to examine how the learning characteristics of individuals affect song variation at the population level (e.g. Williams & Slater 1990; J. Ellers and H. Slabbekoorn, unpublished data).

Further ecological studies will also be crucial to gain insight into the role of bird song in promoting speciation. A shift in focus towards ecology may well serve to re-establish geographical variation in song as the prime tool for investigating the evolutionary importance of behaviour. Integration of studies on assortative mating with ecological approaches, and exploration of gene flow in the context of habitat-dependent acoustic variation, using the latest molecular techniques, are only some of the potential areas of fruitful future research.

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