

Species-specific song convergence in a moving hybrid zone between two passerines

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Moving hybrid zones are receiving increasing attention. However, so far little is known about the proximate mechanisms underlying these movements. Signalling behaviour, by individuals engaged in interspecific sexual and aggressive interactions, may play a crucial role. In this study, we investigated song variation within a moving hybrid zone between two warblers, *Hippolais polyglotta* and *H. icterina*. In these species, song is involved in interspecific territoriality and, probably, in mixed pairings. We showed that allopatric populations of the two species are clearly acoustically differentiated. However, interspecific differences faded out in sympatry as a result of an overall pattern of convergence. Unexpectedly, the two species converged for different song parameters, namely temporal parameters for *H. icterina* and syntax for *H. polyglotta*. Hybridization and interspecific competition could explain convergence in *H. icterina*. Instead, in *H. polyglotta* we suggest that local adaptation to habitat and interspecific learning might contribute to convergence. We particularly stress that cross-species learning, by maintaining high levels of interspecific interactions, may influence the movement of the zone. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, 80, 507–517.

ADDITIONAL KEYWORDS: *Hippolais* – hybridization – interspecific interactions – interspecific territoriality – parapatry.

INTRODUCTION

Hybrid zones have elicited much theoretical, empirical and experimental work (Barton & Hewitt, 1985; Hewitt, 1988; Harrison, 1993; Arnold & Emms, 1998; Butlin, 1998). Recently, the focus has been on moving zones (Gill, 1997; Carney, Gardner & Rieseberg, 2000; Britch, Cain & Howard, 2001; Rohwer, Bermingham & Wood, 2001; Dasmahapatra *et al.*, 2002), challenging the general view of a stable process, acknowledged in spite of the predictions of early theoretical studies (Barton & Hewitt, 1985). Besides, the interest for

moving zones takes place in the context of the growing concern about extinction, assimilation associated with biological invasions (Rhymer & Simberloff, 1996; Allendorf *et al.*, 2001) and distributional changes (Dukes & Mooney, 1999).

Several factors may be involved in the displacement of a contact zone (Shapiro, 1998; Good *et al.*, 2000; Bleeker & Hurka, 2001; Dasmahapatra *et al.*, 2002), among which behavioural aspects may play a crucial role (Pearson, 2000). In particular, the level of differentiation of mating signals often largely determines the degree of prezygotic isolation (Coyne, 1992; Howard, 1993; Gleason & Ritchie, 1998). Mating signals therefore have a direct influence on the frequency of heterospecific pairings (Baker & Boylan, 1999), and potentially on the dynamics of interbreeding populations (Rhymer & Simberloff, 1996;

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Pearson, 2000). However, in several taxonomic groups, mating signals are also used in intrasexual interactions, for example for resource acquisition (Catchpole & Slater, 1995; Ryan & Rand, 1998). Accordingly, they can be involved in interspecific interactions between competing taxa (Reed, 1982; Catchpole & Leisler, 1986), which may also influence the demography of sympatric populations. Both reproductive and territorial interactions are expected particularly between sibling species because of behavioural and ecological similarities due to their common ancestry (McCracken & Sheldon, 1997; Slikas, 1998; Johnson, 1999; Peterson, Soberón & Sánchez-Cordero, 1999). In turn, selection pressures resulting from the balance between hybridization and competition are expected to alter signal designs. Birds provide very good opportunities to investigate signal changes in hybrid zones. First, hybridization is common in this group (Grant & Grant, 1992). Second, pair formation commonly involves exchange of signals between mates, especially in oscines (songbirds). Third, in many species of oscines, song is involved in interspecific territoriality and mixed-pair formation (Gill & Murray, 1972; Emlen, Rising & Thompson, 1975; Baker & Baker, 1990).

THE HYBRID ZONE OF *HIPPOLAIS* WARBLERS IN WESTERN EUROPE

Melodious warblers *Hippolais polyglotta* and icterine warblers *H. icterina* are sibling sylviid species (Helbig & Seibold, 1999). These sexually monomorphic taxa have very similar plumage and morphology but they can be distinguished by wing and song characteristics (Wallace, 1964; Cramp, 1992). They have parapatric distributions (Cramp, 1992), marginally overlapping in Western Europe (Fig. 1A). Although assortative mating is observed in sympatry, the two warblers hybridize and produce viable offspring (Faivre *et al.*, 1999). The position of the hybrid zone has shifted northwards and eastwards during the last decades (Fig. 1B) and morphological variation has been observed in *H. icterina*, the receding taxon (Faivre *et al.*, 1999). This suggests that hybridization might play a role in this process.

In *Hippolais* warblers, song is an important behavioural trait, modulating interspecific interactions. Males are interspecifically territorial (Faivre, 1993), and respond strongly to playbacks of heterospecific songs even in distant allopatric populations (Ferry & Deschaintre, 1974; Secondi, Faivre & Kreutzer, 1999). Song also has a sexual function. As in other related species (Catchpole & Slater, 1995; Feßl & Hoi, 2000), a decrease in singing activity is observed after pairing (B. Faivre, pers. observ.). Fur-

thermore, female *H. polyglotta*, implanted with oestradiol, produced solicitation displays to conspecific songs and, to a lesser extent, to *H. icterina* songs, whereas songs of a more distantly related species were virtually ignored (J. Secondi, unpubl. data). Interspecific interactions are therefore expected to impose selective pressures on signal design.

Two opposite outcomes can be expected in this zone:

(1) Song divergence in *H. polyglotta*

The smaller species (*H. polyglotta*) is usually dominated in aggressive contests (Rice, 1978; Robinson & Terborgh, 1995). It is then expected to diverge in order to avoid the costs of aggressive interactions with a larger species. Recent studies predicted the occurrence of reinforcement in spite of low gene flow (Servedio & Kirkpatrick, 1997; Cain, Andreassen & Howard, 1999; but see also Liou & Price, 1994; Hostert, 1997). There is no data on the actual magnitude of the gene flow between *Hippolais* warblers. However, a previous study suggested it was asymmetric, from *H. polyglotta* to *H. icterina* (Faivre *et al.*, 1999), so that song divergence driven by reinforcement is more likely to occur in *H. polyglotta*.

(2) Song convergence in *H. icterina*

Adult hybrids, viable enough to contribute to the local song pool, are expected to produce intermediate signals. Because of the asymmetrical gene flow from *H. polyglotta* to *H. icterina*, as inferred from morphological variations (Faivre *et al.*, 1999), convergence driven by hybridization is more likely in *H. icterina* than it is in *H. polyglotta*. Interference competition can also drive convergence in *H. icterina*, the larger species, by improving the efficiency of its territorial signalling towards *H. polyglotta* (Cody, 1973; Rohwer, 1973).

In this paper, we investigate the effects of interspecific interactions on song in the contact zone between two sibling taxa. Acoustic parameters, measured on spectrograms from songs of both species recorded in allopatry and in sympatry were analysed separately and in combination through multivariate analyses. We first checked the species-specificity of song. We then tested for differences between sympatric and allopatric populations within a species. Signal divergence can result from either an increase in difference between mean values of signal parameters or a decrease in their variances (Miller, 1982). In contrast, signal convergence can be due to a decrease in differences between mean values or an increase in trait variances. We therefore focused on within-species mean and variance variations in song traits to detect changes and their direction in sympatry.

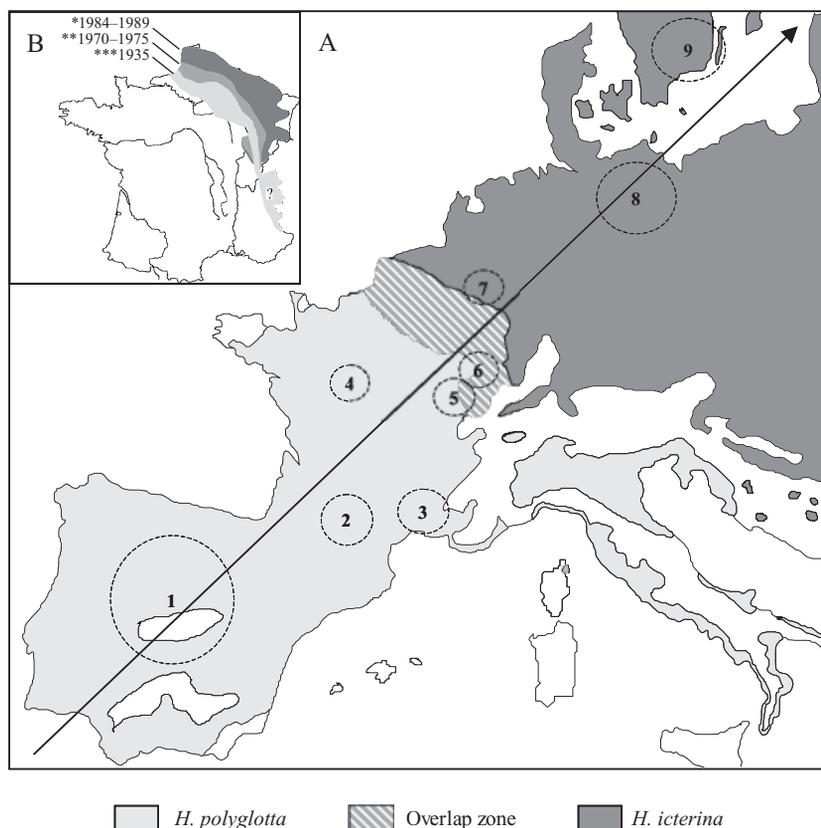


Figure 1. (A) European distributions of *Hippolais icterina* and *H. polyglotta* and sites sampled in this study. Sites are numbered according to their position along a south-west/north-east axis. They are represented by circles whose size accounts for the scattering and/or the accuracy of location of the recording sites. 1: Spain (allopatric *H. polyglotta*, $n = 8$; source J.-C. Roché and R. Ranft); 2: south-western France (allopatric *H. polyglotta*, $n = 4$; source J. Joachim); 3: south-eastern France (allopatric *H. polyglotta*, $n = 11$; source J.-C. Roché); 4: Touraine, central France (allopatric *H. polyglotta*, $n = 7$; source authors); 5: Côte d'Or, eastern France (sympatric *H. polyglotta*, $n = 18$, and *H. icterina*, $n = 15$; source authors); 6: Haute-Saône, eastern France (sympatric *H. polyglotta*, $n = 3$, and *H. icterina*, $n = 14$; source authors); 7: Liège, Belgium (allopatric *H. icterina*, $n = 4$; source authors); 8: northern Germany (allopatric *H. icterina*, $n = 9$; source R. Ranft and G. Tembrock); 9: Sweden (allopatric *H. icterina*, $n = 11$; source R. Ranft). (B) The geographical shift of the sympatric zone during the last 70 years: *Jouard (1935), **Yeatman (1976), ***Yeatman-Berthelot & Jarry (1994).

MATERIAL AND METHODS

SITE AND POPULATION SAMPLING

Fifty-three males of *H. icterina* (24 allopatric and 29 sympatric) and 51 of *H. polyglotta* (30 allopatric and 21 sympatric) were tape-recorded in nine geographical sites, seven allopatric and two sympatric, distributed along an axis encompassing most of the geographical range of these species (Fig. 1A). The two sympatric sites differ in the duration of their contact, ranging from >60 years in Site 5, to <20 years in Site 6 (Secondi *et al.*, 1999). Mixed pairings and morphological introgression have been documented in Site 5 only (Faivre *et al.*, 1999), but as only three *H. polyglotta* were tape-recorded in the recent sympatric site (Site 6), the two sympatric sites were pooled for this species. Therefore, two sympatric populations for *H. icterina*

and one for *H. polyglotta*, and three allopatric populations for *H. icterina* and four for *H. polyglotta* were sampled, providing data on ten populations.

SONG ANALYSES

The *H. polyglotta* song is typically made up of a series of one or two repeated elements followed by a complex and rapid warbling (Cramp, 1992). In contrast, *H. icterina* does not produce well-defined structures, but bouts of elements of various length interspersed with silences of variable duration (Fig. 2A). Because of such differences in syntax, we analysed sequences of constant duration rather than a constant number of bouts. A single sequence of 15–17 s, equivalent to an average duration of two song bouts in *H. polyglotta*, was randomly selected for each individual (J. Secondi,

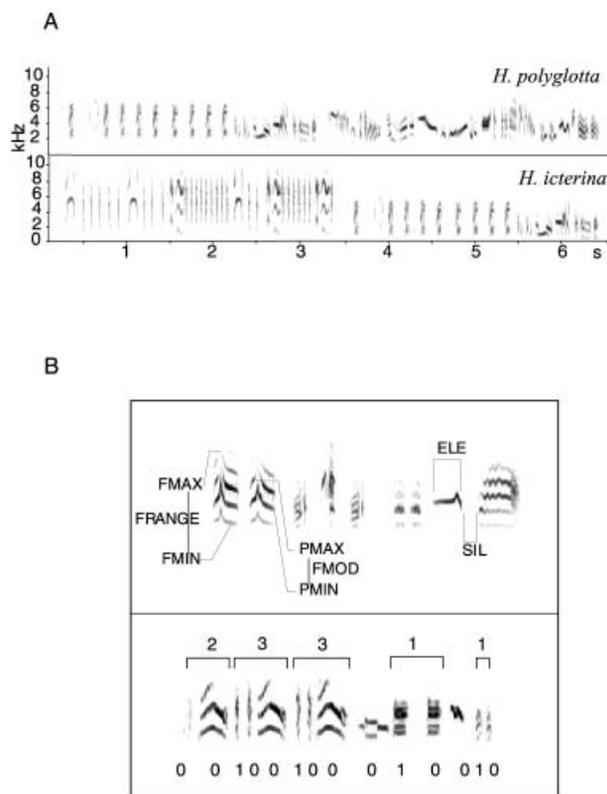


Figure 2. (A) Examples of one song in *Hippolais polyglotta* and one song sequence in *H. icterina*. (B) Spectrograms: measurements of time and frequency variables (upper panel) and syntax variables (lower panel). The binary coding of elements is shown below and the categorization of repetitions according to the number of elements involved is given above the spectrograms. See methods for further details on coding.

unpubl. data). All signals were digitized and analysed on a Macintosh computer using Soundedit 16 (22 255 Hz, 8 bits). Frequency and time resolutions were set, respectively, to 83 Hz and 12 ms with a FFT size of 512 points (Hanning window). Accordingly, to time resolution, two continuous tracings were considered as two elements if they were separated by a gap larger than 12 ms on the spectrogram.

Preliminary analyses indicated a very large repertoire of song elements (i.e. possibly several hundred). We therefore discarded methods based on element categorization that require a good estimate of individual components of the repertoires as well as large samples of individuals for describing realistically the pool of elements present in a population. Instead, we took measurements on all the elements from a sequence (*H. icterina*: 81.6 ± 21.7 elements, range = 50–170; *H. polyglotta*: 116.1 ± 18.2 elements, range = 69–154).

Three categories of acoustic parameters were considered for each single element (Fig. 2). (i) Temporal

parameters included element duration (ELE) and interelement duration (i.e. silence between two successive elements, SIL). (ii) Frequency parameters included frequency range of the element (FRANGE), obtained by the difference between highest and lowest frequencies (FMAX and FMIN in Fig. 2B). We also measured frequency modulation (FMOD) obtained by the difference between highest and lowest frequencies (PMAX and PMIN in Fig. 2B) of the largest frequency modulation in the element. Measurements were taken from the harmonic with the highest amplitude in dB for elements including harmonics. (iii) Syntactical parameters, focusing on the repetition pattern of elements, a suitable method to compare taxa with different singing styles. In our case, icterine warblers repeat elements much more extensively than do melodious warblers. We conducted two distinct analyses. We first analysed single element transitions by counting how many elements were immediately repeated in a sequence. We assigned a value of 1 when an element was identical to the next one, and 0 when it was different (Fig. 2B). We summed all the values to obtain the number of repeated elements REP_1 in the sequence. We secondly considered repetitions of several elements. These repetitions can be simple (i.e. a suite of the same element), or multiple (a suite of several elements immediately followed by the same suite). For each sequence, TOTREP represented the total number of repetitions (i.e. simple and multiple), and TOTMULT the total number of multiple repetitions (Fig. 2B). Lastly, NOREP summed up the number of elements that did not contribute to any of the syntactical variables detailed above. Because the amount of repetition in a sequence of constant duration varies with rhythm or motivation (e.g. fast singers produce more elements than slow singers per time unit), we standardized each syntax variable by dividing all scores by the total number of elements analysed in the sequence.

STATISTICAL ANALYSES

As we sampled a large and variable number of song elements for each individual, we computed average values and coefficients of variation (CVs), an indicator of within-individual variability, for time and frequency parameters. For syntax parameters, we used the standardized scores. Overall, 12 acoustic parameters (including CVs) were used for each of the 104 individuals. We first checked that the acoustic parameters we analysed reliably discriminated between the two species by comparing allopatric groups only. We then considered sympatric groups only and in combination with allopatric individuals to test whether song variation occurred in sympatry. Lastly, clinal or spatial variation across Western Europe was investigated, in

which case each population (i.e. geographical population or site) was considered as a group.

Univariate analyses tested for variations in individual acoustic parameters (ANOVA), whereas multivariate approaches considered song as a whole using all acoustic parameters. We first used multiple analysis of variance (MANOVA) to obtain multivariate statistics. We then carried out quadratic discriminant function analysis (DFA) on the 12 acoustic parameters. We used quadratic DFA rather than linear DFA as the criterion of homoscedasticity was not met. Following each DFA, we calculated four estimates of classification power. The first one, simply derived from resubstitution of all individuals, provides an apparent error rate (the error count), but has an optimistic bias. The second obtained by a cross-validation technique (a jackknife procedure) is probably more realistic. However, the allocation rule, which is either 0 or 1 depending on whether the observation is wrongly or correctly classified, yields a high variance. Therefore, we also applied to both techniques a smoothing procedure that gives the probability of allocation of the observation in each of the groups (see SAS, 1999). Stepwise DFA was also used to detect the most informative acoustic parameters regarding species discrimination, taking into account autocorrelation between variables. Canonical discriminant analysis was finally used to derive scores for each individual and allow graphic representation. We checked for normality of variables before performing parametric tests. Temporal acoustic parameters, which did not follow normal distributions, were log-transformed prior to statistical analyses. All statistical analyses were performed on the SAS 8.0 package.

RESULTS

SONG SPECIES-SPECIFICITY

Nine acoustic parameters were statistically informative with regard to species discrimination in allopatry (see between-species *F*-values in Table 1). All four syntactic parameters were highly divergent between species, as were temporal ones, but the situation was less clear for frequency parameters. The level of within-individual variability (i.e. interelement variation) also differed between species, though on frequency parameters only (Table 1). Consistently, within-species variation (sympatry vs. allopatry) was much lower than was between-species variation (nested ANOVA, population category nested within species in Table 1). This was, however, not true for SIL and NOREP, which showed similar levels of variation, and was actually reversed for FRANGE which was more divergent within than between species (Table 1).

Table 1. Average values (and standard errors) for the 12 acoustic parameters, according to species and population category (sympatry vs. allopatry)

Taxon	Population category	<i>N</i>	ELE ¹	CV-ELE (%)	SIL ¹	CV-SIL (%)	FRANGE	CV-FRANGE (%)	FMOD	CV-FMOD (%)	NOREP	REP ₁	TOTREP	TOTMULT
<i>H. polyglotta</i>	allopatric	30	1.82 (0.01)	16.93 (0.43)	1.63 (0.01)	17.98 (0.48)	4871.8 (182)	30.69 (1.81)	1717.9 (54.3)	59.44 (1.72)	0.53 (0.05)	0.41 (0.04)	0.21 (0.01)	0.07 (0.01)
<i>H. polyglotta</i>	sympatric	21	1.80 (0.02)	17.58 (0.57)	1.63 (0.02)	17.57 (0.49)	4641.5 (137)	32.72 (1.71)	1706.4 (46.5)	61.25 (1.82)	0.33 (0.03)	0.30 (0.04)	0.27 (0.02)	0.11 (0.02)
<i>H. icterina</i>	sympatric	29	1.92 (0.02)	16.26 (0.71)	1.77 (0.02)	16.79 (0.92)	5452.1 (202)	37.71 (1.53)	2070.4 (89.1)	50.74 (1.93)	0.29 (0.02)	0.17 (0.02)	0.34 (0.02)	0.20 (0.01)
<i>H. icterina</i>	allopatric	24	1.95 (0.02)	16.72 (0.55)	1.88 (0.03)	17.06 (0.67)	4528.9 (215)	45.55 (3.32)	1858.5 (65.4)	55.21 (1.93)	0.31 (0.03)	0.18 (0.03)	0.36 (0.02)	0.20 (0.02)
Between-taxon			38.7	1.68	88.38	1.49	1.46	20.82	13.20	13.91	12.42	28.93	39.25	51.39
<i>F</i> -statistic	(<i>P</i>)		<0.0001	0.19	<0.0001	0.29	0.23	<0.0001	0.0004	0.0003	0.0006	<0.0001	<0.0001	<0.0001
Within-taxon			0.95	0.46	7.00	0.12	6.22	3.55	2.41	1.52	7.00	2.38	3.16	2.09
<i>F</i> -statistic	(<i>P</i>)		0.39	0.63	0.001	0.88	0.003	0.032	0.09	0.22	0.001	0.09	0.05	0.13

A nested ANOVA was performed to test for significant effect of taxon and population category nested within taxon. A sequential Bonferroni correction was applied for each analysis (i.e. between and within taxon *F*-statistics, with alpha = 0.05/12).

¹Temporal parameters were log-transformed to meet normality distribution.

A multivariate approach confirmed these results (Table 2). Of 54 allopatric individuals, only one individual (*H. icterina*) was misclassified using the resubstitution technique. The cross-validation technique yielded similar results, though, as expected, the error rate was higher. Smoothed error rates were, however, very low with in both cases (Table 2, second analysis). This suggested a very strong acoustic separation between the two species on the basis of the 12 parameters measured. The most powerful parameters leading to the separation, as shown by stepwise DFA, were SIL and ELE, and three of the four syntactic parameters.

COMPARISON OF SONG IN ALLOPATRIC AND SYMPATRIC POPULATIONS

We tested whether means and variances differed between allopatric and sympatric populations within each species. The mean values of three acoustic parameters differed statistically. In two cases (SIL for *H. icterina* and REP₁ for *H. polyglotta*), the mean value converged from the allopatric to the sympatric situation (see Fig. 3). The situation was less clear with regard to variance. In two cases (NOREP for *H. polyglotta*, and CV-FRANGE for *H. icterina*), variance decreased from allopatry to sympatry. However, in two other cases (FMOD for *H. icterina*, and TOTREP for *H. polyglotta*), the reverse was true (although in those two latter cases, differences were not significant after Bonferroni adjustment). Interestingly, parameters which varied most in sympatry were those which differed most between both species in allopatry, namely temporal parameters for *H. icterina* and syntax variables for *H. polyglotta*. *H. icterina* converged for temporal parameters, diverged for frequency parameters, and stayed unchanged for all syntactic parameters. The reverse was true for *H. polyglotta*, which stayed unchanged for both temporal and frequency parameters, but converged for all syntactic parameters (Fig. 3).

Similarly, the canonical discriminant analysis on all individuals indicated that interspecific differences in song varied according to whether populations were in sympatry or in allopatry (Table 2 first analysis; Fig. 4). A scatterplot of the first two canonical axes showed substantial overlap in sympatric populations but a complete separation between allopatric populations. Furthermore, overlap seemed to occur due to *H. icterina* individuals rather than to *H. polyglotta*, suggesting an asymmetric convergence between the two taxa in sympatry (Fig. 4). In summary, convergence in mean values was observed in sympatric populations of the two species while larger song variability in sympatry was detected in *H. polyglotta* only (Fig. 3).

Table 2. Results of the MANOVA, and discriminant function analyses

Discrimination between	Sample size	MANOVA		Discriminant analysis		*Incorrect <i>H. icterina</i> in		*Incorrect <i>H. polyglotta</i> in	
		Wilks' lambda	<i>P</i>	Resubstitution method	Cross validation method	allopatry	sympatry	allopatry	sympatry
<i>H. icterina</i> and <i>H. polyglotta</i>	104	0.32	<0.0001	4.8 (0.029)	12.5 (0.032)	1	3	0	1
Allopatric populations	54	0.17	<0.0001	1.8 (0.011)	11.1 (0.011)	1	–	0	–
Sympatric populations	50	0.46	0.0013	4.0 (0.014)	30.0 (0.027)	–	2	–	0
Allopatric classification ¹						–	5	–	3

Due to heterogeneity between variances in groups, a within-group covariance matrix and a quadratic discriminant function were used. Discriminant power is evaluated using resubstitution and cross-validation. Both error counts and posterior probabilities of classification (in parentheses) are reported (see Methods).

^{*}The last four columns provide the number of individuals incorrectly classified using the resubstitution technique.

¹In this analysis, sympatric individuals were classified using the formula based on allopatric individuals, i.e. sympatric individuals did not contribute to the discriminant function.

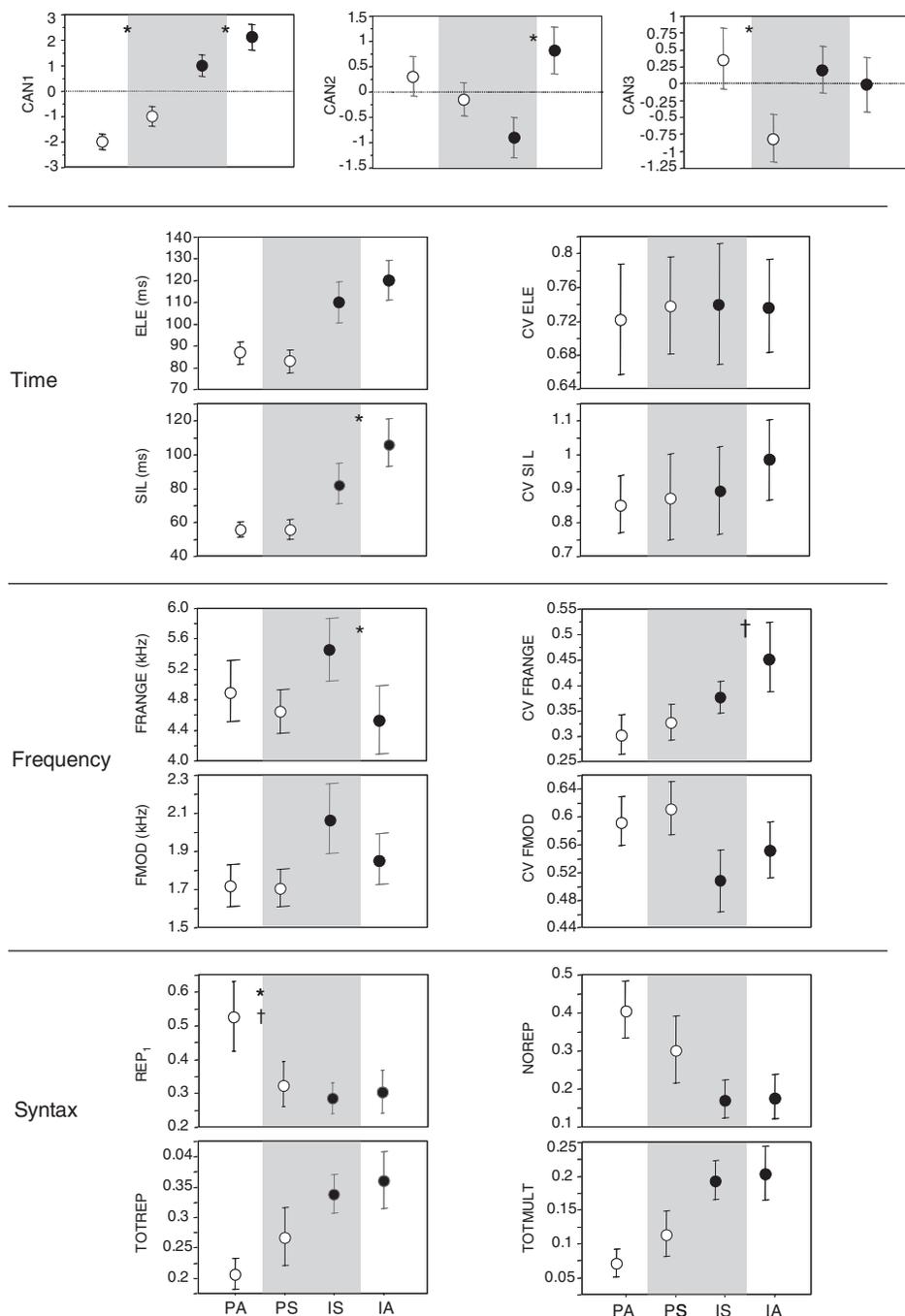


Figure 3. Song variation in sympatric and allopatric populations of *Hippolais polyglotta* (○) and *H. icterina* (●). Population means \pm 95% confidence intervals are given for the three canonical variables (CAN) from the discriminant function analysis and for the 12 song variables (defined in the text). Shaded areas indicate sympatric populations. (*) for mean values and (†) for variances indicate significant within-species differences after sequential Bonferroni correction. A correction was applied for each set of tests (e.g. comparison of mean values in *H. icterina*, 12 tests, $\alpha = 0.05/12$). PA, allopatric *H. polyglotta*; PS, sympatric *Hippolais polyglotta*; IS, sympatric *H. icterina*; IA, allopatric *H. icterina*.

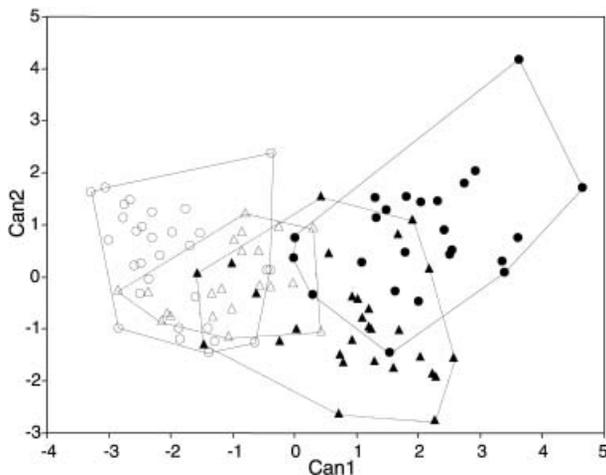


Figure 4. Scatterplots of sympatric and allopatric populations of *Hippolais polyglotta* and *H. icterina*, using scores on the two first axes of a canonical discriminant analysis with the two species as the two groups, but the four populations are shown: *H. icterina* in allopatry (●) and in sympatry (▲), and *H. polyglotta* in allopatry (○) and in sympatry (△).

Discriminatory power actually dropped when we considered sympatric individuals only, particularly when using the cross-validation technique (Table 2, third analysis). The pattern was even more marked when we used the dataset of allopatric populations as a training set, and then used its classification rule to allocate sympatric individuals into species categories (Table 2). The discrepancy between these two analyses was rather high (eight vs. two misclassified birds using, respectively, sympatric and allopatric classifications). This suggests that acoustic parameters changed in sympatry compared with allopatry, and that information regarding species-specificity in allopatric populations was no longer present in sympatric populations.

SPATIAL VARIATION IN SONG

Because recording sites differed in size and in accuracy for the location of tape-recorded individuals, we did not analyse clinal variations in song formally. Nevertheless, clines may occur across the range of the two species, as suggested in Figure 5.

DISCUSSION

SONG SPECIES-SPECIFICITY AND SONG VARIATION IN SYMPATRY

Icterine and melodious warblers are two distinct species based on morphological, ecological and molecular evidence (Cramp, 1992; Faivre, 1993; Helbig & Sei-

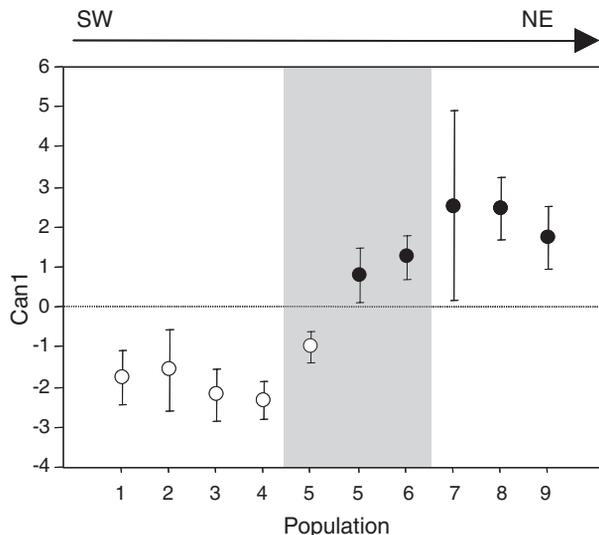


Figure 5. Spatial variation in the song of *Hippolais polyglotta* (○) and *H. icterina* (●). Population means \pm 95% confidence intervals are given for the first canonical axis calculated from 12 song variables. Shaded areas indicate sympatric sites. Populations are ordered as in Fig. 1.

bold, 1999). In this study, we have further shown that both taxa are well separated acoustically on most song parameters, resulting in a lack of overlap between allopatric populations (*c.*1% misclassified individuals). Acoustic separation is particularly marked for syntax and temporal acoustic features, underlying the fact that *H. icterina* sings more slowly and produces more repetitions than does its sibling counterpart.

However, interspecific song differences faded out in the contact zone, as indicated by higher rates of cross-species misclassification of sympatric individuals. Accordingly, univariate analyses revealed convergence, particularly for those song parameters that were shown to be the most divergent between the two taxa in allopatry (*i.e.* syntax for *H. polyglotta* and temporal variables for *H. icterina*). Unexpectedly, *H. polyglotta* populations were to some extent less variable in sympatry than they were in allopatry whereas either hybridization or competition is likely to increase trait variability. We do not have a clear explanation for this result. However, we cannot rule out the possibility of an artefact due to a sampling bias. We sampled more allopatric than we did sympatric populations, and the geographical area covered by the former was much larger. Differences in variability may therefore simply reflect geographical song variation.

ECOLOGICAL AND BEHAVIOURAL EXPLANATIONS FOR SONG CONVERGENCE

The data clearly do not support our prediction on song divergence in *H. polyglotta*. Interspecific territorial

interactions are apparently not costly or frequent enough to drive song differentiation. Further divergence may actually be unnecessary considering the clear-cut acoustic separation between the two species. In contrast, the song variation pattern is consistent with our prediction of convergence in *H. icterina*. Hybridization may be involved here since the spatial variation of song suggests the presence of a vocal cline as usually observed for allelic frequencies or genetically determined traits in hybrid zones (Sanderson, Szymura & Barton, 1992; Mousseau & Howard, 1998). A role for competition in convergence is also indirectly supported in *H. icterina* by the maintenance of a strong response to *H. polyglotta* songs in sympatry (Secondi *et al.*, 1999). Convergence could therefore increase the efficiency of territorial signalling directed towards heterospecific males, and help to achieve adaptive interspecific territoriality (Cody, 1973).

Interpreting song convergence in *H. polyglotta* is more difficult. Because it would increase the risks of interacting with a larger species, an effect of interspecific competition is unlikely. Hybridization does not seem to provide a good explanation either. Melodious warblers have been recently sampled for DNA on the same study site from which they were previously sampled for morphology (Faivre *et al.*, 1999). In this population, which has been in allopatry for five years now, none of the 27 birds analysed had any *H. icterina* mitochondrial DNA (J. Secondi, unpubl. data). This sharply contrasts with results from a similar study by Rohwer *et al.* (2001) of two *Dendroica* warblers. The authors observed up to 100% of heterospecific mitochondrial haplotypes in phenotypically pure populations of the expanding species. In comparison, it seems that introgression has never been extensive in *H. polyglotta*. Although we cannot completely exclude the presence of undetected hybrids or introgressed individuals in our sample, hybridization does not convincingly explain large song variations in sympatry. An intriguing result supports the idea that other mechanisms could influence song variation in sympatry. One would expect introgression to affect the same vocal traits in both taxa. In this regard, the convergence of different song parameters in the two species is particularly striking. We suggest two mechanisms, one ecological and one behavioural, that could have played a role in song variation.

First, the two species differ for habitat selection and singing behaviour. *H. icterina* sings mainly in the cover of dense and high bushes whereas *H. polyglotta* uses song perches dominating the canopy in more open areas (Cramp, 1992; Faivre, 1993). Clinal habitat variations may therefore induce song convergence in the contact zone. We do not favour this hypothesis, as we did not observe obvious variations between adjacent areas inside and outside the hybrid zone. How-

ever, detailed studies on habitat selection and measurements of song degradation in different populations would be required to evaluate habitat constraints.

Second, cross-species learning, i.e. song copied from heterospecific tutors, has been repeatedly reported in natural populations of songbirds (reviewed in Helb *et al.*, 1985). This is very likely influenced by the degree of signal similarity as well as the frequency of interactions with heterospecifics (Emlen *et al.*, 1975; Helb *et al.*, 1985). A consequence is that song characteristics may become uncoupled from genetically determined traits like morphology (Emlen *et al.*, 1975) or from the genetic background of individuals (Grant & Grant, 1997b). Such a phenomenon would be expected in *Hippolais* warblers. Indeed, the strong reactions of males to heterospecific songs in distant allopatric populations (Ferry & Deschaintre, 1974) support the view that there is no vocal barrier between the two species. Also, *Hippolais* warblers form interspecific clusters of territories when in syntopy (Faivre, 1993), so that fledglings have many opportunities to learn songs from heterospecific neighbours. Morphological similarity between both species might ease this process since morphology is involved in tutor choice in birds (Mann *et al.*, 1991; Grant & Grant, 1997a). Finally, it is worth noting that *Hippolais* warblers are skilled mimics (Cramp, 1992), so songs of close relatives might be easily imitated.

EVOLUTIONARY CONSEQUENCES OF SONG CONVERGENCE

Several mechanisms can drive song convergence and it is not clear which one prevails nor whether they are identical for both warblers. Nevertheless, a possible consequence of song convergence, irrespective of the actual mechanism, is an increase in the frequency of mismatings that could have long-term consequences on sympatric populations. Mixed pairs actually did increase over a 20-year period in our main sympatric site (Faivre *et al.*, 1999). Although other cues, such as territory quality, can be used for mate choice, song is probably prominent in *Hippolais* warblers. Measuring female sexual preferences to convergent and non-convergent heterospecific songs in *H. icterina*, the receding species, would therefore be crucial to assess the effect of song convergence on hybridization rate.

In general, the interplay between hybrid zones, signals and mating patterns has been relatively little studied in birds (but see Robbins, Braun & Tobey, 1986; Moore, 1987; Grant & Grant, 1996; Grant & Grant, 1997b). In particular, the actual importance of cultural processes in the hybridization process remains virtually unknown. As pointed out by Robbins

et al. (1986), it is difficult to identify which mechanism drives song variation in oscines, because alternative hypotheses, involving selective and non-selective factors, can lead to exactly the same pattern. Studies coupling behavioural and genetic data are therefore needed to provide insight into the mechanisms underlying song variation in hybridizing populations of passerines, and to understand the consequences of such variations on the dynamics of hybrid zones.

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