

A comparative study of the function of heterospecific vocal mimicry in European passerines

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Although heterospecific vocal imitation is well documented in passerines, the evolutionary correlates of this phenomenon are poorly known. Here, we studied interspecific variation in vocal mimicry in a comparative study of 241 European songbirds. We tested whether vocal mimicry is a mode of repertoire acquisition or whether it resulted from imperfect song learning. We also investigated the effect of the degree of contact with the vocal environment (with species having larger ranges, abundance, or being long lived having a higher degree of mimicry) and a possible link with cognitive capacity (an overall larger brain in species with mimicry). Finally, we determined the potential evolutionary role of vocal mimicry in different interspecific contexts, predicting that mimicry may affect the intensity of brood parasitism, predation, or degree of hybridization. While controlling for research effort and phylogenetic relationships among taxa, we found that effect sizes for intersong interval, brain size, breeding dispersal, abundance, age-dependent expression of repertoires, and predation risk reached a level that may indicate evolutionary importance. Vocal mimicry seems to be a consequence of song continuity rather than song complexity, may partially have some cognitive component but may also be dependent on the vocal environment, and may attract the attention of predators. However, estimates of sexual selection and interspecific contacts due to brood parasitism and hybridization varied independently of vocal mimicry. Therefore, mimicry may have no function in female choice for complex songs and may be weakly selected via interspecific associations. These findings provide little evidence for vocal mimicry having evolved to serve important functions in most birds. *Key words*: bird song, comparative study, learning, repertoire size, sexual selection. [*Behav Ecol*]

Avian vocal mimicry is a conspicuous but puzzling phenomenon, and it shows striking interspecific variation even between closely related species (Hindmarsh 1984a). For example, marsh warblers *Acrocephalus palustris* mimic more than 100 species (Dowsett-Lemaire 1979), whereas other *Acrocephalus* warblers imitate fewer species with more uniform timing and slower tempo (e.g., Hamao and Eda-Fujiwara 2004), and some members of the family do not mimic at all (Cramp and Perrins 1985–1994). As vocal mimicry corresponds to certain social and ecological contexts (Dobkin 1979; Baylis 1982), its interspecific variation may be expected to be associated with the intensity of natural and sexual selection (Hindmarsh 1984a). Accordingly, several evolutionary constraints may favor vocal mimicry and can explain why 15–20% of passerines incorporate heterospecific elements in their songs (reviews in Dobkin 1979; Baylis 1982).

First, as vocal mimicry may be a means by which males acquire large repertoires (Dobkin 1979; Baylis 1982), it can enhance sexual selection via female preferences (Hindmarsh 1986). Hence, if the rate of heterospecific imitation determines repertoire size, selection for complex songs should have consequences for vocal mimicry. However, sexual selection may directly act on vocal mimicry, if it reflects individual

learning capacities, and the preference for such abilities involves potential benefits for females (see Nowicki et al. 2002). Accordingly, the accuracy of vocal mimicry and the number of model species mimicked both seem to determine mating success of male satin bowerbirds *Ptilonorhynchus violaceus* (Coleman et al. 2007). Moreover, males of the European starling *Sturnus vulgaris* with a large mimicked repertoire size experience high fecundity in terms of clutch size (Hindmarsh 1984b, but see Hamao and Eda-Fujiwara 2004 for negative evidence for female preference). Similarly, the list of species mimicked by particular males may reflect certain attributes of these males (e.g., wintering sites [Dowsett-Lemaire 1979] or habitats), which may be useful in the context of sexual selection.

Second, large repertoire size may result in an increase in vocal mimicry, and not vice versa as the sexual selection model would predict, as it can be associated with complex songs due to learning mistakes (Hindmarsh 1986). To obtain large repertoires, males need to learn several sounds. If complexity is what matters, fine syllable structure (e.g., frequency contour) may become less important. Hence, criteria for selecting sounds for learning should be relaxed, and different filters that control the inclusion of new sounds into the repertoire will become weakened. As an artifact, this will increase the probability of mistakes in terms of incorporating songs from other species. If there is no selection against such learning mistakes, as they do not alter the signaling effectiveness of the song, heterospecific sounds will remain in the repertoire. Species with large repertoire size may have the motor

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apparatus to produce various sounds. Such species will easily match the motor pattern of the model species, which is often required for accurate heterospecific vocal imitation (Zollinger and Suthers 2004).

Third, if vocal mimicry is a mode of active repertoire acquisition, it should involve cognitive functions to cope with the variable vocal environment. In general, to efficiently deal with environmental complexity by behavioral means, superior cognitive capacities may be required (Lefebvre et al. 2004). In particular, learning, production, and perception of heterospecific songs may be a cognitively challenging task, and mimicking species will need to store and manipulate considerable amounts of information about their vocal environment. Mimicry is not necessarily restricted to the simple copy of vocal patterns, but birds may actually learn the appropriate usage and remember the social context of mimetic songs with different meaning (Greenlaw et al. 1998; Goodale and Kotagama 2006). Additionally, vocal mimicry does not always reflect the abundance of species in the environment (Hindmarsh 1984b; Hausberger et al. 1991; Chu 2001), and such selectivity in copying may suggest a certain degree of cognitive adaptation to the vocal environment.

Fourth, if vocal mimicry is a passive process to some degree, it may be partially influenced by the exposed vocal environments. The starling has been introduced throughout the world, and everywhere, it only mimics local species (Baylis 1982). The effect of the vocal environment is even obvious at the local scale in this species because certain mimicked components of the song occur with a frequency that matches with the models' abundance (Hausberger et al. 1991). Similarly, 5 African *Cossypha* robin-chat species mimic different species groups corresponding to differences in their acoustic environments (Ferguson et al. 2002). Interestingly, mimetic vocal learning encompasses the migration season in the marsh warbler, and about 20% of mimicked song elements represent African species (Dowsett-Lemaire 1979).

Fifth, vocal mimicry is sometimes thought to function in various interspecific contexts (Baylis 1982). For example, vocal mimicry can be used to deter other species from contested resources, and thus, it may mediate interspecific territoriality (Hartshorne 1973). Moreover, vocal mimicry can effectively disturb host recognition of brood parasites via acoustic cues if the parasite becomes unfamiliar with incorporated new sounds (Baylis 1982). Additionally, as attacked birds often produce mobbing or alarm sounds from various species that distract a predator's interest from hunting, vocal mimicry can be used as a vocal threat against predators (Robinson 1974). Finally, mimetic song may serve a role in species isolation, and extensive mimicry may be a way by which a species avoids hybridization (Lemaire 1977).

Here, we investigated these evolutionary pathways that may produce interspecific variation in vocal mimicry in European passerines. We used several predictor variables and tested whether the proposed factors accompany evolutionary transitions in vocal mimicry. Accordingly, we can formulate 5 major predictions. 1) If vocal mimicry is favored to increase repertoire size via female preference for complex songs, we predicted that vocal mimicry is primarily associated with measures of song complexity, and it is positively associated with intensity of sexual selection. 2) If vocal mimicry is a simple consequence of large repertoires due to learning mistakes, we predicted positive associations with song complexity and song output, as longer or more continuous songs increases the probability of passive uptake of heterospecific sounds into the repertoire, but no relationship with estimates of the intensity of sexual selection. 3) If vocal mimicry involves cognition and learning, we expected a positive interspecific relationship with relative brain size used as a proxy for cogni-

tive capacities. 4) If the link between vocal environment and vocal mimicry is a general phenomenon because it is basically a passive process, we should expect a higher degree of heterospecific vocal imitation in species that encounter various acoustic environments than species that are confronted with a single vocal milieu. This prediction may also be expanded to a temporal scale, as long-lived animals may hear and learn more sounds during their lifetime than species with a short lifespan. Additionally, open-ended learners that flexibly increase their repertoires in adulthood have a more extended period to acquire mimetic sounds than species in which repertoire size stabilizes when young. 5) If any of the interspecific contacts affects vocal mimicry, we predicted an association with the corresponding estimate of the operating selective factor.

MATERIALS AND METHODS

Vocal mimicry

We compiled information on vocal mimicry from *The Birds of the Western Palearctic*, which provides detailed information on singing behavior (Cramp and Perrins 1985–1994). Although each section was written by different groups of authors, they all follow a standard format and rely on the primary literature facilitating cross-species comparisons. We collected data for 241 passerine species, spanning 26 families and 85 genera, as summarized in the Supplementary Appendix.

We found more or less detailed descriptions on vocal mimicry. Authors usually provide a list of typically mimicked species with representative mimicking patterns. We collected qualitative and quantitative information for our comparative purposes. First, we categorized vocal mimicry by giving a score of “1” to species, for which the presence of vocal mimicry was clearly stated. The remainder of the species were considered to be nonmimetic species and were given a score of “0.” Second, as a continuous measure of mimicry, we counted the total number of stems “mimic*,” “mime*,” “imitat*,” and “copy” (or “copie*”) within the relevant section (words used in a negative sense were not counted). Third, we counted the number of species that were imitated. We applied a broad-sense criterion and accepted positive observations in captive animals as supporting evidence. We equally considered songs and subsongs but not calls. The 2 continuous measures were strongly positively correlated ($r = 0.947$, $N = 215$, $P < 0.001$). We used the \log_{10} -transformed total number of stems in association with mimicry, as this could be estimated for all species involved. Our estimates seemed to be reliable because they were strongly positively associated with data of Hindmarsh (1984a) (mimicry on a discrete scale: $t_{68} = 4.63$, $P < 0.001$; mimicry on a continuous scale, $r = 0.776$, $N = 70$, $P < 0.001$). There was no mimicking species in Hindmarsh's list that was identified as a nonmimicking species in our survey. In contrast, Hindmarsh gave a score of “0” to some species for which we found evidence of vocal mimicry in Cramp and Perrins (1985–1994). This difference is likely due to differences in study effort as Hindmarsh relied on Witherby et al. (1943). Information in our source originates from more recent and updated references.

Research effort

The probability of finding a report on vocal mimicry in a species may depend on the intensity of studies on the species' song. Therefore, we estimated research effort on song to control for its confounding effects. We counted the number of words in the song sections (Song Display and Calls of Adults) in the electronic version of Cramp and Perrins (1985–1994). We assumed that this measure reflects the intensity of research

on song because the number of words was larger in species in which quantitative information is available on male song (e.g., listed in Read and Weary 1992) than in species without such quantitative information ($t_{239} = 6.649$, $P < 0.001$).

We also estimated the degree of research effort in general because it may affect some predictor variables (see below). We counted the number of papers published since 1972 on each species as cited in the ISI Web of Science (<http://www.isiknowledge.com/>).

Song variables

We used 4 variables to represent song output and song complexity, following the definitions in Read and Weary (1992). Song output was measured as song duration (seconds) and intersong interval (seconds). We did not derive song continuity and song rate as defined by Read and Weary (1992) because they are directly calculated from song duration and intersong interval. Interpretations for song continuity and rate can be made from statistical models that include both song duration and intersong interval. Between-song complexity was estimated as song type repertoire size (number of different song types in an individual's repertoire). We used the syllable repertoire size (number of different syllable types within a song) to reflect within-song complexity. For species with extreme song complexity, general sources provide near-infinite data on repertoire size because it is difficult to estimate. In such cases, syllables are combined randomly and a particular combination occurs rarely, leading to the detection of numerous song types. Following common practice, for species with infinitely large song type repertoire size (>100) we assigned an arbitrary value of 1000 (see Read and Weary 1992; Garamszegi and Møller 2004).

We used song data from Read and Weary (1992), supplemented with information from other sources (listed in Møller et al. 2006; Garamszegi, Biard, et al. 2007). The use of song parameters in comparative analyses raises issues about comparability. We have previously addressed this issue in detail (Garamszegi and Møller 2004), and here we assume that our song variables provide reliable information.

Cognitive capacity

Data for brain size (in grams) and the associated body mass to control for allometric effects were derived from 3 different sources (Mlikovsky 1990; Garamszegi et al. 2002; Iwaniuk and Nelson 2003). Highly significant repeatabilities among studies indicate that information on relative brain size can be combined across sources (Garamszegi et al. 2005).

The intensity or the degree of contact with different vocal environments

Range size

We estimated total geographical range size as the area surrounded by the maximum latitude and longitude of each species' breeding range to the nearest 0.1 degrees in Cramp and Perrins (1985–1994). To take into account the spherical curvature of the earth, we used the equation $\text{area} = R^2 \times (\text{longitude}_1 - \text{longitude}_2) \times (\sin(\text{latitude}_1) - \sin(\text{latitude}_2))$, when R is the radius of the earth (6366.2 km) and latitude and longitude are expressed in radians. In widespread species, Old and New World ranges were calculated separately and subsequently summed. This method overestimates true geographical range, but the error should be random in the current focus. However, we tested the relationship between different estimates of range size, which all proved that our approach was reliable. Our estimate of area was strongly positively cor-

related with geographical range size as calculated by the number of one-degree grid cells covering species' distribution ($r = 0.871$, $P < 0.001$, $N = 20$ Palearctic and Nearctic species), with range size as reported for a sample of 11 threatened species (Stattersfield and Capper 2000) ($r = 0.976$, $P < 0.001$), with range size as estimated based on image analysis of digital breeding distribution maps from Cramp and Perrins (1985–1994) ($r = 0.524$, $N = 60$, $P < 0.001$). In our analyses of range size, we took into account differences between species in abundance. Abundance may reflect the degree to which they experience interspecific vocal influence because common species are more likely to be exposed to various sounds than rare species. Accordingly, we obtained information on population size from Burfield and van Bommel (1997) and included it in analyses of range size.

Migration distance

We used the mean of the northernmost and southernmost latitudes during the breeding season minus the mean of the northernmost and southernmost latitudes during winter.

Dispersal

We used the arithmetic mean breeding dispersal distance (birds ringed as adults and recovered at least 1 year later) for birds from the British Isles reported by Paradis et al. (1998), which relies on European Union for Bird Ringing standards and corresponds to 400 000 ringing recoveries.

Number of breeding habitats

Cramp and Perrins (1985–1994) defined the principal breeding habitat categories in a glossary, and we used these to characterize habitat diversity. We searched for these terms in the breeding habitat descriptions, where we counted the total number of habitat categories. A large number of habitats may simply reflect large research activity because intensively studied species may be observed in more different habitats. Hence, research effort should be considered in analyses of habitat diversity.

Longevity

We extracted information on maximum longevity of birds from standard ornithological handbooks (Cramp and Perrins 1985–1994; Glutz von Blotzheim and Bauer 1985–1997). The available information is based on extensive literature search and data provided by major bird-ringing schemes. The probability of finding rare and very old individuals in a species may be dependent on research intensity, and thus, longevity should be adjusted for sampling effort (Møller 2006).

Age-dependent expression of repertoires

We used information from Cucco and Malacarne (2000), which we updated with recent findings (Galeotti et al. 2001; Gil et al. 2001; Bell et al. 2004; Forstmeier et al. 2006; Kipper et al. 2006; Garamszegi, Török, et al. 2007) to classify species according to whether repertoire size is the same in yearling and older males. We assumed that age-dependent expression of repertoires reflects the incorporation of new sounds into the repertoire but not phenotype-dependent survival or immigration. Several studies have suggested that differences in repertoire size between age categories result from consistent increase in song complexity (Gil et al. 2001). In cases when age dependence may be different between populations (e.g., Forstmeier et al. 2006), we used the strongest effect known for the species.

Intensity of sexual selection

Polygyny

We recorded the maximum frequency of polygyny in Cramp and Perrins (1985–1994). In our list, there was no lekking

species, for which the meaning of polygyny may be obscure. However, finding no evidence for polygyny in a species may arise not only due to biological reasons but also due to absence of observations. As such, differences in research effort may bias estimates of polygyny, which therefore should be controlled.

Sexual dichromatism

We scored species as sexually monochromatic or dichromatic, using a dichotomous classification. Species were considered to be monochromatic, if males and females could not be reliably distinguished based on plumage characters according to field guides (e.g., Svensson 1984; Mullarney et al. 2000). Any sex difference in plumage coloration independently of its magnitude was considered to represent sexual dichromatism.

Extrapair paternity

We used the relative frequency of extrapair offspring as a measure of extrapair paternity, defined as the number of extrapair offspring divided by the total number of offspring. Data were extracted from Griffith et al. (2002) and Spottiswoode and Møller (2004), and repeatability and reliability are reported therein.

Interspecific associations

Predation pressure

We characterized predation pressure due to the European sparrow hawk *Accipiter nisus*, which is the most common avian predator in forested and agricultural regions of the Palearctic, as defined by Møller et al. (2006). This estimate relies on a long-term study of passerine prey items. A prey selection index was calculated by controlling prey abundance for population densities, with positive values signifying an overrepresentation relative to the abundance and negative values an underrepresentation.

Brood parasitism

Level of parasitism relied on the percentage of nests parasitized by the cuckoo *Cuculus canorus*, as reported in the literature (Avilés and Garamszegi 2007). Previous analyses have revealed consistently greater variance among than within species in parasitism rate by the cuckoo (Soler et al. 1999; Avilés and Garamszegi 2007), which suggests that the mean estimate of the rate of parasitism can be regarded as a species-specific trait.

Hybridization

We used the extensive review of all available information on hybridization in birds compiled by Panov (1989), combined with information from Randler (2002), McCarthy (2006), and Gray (1958) and an extensive search of the literature on the Web of Science. We did not consider studies on captive birds to avoid any bias. However, a larger number of publications would reflect a larger research activity and hence a greater probability of hybrids having been reported. Therefore, in the corresponding analyses, a control for sampling effort may be required.

Statistical and phylogenetic analyses

Variables were accurately transformed for the analyses (\log_{10} , or arcsine square root). We tested our predictions at the interspecific level by calculating the associations between vocal mimicry and the predictor variables by using multivariate models, which involved the potentially confounding effects of research effort at different levels.

Closely related species are more likely to share phenotypes than more distantly related species, and thus, phylogenetic

relationship among species should be controlled. We used phylogenetic generalized least squares models (PGLM), which incorporate a matrix of the expected covariances among species based on likelihood ratio statistics (Martins and Hansen 1997; Pagel 1999). This method also enabled us to estimate the importance of phylogenetic corrections (Freckleton et al. 2002); thus, we conducted all analyses by setting the degree of phylogenetic dependence (λ) to the most appropriate degree evaluated for each model. These exercises were performed in the R statistical computing environment, with additional unpublished functions by Freckleton R (University of Sheffield, available on request) for the PGLM procedure developed for continuous and discrete variables and multivariate models.

The composite phylogeny for birds used in the phylogenetic models was mainly based on Sibley and Ahlquist (1990), combined with information from other sources (Sheldon et al. 1992; Blondel et al. 1996; Badyaev 1997; Cibois and Pasquet 1999; Møller et al. 2001). We applied branch lengths from Sibley and Ahlquist (1990) for higher taxonomic levels. Within families, the distance between different genera was set to 3.4 ΔT_{50H} units and between species within genera to 1.1 ΔT_{50H} units. Using equal branch lengths, which is equivalent to an assumption of a punctuated model of evolution, gave very similar results.

To determine the strength and direction of the predicted relationships, we estimated effect sizes (such as correlation effect size “ r ,” sensu Cohen 1988) and the associated 95% confidence intervals (CIs) for each particular relationship. We preferred focusing on effect sizes instead of using Bonferroni adjustment of P values because the latter approach has been criticized in the field of ecology and behavioral ecology for mathematical and logical reasons (Moran 2003; Nakagawa 2004; Garamszegi 2006). We used the software Comprehensive Meta-Analysis (BioStat 2000; <http://www.meta-analysis.com/>) to calculate effect sizes and corresponding CIs. For demonstrative purposes, we also present significance levels.

RESULTS

First, we assessed the degree to which research effort should be considered in our analyses. The 2 independent estimates of research effort were significantly positively associated with each other implying that they reflect similar phenomena ($r = 0.466$, $N = 241$, $P < 0.001$). We found a positive relationship between vocal mimicry and both estimates of research effort (research effort on song: mimicry, discrete, $t_{239} = 6.528$, $P < 0.001$; mimicry, continuous, $r = 0.426$, $P < 0.001$, $N = 241$; Figure 1; research effort in general: mimicry, discrete, $t_{239} = 3.176$, $P = 0.002$; mimicry, continuous, $r = 0.230$, $P < 0.001$, $N = 241$). However, partial correlations revealed that research effort on song was a better predictor of vocal mimicry than research effort in general (research effort on song: $r = 0.370$, $P < 0.001$; research effort in general: $r = 0.030$, $P = 0.643$). As predicted, research effort in general was significantly related to habitat diversity ($r = 0.289$, $N = 241$, $P < 0.001$), longevity ($r = 0.392$, $N = 86$, $P < 0.001$), polygyny ($r = 0.234$, $N = 240$, $P < 0.001$), and hybridization ($r = 0.491$, $N = 241$, $P < 0.001$). Therefore, we controlled for research effort on song in all analyses of vocal mimicry but only considered research effort in general when the predictor variable required so.

Pairwise associations between vocal mimicry and the predictor variables while holding research effort on song constant are given in Table 1. Models based on discrete and continuous estimates of mimicry revealed qualitatively similar results. Using the species-specific data, we found effect sizes corresponding to intermediate effects for song variables that varied in the expected direction. Effects with similar magnitudes were found for dispersal and age-dependent expression

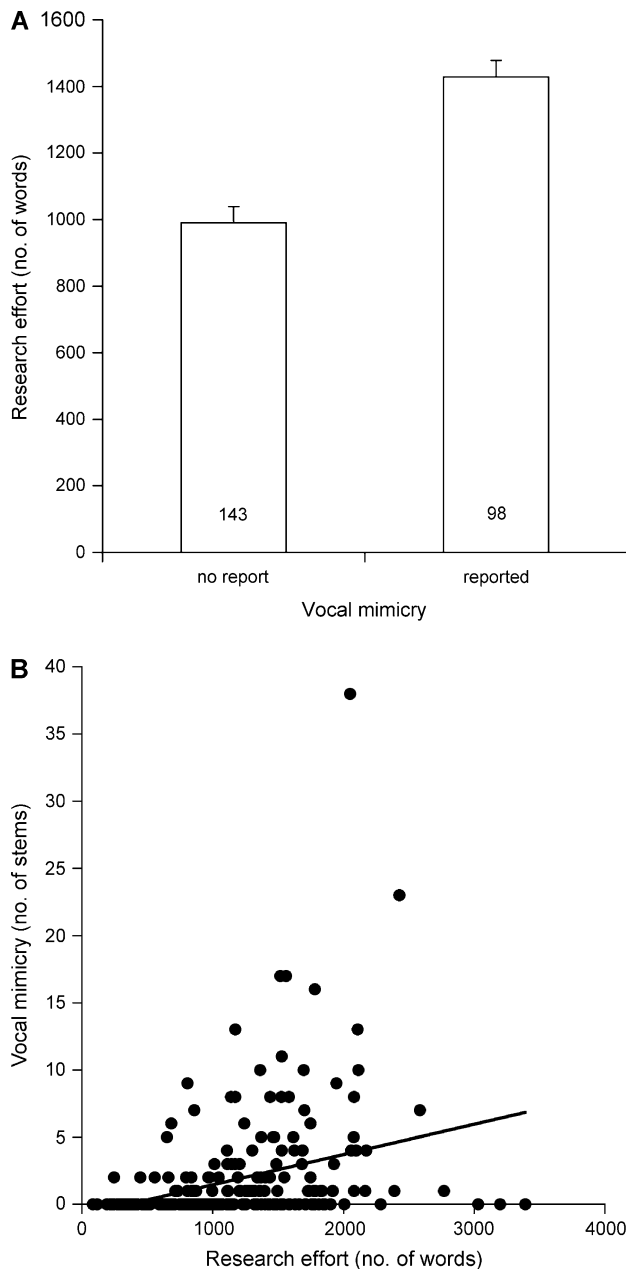


Figure 1
The relationship between research effort and the estimation on vocal mimicry, when research effort was estimated as the number of words in the song sections of *The Birds of the Western Palearctic* (Cramp and Perrins 1985–1994). (A) Vocal mimicry as a binary-state variable (bars are standard errors, numbers are number of species). (B) Vocal mimicry is a continuous variable measured as the number of stems in association with mimicry found in handbook descriptions (the line is the regression line). See text for statistics.

of repertoire size and brood parasitism. These effects were also in the expected direction. In contrast, effect sizes for sexual selection and brain size were generally small. Note that in many cases, small effect sizes were associated with narrow CIs indicating that due to the large sample size, we could precisely estimate true effects that are close to zero.

The control for phylogenetic effects slightly modified the above patterns. We still found effects of immediate magnitude for variables describing features of song and dispersal and for age-dependent expression of repertoire size (Table 1). Some

of these relationships were weakened, but this may also indicate the imprecision of our estimates, as the corresponding CI remained wide due to smaller sample size. Additional changes were that the relationship of vocal mimicry with brood parasitism considerably weakened, although it became stronger with brain size, abundance, and predation risk. A PGLM with all song variables revealed that the most important predictor of heterospecific vocal mimicry was intersong interval (Table 2). Song performance with short intersong intervals, reflecting higher song continuity when song duration was held constant, was accompanied with more likely heterospecific vocal imitation than singing with long intersong intervals.

DISCUSSION

Several hypotheses may explain the evolution of avian vocal mimicry, generating testable predictions at the interspecific level (see Introduction). Hindmarsh (1984a) made a pioneering attempt to unravel correlates of vocal mimicry across species. However, his otherwise exhaustive study included a subset of birds only, relied on a subjective scoring of mimicry, and did not control for research effort and phylogenetic relationships. Here, we demonstrated that the latter 2 factors have important effects (Figure 1 and Table 1, the values of λ were significantly larger than zero). When we held these confounding effects constant, we found effect sizes indicating that song continuity, brain size, dispersal distance, abundance, age-dependent expression of repertoire size, and predation risk may predict vocal mimicry with a magnitude that is evolutionarily relevant (*sensu* Møller and Jennions 2002). Other traits, such as estimates of sexual selection, seemed to be unrelated to mimicry.

Hindmarsh (1984a) concluded that song complexity predicts vocal mimicry better than song output, which supported 2 causal mechanisms linking song complexity to mimicry. Our pairwise correlations factoring research effort out also suggested relationships with song complexity (Table 1). However, phylogenetic models revealed consistently weaker effects for song type and syllable repertoire size than models relying on the raw species data (Table 1). This may indicate that the apparently strong relationship between vocal mimicry and song complexity may be partially caused by the phylogenetic associations of species. In addition, when we considered covariation between song traits, song output in terms of intersong interval was the strongest correlate of mimicry (Table 2). This model showed that heterospecific imitation is more likely when singing with shorter intervals between songs than in songs with longer intervals. Therefore, in a phylogenetic context when the correlations between song traits are held constant, song continuity seems to be the most important predictor of vocal mimicry.

We failed to detect strong relationships between different components of sexual selection and vocal mimicry (Table 1). Intense sexual selection enhances the evolution of complex songs leading to a positive association between polygyny and repertoire size (Read and Weary 1992). If the acquisition of large repertoires is achieved by copying from other birds, we should have observed vocal mimicry positively related to both song complexity and polygyny. Moreover, if vocal mimicry is a signal of learning abilities, which may be relevant in sexual selection (e.g., Nowicki et al. 2002), such mechanisms should also have generated frequent mimicry in species with high degree of polygyny or extrapair paternity. Our results do not support these predictions, and thus, sexual selection does not seem to favor vocal mimicry via female preference for large repertoires or learning abilities.

Some evidence suggests that vocal mimicry may involve learning and may be cognitively demanding (Greenlaw et al.

Table 1
Effect sizes (estimated as partial correlations “*r*”) and the associated 95% CIs for the relationship between vocal mimicry and different predictor variables

Predictor variables (<i>N</i> = species-specific data; contrasts)	Dependent variable: vocal mimicry					
	Discrete model		Continuous model		Phylogenetic model	
	<i>r</i>	95% CI	<i>r</i>	95% CI	<i>r</i>	95% CI
Song complexity and output						
Song duration (<i>N</i> = 58)	0.202	-0.059 to 0.437, <i>P</i> = 0.124	0.326	0.074 to 0.539, <i>P</i> = 0.013	0.288, λ = 0.671	0.032 to 0.508, <i>P</i> = 0.029
Intersong interval (<i>N</i> = 34)	-0.290	-0.572 to 0.053, <i>P</i> = 0.091	-0.504	-0.720 to -0.200, <i>P</i> = 0.003	-0.404, λ = 0.554	-0.653 to -0.076, <i>P</i> = 0.020
Song type repertoire size (<i>N</i> = 53)	0.293	0.025 to 0.522, <i>P</i> = 0.033	0.426	0.176 to 0.624, <i>P</i> = 0.002	0.198, λ = 0.734	-0.076 to 0.445, <i>P</i> = 0.160
Syllable repertoire size (<i>N</i> = 62)	0.221	-0.030 to 0.446, <i>P</i> = 0.082	0.405	0.173 to 0.595, <i>P</i> = 0.001	0.254, λ = 0.774	0.005 to 0.474, <i>P</i> = 0.048
Cognitive capacity						
Brain size ^a (<i>N</i> = 102)	-0.048	-0.240 to 0.148, <i>P</i> = 0.625	-0.010	-0.204 to 0.185, <i>P</i> = 0.919	0.204, λ = 0.585	0.010 to 0.383, <i>P</i> = 0.042
The intensity or the degree of contact with the vocal environment						
Range size ^b (<i>N</i> = 203)	-0.084	-0.219 to 0.054, <i>P</i> = 0.236	-0.087	-0.222 to 0.051, <i>P</i> = 0.221	-0.092, λ = 0.558	-0.227 to 0.046, <i>P</i> = 0.518
Population size ^b (<i>N</i> = 203)	0.080	-0.058 to 0.215, <i>P</i> = 0.256	0.100	-0.038 to 0.234, <i>P</i> = 0.157	0.194, λ = 0.558	0.058 to 0.323, <i>P</i> = 0.006
Migration distance ^c (<i>N</i> = 241)	0.183	0.058 to 0.302, <i>P</i> = 0.005	0.197	0.072 to 0.316, <i>P</i> = 0.002	0.097, λ = 0.541	-0.030 to 0.221, <i>P</i> = 0.137
Longevity ^c (<i>N</i> = 86)	-0.034	-0.244 to 0.179, <i>P</i> = 0.750	-0.001	-0.213 to 0.211, <i>P</i> = 0.998	0.057, λ = 0.633	-0.157 to 0.266, <i>P</i> = 0.604
Dispersal (<i>N</i> = 44)	0.245	-0.056 to 0.505, <i>P</i> = 0.105	0.408	0.126 to 0.629, <i>P</i> = 0.007	0.249, λ = 0.866	-0.052 to 0.508, <i>P</i> = 0.108
Number of breeding habitats ^{cd} (<i>N</i> = 241)	0.039	-0.088 to 0.165, <i>P</i> = 0.541	0.035	-0.092 to 0.161, <i>P</i> = 0.588	-0.026, λ = 0.562	-0.152 to 0.101, <i>P</i> = 0.686
Age-dependent repertoires (<i>N</i> = 33)	0.267	-0.084 to 0.559, <i>P</i> = 0.125	0.412 ^c	0.080 to 0.662, <i>P</i> = 0.017	0.196, λ = 0.719	-0.158 to 0.505, <i>P</i> = 0.282
Sexual selection						
Polygyny ^d (<i>N</i> = 240)	-0.109	-0.232 to 0.018, <i>P</i> = 0.092	-0.011	-0.137 to 0.116, <i>P</i> = 0.867	-0.032, λ = 0.552	-0.158 to 0.095, <i>P</i> = 0.619
Extrapair paternity (<i>N</i> = 49)	0.008	-0.274 to 0.289, <i>P</i> = 0.956	0.027	-0.256 to 0.306, <i>P</i> = 0.856	0.006, λ = 0.894	-0.276 to 0.287, <i>P</i> = 0.966
Sexual dichromatism (<i>N</i> = 241)	0.023	-0.104 to 0.149, <i>P</i> = 0.722	-0.043 ^c	-0.168 to 0.084, <i>P</i> = 0.501	-0.097, λ = 0.536	-0.221 to 0.030, <i>P</i> = 0.134
Interspecific associations						
Predation risk (<i>N</i> = 62)	0.023	-0.228 to 0.271, <i>P</i> = 0.859	0.070	-0.183 to 0.314, <i>P</i> = 0.591	0.234, λ = 0.653	-0.017 to 0.457, <i>P</i> = 0.069
Brood parasitism (<i>N</i> = 85)	0.184	-0.030 to 0.382, <i>P</i> = 0.092	0.271	0.061 to 0.458, <i>P</i> = 0.013	0.077, λ = 0.657	-0.138 to 0.285, <i>P</i> = 0.484
Hybridization ^{cd} (<i>N</i> = 241)	0.039	-0.088 to 0.165, <i>P</i> = 0.547	0.057	-0.07 to 0.182, <i>P</i> = 0.379	0.066, λ = 0.540	-0.061 to 0.191, <i>P</i> = 0.308

Discrete models correspond to analyses on the species-specific data, in which we used vocal mimicry as a binary-state variable. Effect sizes were calculated from multivariate logistic models, in which research effort on song (the number of words in the song section) was held constant. Continuous models relied on the number of stems associated with mimicry as counted in the song sections; partial correlations were computed (research effort on song controlled), and these correlation coefficients provide estimates of effect sizes. Phylogenetic models are PGLM, from which effect sizes for the relationship of interest were derived. The phylogeny scaling factor is given for each model. In some models, we included other obvious potentially confounding variables (see Materials and Methods and notes). Effect size conventions: *r* = 0.10 small effect, *r* = 0.30 intermediate effect, and *r* = 0.50 large effect (Cohen 1988). Signs of effects show the untransformed direction of the relationship, that is, they do not indicate whether the patterns are in the expected or the opposite direction.

^a Models that included body size.

^b Effects from the same model that included range size and population size to control for abundance.

^c Models that included range size.

^d Models that included research effort in general (number of papers in the Web of Science).

^e Effect sizes were calculated from multivariate logistic models using the bivariate variable as the dependent variable (research effort on song included).

Table 2

Phylogenetic model (PGLM) testing for the relationships between vocal mimicry and song variables simultaneously, which controls for the covariation of song traits

Predictor variables	Dependent variable: vocal mimicry		
	Slope (\pm standard error)	r (95% CI)	P
Song duration	0.091 (\pm 0.203)	0.103 (−0.305 to 0.479)	0.658
Intersong interval	−0.299 (\pm 0.116)	−0.509 (−0.753 to −0.143)	0.018
Song type repertoire size	0.127 (\pm 0.197)	0.146 (−0.264 to 0.512)	0.528
Syllable repertoire size	0.188 (\pm 0.117)	0.346 (−0.057 to 0.652)	0.125
Number of words	−0.820 (\pm 0.742)	−0.251 (−0.588 to 0.160)	0.272

The number of words in the song sections of our source was included to control for differences in research effort on song. The full model has the following statistics: $F = 3.376$, $N = 25$, number of parameters = 6, $P = 0.024$, $\lambda = 0.540$, log likelihood = −12.606, adjusted $R^2 = 0.331$.

1998; Goodale and Kotagama 2006). If this is a general role, we predicted that species that possess relatively larger brains would generally cope with these cognitive functions better than small-brained species. A PGLM controlling for phylogenetic inertia revealed a positive relationship between relative brain size and vocal mimicry, and thus, the integration of this behavior into the brain seems to require some general neural augmentation. Selection may act on the volume of a specific structure of the brain that stores heterospecific sounds, which is translated into similar relationships for overall brain size (e.g., Garamszegi and Eens 2004). It is also possible that vocal mimicry is not associated with a certain neural structure but is a component of a cognitive complex, and thus, species with larger brains are generally good at performing several cognitively demanding tasks (e.g., Lefebvre et al. 2004) involving vocal mimicry.

The assimilation of new sounds from the environment may be a passive process to some degree because sound uptake can be determined by the vocal environment (e.g., Dowsett-Lemaire 1979; Hausberger et al. 1991; Ferguson et al. 2002). Accordingly, lifestyles, distributions, or movements that involve frequent contacts with different acoustic environments on a spatial or temporal scale were predicted to facilitate heterospecific song imitation. In a phylogenetic context, effect sizes for breeding dispersal, abundance, and age-dependent expression of repertoires may lend some support for these predictions. Species may be exposed to different vocal environments if they disperse long distances or if they are relatively abundant, which can leave signatures in their mimicry. Moreover, species with extended periods for repertoire acquisition may be more susceptible to heterospecific sounds than species in which repertoire size stabilizes early in life (Table 1). However, given the correlative nature of this study, alternative explanations driven by additional factors are also possible. For example, dispersal and abundance may determine the outcome of competition among species (Friedenberg 2003), which may be also related to vocal mimicry (Baylis 1982), and the relationship between dispersal, abundance, and mimicry can be a result of interspecific competition. In addition, some effects should be interpreted with caution due to their wide CIs. Although our results are in accordance with the hypothesis that the degree of contact with the vocal environment may affect vocal mimicry, the underlying mechanisms require further investigation.

If vocal mimicry is used in other interspecific contexts, species may develop this behavior to escape predation, brood parasitism, or hybridization. If mimicking species are inherently successful at avoiding such interspecific interactions, they may experience a lower rate of predation, brood parasitism, or hybridization. These causal mechanisms assuming that

mimicry affects the outcome of these interactions predict negative associations between vocal mimicry and the intensity of interspecific relationships. In contrast, an opposite causal mechanism may be at work, if predation, brood parasitism, or hybridization constrains the evolution of vocal mimicry. As such, species that experience high costs due to these interspecific effects may be expected to adopt pronounced vocal mimicry as a response, resulting in a positive association between traits. An analysis of vocal mimicry across *Cossypha* robin-chats found no evidence for a relationship with brood parasitism, predation, or interspecific competition (Ferguson et al. 2002). On the other hand, our comparative analyses revealed a phylogenetically adjusted effect size for predation rate that may be relevant for the second scenario (Table 1). Strong selection pressures by predators may favor the use of heterospecific sounds in the song of prey species that disturb the prey recognition of their enemies. However, our results may also indicate that species that sing songs with mimicked elements are more likely to have song elements in their repertoires that attract the interest of predators than nonmimicking species. Note that we could only estimate vocal mimicry for songs, and thus, we were unable to deal with adaptive response of heterospecific mimicry to increased predation rate in alarm calls.

As comparative studies are based on correlations and are constrained by data availability, these limitations warrant some attention. First, the definition and the use of variables were conditional on certain assumptions. We assumed that our measures of vocal mimicry (the number of stems in association with the phenomenon as counted in the handbook) truly reflected the rate at which species imitate others. We tested this assumption by investigating correlations with independent variables that have a supposedly similar biological meaning. The only confounding factor we could imagine was research effort (Figure 1), for which we controlled. Any further noise in the data should be random for the questions at hand and should not confound the results. We note that we detected similar patterns when we used continuous and bivariate variables reflecting mimicry, and the relationships were biologically meaningful both at the species-specific level and in a comparative context.

To conclude, we were more likely to find effect sizes to support that in the majority of songbirds, heterospecific vocal mimicry is a side effect of song learning than strong evidence for an adaptive role. Heterospecific imitation seems to be more common in species with continuous song and in species with frequent contacts with different vocal environments suggesting mechanisms for passive sound acquisition. We cannot exclude that vocal mimicry may have some cognitive component, but its link with brain space warrants further investigation.

Importantly, vocal mimicry does not seem to function in a context of sexual selection. Learning mistakes can remain, if this does not involve fitness costs, and does not alter the effectiveness of song in female attraction. However, such primarily functionless heterospecific elements can be subject to selection, and may be functional, as seen in some species. Perhaps, predator avoidance has evolved for such a function, and thus, the phenomenon of vocal mimicry could be better understood in an interspecific than in an intraspecific context. It is also possible that different taxa may have evolved mimicry for different adaptive advantages, and there is no single “all purpose” functional explanation for mimicry in different lineages. This may explain why we failed to find strong effect sizes for the majority of the predicted relationships.

SUPPLEMENTARY MATERIAL

Supplementary Appendix can be found at <http://www.behco.oxfordjournals.org/>.

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