Interspecific territoriality in two songbird species: potential role of song convergence in male aggressive interactions

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In animals, interspecific interference competition is often associated with their aggressive behaviour. The intensity of interspecific aggression and the outcomes of interference competition between closely related species might be substantially modified by copying of vocal signals used in territory defence. Here we tested the hypothesis that song convergence observed in a secondary contact zone of two songbird species, the common nightingale. *Luscinia megarhynchos*, and the thrush nightingale, *Luscinia luscinia*, might be an adaptive response to interspecific interference competition. These species are morphologically and ecologically very similar. However, the thrush nightingale is slightly larger and several lines of evidence indicate its competitive dominance. In the secondary contact zone most thrush nightingales incorporate common nightingale song types in their repertoires. Using playback experiments, we evaluated the strength of nonvocal aggressive responses of both species to conspecific and heterospecific stimuli. The species did not differ in aggressive responses to a heterospecific stimulus, suggesting that competitive dominance is not associated with higher interspecific aggressiveness in nightingales. Interestingly, while the common nightingale reacted significantly more aggressively to the conspecific than the heterospecific stimulus, the thrush nightingale showed similarly strong responses to both stimuli. We suggest that this similar level of interspecific and conspecific aggression in the thrush nightingale results from mixed singing of this species in sympatry, as males may not distinguish conspecifics from heterospecifics by song alone. Our results are consistent with the concept of convergent agonistic character displacement. According to this theory, vocal convergence might be adaptive in species that overlap broadly in resource use, as it leads to better distinction of territory boundaries between the species and thus reduces the level of interspecific competition.

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Aggressive behaviour connected with territory defence is the predominant form of interference competition in animals (Cody, 1974; Langkilde & Shine, 2004; Robinson & Terborgh, 1995) with important ecological consequences (Pigot & Tobias, 2013). It can occur between individuals of the same species as well as between individuals belonging to different species. Ecological and evolutionary aspects of interspecific aggression are, however, understudied compared to other interspecific interactions (Grether et al., 2013).

In some animal groups including birds, acoustic signals facilitate territory defence besides their function in mate choice and changes in such signals can have important consequences for aggressive interactions (Maynard Smith & Harper, 2003). Such changes often occur in secondary contact zones of closely related species (reviewed in Grether, Losin, Anderson, & Okamoto, 2009). It is often assumed that divergence in vocalization will evolve after secondary contact to minimize hybridization (Kirschel, Blumstein, & Smith, 2009; Sætre et al., 1997; Seddon, 2005). Convergence of acoustic signals in secondary contact zones, however, is also frequent, especially in birds (Haavie et al., 2004; Helb, Dowsett–Lemaire, Bergmann, & Conrads, 1985; Lemaire, 1977). This is probably because in many birds, particularly in passerines, vocalization is not genetically determined but learned through an imprinting-like process (Price, 2008). Misdirected imprinting and heterospecific

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learning can lead to transfer of vocal characters from one species to another resulting in song convergence in sympatry (Dalziell, Welbergen, Igic, & Magrath, 2014; Haavie et al., 2004; Helb et al., 1985). Such song convergence is usually considered to be mal-adaptive, as it can increase the rate of interspecific hybridization (Qvarnström, Haavie, Sæther, Eriksson, & Pärt, 2006). However, according to the theory of agonistic character displacement, song convergence can be positively selected in species that overlap broadly in resource use as it leads to better distinction of territory boundaries between the species and thus reduces the level of interspecific competition (Cody, 1969; Grether et al., 2009). Empirical evidence for such convergent agonistic character displacement, however, is so far scarce (Tobias & Seddon, 2009).

Two closely related songbird species, the common nightingale, *Luscinia megarhynchos*, and the thrush nightingale, *Luscinia luscinia*, represent a particularly interesting system to study how conver-gence in vocal signals affects competitive interactions and the speciation process. These species diverged approximately 1.8 million years ago (Storchová, Reif, & Nachman, 2010), and their ranges came into secondary contact with a narrow zone of sym-patric occurrence in central and eastern Europe (Cramp, 1988), where they occasionally hybridize (Becker, 2007; Kverek, Storchová, Reif, & Nachman, 2008; Reifová, Kverek, & Reif, 2011). The species are morphologically very similar, but some distinctive species-specific diagnostic traits exist in body size, coloration and plumage (Svensson, 1992). The common nightingale and the thrush nightingale prefer the same dense shrubby habitats, mostly on moist sites (Cramp, 1988), and their territories are often in close proximity (Becker, 1995). Interspecific competition between these species can be inferred from spatially exclusive territories in sym-patry (Sorjonen, 1986) and ecological character displacement in beak morphology (Reifová, Reif, Antczak, & Nachman, 2011). Several lines of evidence suggest that the thrush nightingale, which is slightly larger than the common nightingale, is competitively more dominant (Reifová, Reif, et al., 2011; Stadie, 1991). In sym-patry, asymmetrical convergence in vocalization occurs: most thrush nightingales are mixed singers, incorporating common nightingale song types in their repertoires (Becker, 2007; Lille, 1988; Vokurková et al., 2013). The convergence is not caused by genetic introgression, but rather by heterospecific learning (Vokurková et al., 2013). This, however, does not mean that the tendency to asymmetric heterospecific learning cannot be geneti-cally determined (Grether et al., 2009). The interesting question thus remains whether the mixed singing in the thrush nightingale is adaptive in terms of improving competitor recognition, increasing interspecific territoriality and reducing the intensity of interspecific competition.

In this study, we performed playback experiments to study the intensity of aggressive reaction towards conspecific and hetero-specific males in both nightingale species in sympatry. Similar ex-periments on these species have been performed by Sorjonen (1986). However, Sorjonen (1986) only evaluated whether or not tested males reacted to the stimuli without quantification of reac-tion strength. Moreover, his methodology could have introduced substantial bias in the tested birds' responses owing to the nonin-dependence of the stimuli presented, and probably also by reuse of the same playback stimuli across experiments, resulting in pseu-doreplication (Kroodsma, Byers, Goodale, Johnson, & Liu, 2001).

Here we conducted playback experiments testing the response of males of both species in a sympatric zone in a rigorous design overcoming the methodological problems mentioned above. We focused on the following questions. First, does the thrush nightin-gale, as a larger and presumably competitively dominant species, show a stronger response to the heterospecific stimuli than the common nightingale? Second, does the mixed singing of the thrush

nightingale affect the intensity of its interspecific aggressive reac-tion? Based on the current knowledge of agonistic character displacement (Grether et al., 2009), we expected the strength of the thrush nightingale response to be similar to conspecific and het-erospecific stimuli, while a stronger response to the conspecific than to the heterospecific stimulus was expected in the common nightingale.

METHODS

Study Area

The study was conducted in a ca. 200 km^2 area near the towns of Pleszew and Zagorow in central Poland (Wielkopolska region; 52°01′N, 17°48′E), in a central area of sympatry where both species occur in similar densities. In this region, nightingales were studied in floodplains of the rivers Prosna and Warta providing ample suitable habitats. Both species were present at the same sites, and in most cases we did not observe any habitat segregation. Terri-tories of individual males did not overlap, and were often adjacent to each other irrespective of species identity.

Recording of Songs used as Playback Stimuli

Songs used for experiments were recorded in two areas of close allopatry: in the Czech Republic in 2007–2010 (common nightin-gale) and in northeastern Poland in 2009 (thrush nightingale). These allopatric areas were located 300 km and 350 km, respec-tively, from the sympatric study area and previous analyses confirmed that none of the individuals from these localities showed interspecific copying of song (Vokurková et al., 2013). As a control stimulus, we used songs of the willow warbler, *Phylloscopus tro-chilus*, a species occurring in high densities on the study sites among breeding nightingales. From each recording of an individual of a given species, a unique 150 s interval of good quality was cleaned from the background noise in the software Avisoft SASLab Pro version 5.2 (Specht, 2007) and then duplicated to create a 5 min long playback recording. In total, we had 58 of these 5 min re-cordings available for the experiments.

Experimental Design

The experiments were conducted in May 2011–2013, soon after the arrival of both species to their breeding sites, always within a 2-week period at the beginning of the breeding season to cover the period of the highest territorial activity of both species. Weather permitting; we worked in the morning (0600–1000 hours) and late afternoon (1600–2000 hours) when nightingales show high singing activity.

The general design of the experiment followed that of Turčoková, Pavel, Chutný, Petrusek, and Petrusková (2011) and was based on presenting playback songs of the focal species together with a corresponding taxidermic dummy (i.e. a specific dummy for each species). The taxidermic dummies were supplied by the Department of Zoology, Charles University in Prague, and showed all species-specific diagnostic traits (see Svensson, 1992). We first checked for individual territories by walking through the breeding sites and registering individual nightingales and their singing posts for several days at the beginning of the nightingale breeding sea-son. Before each experiment, we first detected the position of an individual selected for the experiment to confirm its presence in the territory. Then we placed a loudspeaker MIPRO MA-101 and a taxidermic dummy (of the species corresponding to the playback stimulus) into a territory of the target individual near its singing post. Once the focal male was detected visually or acoustically in its

territory, we played the song of either the common nightingale or the thrush nightingale for 5 min. The observers were hidden ca. 20 m from the loudspeaker and dummy, to avoid any influence of human presence on the bird's behaviour. We noted the behaviour of the tested male and recorded its vocal activity (using the Marantz PMD 660 recorder and Sennheiser ME 67 shotgun microphone) for 5 min during the playback. After this session, the first part of the experiment was finished.

We presented the stimuli in a random order to avoid possible order effects. To avoid habituation and interaction between subsequent stimuli, the tested male was exposed to the stimulus of the second nightingale species (with the same design) a day after we conducted the first experiment, at approximately the same time of day and in the same fashion. On the same day, we never tested individuals occupying territories situated within hearing distance of the bird exposed to playback. All experiments were conducted by M.J. (playbacks and recording songs of tested individuals) and J.R. (observing and noting behavioural activity).

The control stimulus (represented by the willow warbler) was presented a day after the second part of the experiment to some of the tested birds each year of the study. However, we never observed any response to this type of stimulus. Therefore, we performed the experiment with the control with nine birds only to show that the lack of response is consistent (see below). Reducing the number of experiments with the control stimulus allowed us to maximize the number of experiments with conspecific and heterospecific nightingale stimuli during the short period when males are willing to respond to the playback, as, in many species, males cease aggressive responses towards an intruder after their mates start incubation (e.g. Nowicki, Searcy, Krueger, & Hughes, 2002).

Data Analysis

In total, we tested 15 common nightingale and 15 thrush nightingale individuals with both conspecific and heterospecific stimuli. Data from presentations of the control stimulus were obtained from five common nightingales and four thrush nightingales.

The behavioural response was recorded during the 5 min period when the playback was presented. Our description of the behavioural response is generally based on approach measures because approaching the rival has been found to be a key component of aggressive behaviour in both species (Stadie, 1991). Although some specific song patterns also play a role in aggressive interactions in the common nightingale (e.g. Schmidt, Kunc, Amrhein, & Naguib, 2008), it would be difficult to apply them to the thrush nightingale, as the song structure of the latter species has been much less studied. We categorized responses as follows (adapted from Petrusková, Petrusek, Pavel, & Fuchs, 2007): approach (individual approaches close to the dummy suggesting an interest in it; the approach is repeated or prolonged, not caused by accidental movement of the tested bird), flyover (flight over or behind the dummy, at a distance of more than 1 m), running (excited running on the ground below the dummy), flight-attack (flight directed at the dummy, within 1 m, but not resulting in physical contact), physical contact (attack on the dummy; individual typically sitting on its back and pecking).

These behavioural categories were mutually exclusive (i.e. an individual could not show behaviour of more than one category at the same time), and for each individual we calculated the proportion of time spent performing the behaviour in each category during an experiment. In one experiment, the sum of these proportions equals the time when a given individual showed any response to a given stimulus. We also calculated the percentage of time spent singing during the experiment. This activity was

recorded independently of the five behavioural categories (see above); and we added the percentage of time singing to the analysis of the behavioural response.

All six variables summarizing the time investment in the five categories of nonvocal behavioural response (as defined above) and singing activity were subjected to a principal component analysis (PCA) because some variables were closely correlated with each other and thus were not independent (Table 1). The PCA was done on a correlation matrix of the arcsine-transformed variables (all variables were proportions). By means of PCA, we obtained new independent variables (PC axes) describing the most important gradients in the responses of tested individuals. The first two PC axes, which accounted for the largest part of the variability in nightingale responses (see Results), were taken as response variables for further analyses. We also estimated the minimum distance (m) to the dummy during the playback, and used it as an additional response variable in statistical analyses.

To test the differences between species in responses to the respective stimuli, we employed linear mixed-effects models relating the first PC axis, the second PC axis and the minimum distance to the dummy as the respective response variables to fixed effects of species (categorical variable with two levels: common nightingale and thrush nightingale), stimulus (categorical variable with two levels: conspecific and heterospecific) and their interaction. Although we presented the stimuli in random order (see above), we included the information about the order of a given stimulus presented (i.e. first or second) as a covariate to control for a possible order effect in the data (Petrusková, Petrusek, Pavel, & Fuchs, 2008). Since we presented two stimuli to each individual tested, we included the identification code of each individual as a categorical variable with random effects (as in Farwell & Marzluff, 2013).

The nightingale males never showed any interest during the playback of the willow warbler control stimulus (consistent with observations of Sorjonen (1986) who used the song of the bluethroat, *Luscinia svecica*, as a control). Thus, we did not include experiments with the control stimulus in the PCA and further analyses. Rather, we compared proportional time spent in aggressive responses (sum of all behavioural categories together, see above) between the control (willow warbler) and congeneric (i.e. the heterospecific nightingale) stimulus for each species separately by the linear mixed-effects model. The model contained the fixed-effect stimulus and order and the random effect of nightingale individual. The test confirmed a highly significant difference in the time spent in aggressive responses between the congeneric and control stimulus for both tested species: common nightingale – congeneric stimulus: mean = 95.20% of time spent in aggressive responses (SE = 0.91), control stimulus: mean = 0.00% (SE = 0.91), $F_{1,2} = 4811$, $P < 0.001$; thrush nightingale – congeneric stimulus: mean = 97.40% (SE = 1.09), control stimulus: mean = 0.00% (SE = 1.09), $F_{1,2} = 3550$, $P < 0.001$.

Ethical Note

Our study involved field observations of aggressive behaviour of 30 birds in response to two 5 min long playbacks. After the playback experiments, individual birds were caught, ringed and released by P.T.D. (ringing licence no. 55 and 61). Trapping and ringing were done in accord with The Nature Protection Act (Disposition no. 627 from 2013) in Poland. No birds were invasively sampled. Our research did not require approval by the Local Ethical Commission because the playback experiments do not fall within its authority in Poland according to The Act on Experiments on Animals (Disposition no. 289 from 2005). The playback was kept as short as possible to obtain data for the purposes of the current

Table 1
Variables describing behavioural response of males of the common nightingale and the thrush nightingale during playback experiments

Variable	Description	PC1	PC2	PC3	PC4
Approach	Approach to the dummy with signs of interest	−0.98	−0.15	0.13	0.01
Flyover	Flight over or behind the dummy	−0.05	0.13	−0.10	0.38
Running	Excited running below the dummy	0.15	0.01	−0.04	0.95
Flight-attack	Flight directed at the dummy (within 1 m)	0.00	−0.03	−0.04	0.35
Physical contact	Attack on the dummy	0.76	−0.25	0.60	0.00
Singing	Percentage of time spent singing	−0.34	0.90	0.27	0.00

The behavioural response was characterized by five variables represented by the mutually exclusive categories of behaviour (ordered by increasing aggressiveness from approach to physical contact) and one additional variable represented by singing. All six variables were subject to a principal component analysis. Relations of these variables to the four most important principal components (PC) are shown.

study and we are not aware of any consequences for subjects' breeding or welfare.

RESULTS

All males showed at least an interest in or, often, a stronger level of behavioural response to both conspecific and heterospecific playbacks. In other words, all individuals approached the dummy when exposed to the playback and 'approach' was also the behavioural category taking the highest proportion of time during the experiment (75% in the common nightingale and 85% in the thrush nightingale). Physical attacks on the dummy in response to the playback were also observed in both species. These attacks were more frequent among common nightingales (eight of 15 males attacked the dummy at least once) than thrush nightingales (five of 15 males).

The results of the PCA showed that the first PC axis (eigenvalue = 2.77) explained over 73.5% of the variability in nightingale responses to conspecific and heterospecific stimuli and was the only axis with an eigenvalue >1. This axis showed a gradient of increasing aggressiveness from weak responses represented by approaching to strong responses represented by physical attack and, to lesser extent, by running on the ground close to the dummy (Table 1, Appendix Fig. 1). The second PC axis (eigenvalue = 0.20) expressed the increasing proportion of time devoted to singing (Table 1, Appendix Fig. 1) but explained only 16.4% of the variability in responses. The remaining two axes did not provide a clear interpretation (Table 1) and accounted for a negligible part of the variability in responses (PC3: eigenvalue = 0.11, variability explained = 9.7%; PC4 eigenvalue = 0.00, variability explained = 0.2%).

The mixed-effects model performed with the first PC axis as a response variable showed that common nightingales generally responded more aggressively than thrush nightingales, irrespective of the stimulus (Table 2). Overall, the tested males (irrespective of species) were not more aggressive to the conspecific than to the heterospecific stimulus (Table 2). However, a significant interaction between species and stimulus indicates that responses to the two types of stimuli differed between the species (Table 2). The order effect was significant indicating that the stimuli presented first provoked a more aggressive response than the stimuli presented afterwards (Table 2). The order of stimuli was thus kept in the model to control for its effect.

The interpretation of the interaction between species and stimulus was elucidated by the analysis of contrasts (Fig. 1). The species did not differ in overall aggressiveness in response to the heterospecific stimulus ($t = 0.10$, $P = 0.923$), but the common nightingale was more aggressive in response to the conspecific stimulus than the thrush nightingale ($t = 2.12$, $P = 0.043$). The common nightingale responded significantly more aggressively to the conspecific than to the heterospecific stimulus ($t = 2.20$, $P = 0.036$; Fig. 1), but no difference was observed in the thrush nightingale ($t = -0.80$, $P = 0.432$; Fig. 1).

The mixed-effect models run for the second PC axis and for the minimum distance to the dummy as respective response variables did not find significant effects of any predictors (Table 2).

DISCUSSION

Our experiments, which quantified behavioural responses of two nightingale species to conspecific and heterospecific playbacks, revealed three important patterns. (1) Males of both species showed aggressive responses to each other's song (accompanied with a species-specific taxidermic dummy) but did not react to control stimuli. (2) The species did not differ in the level of aggressiveness in response to the heterospecific stimulus. (3) The common nightingale reacted significantly more aggressively to the conspecific stimulus than to the heterospecific stimulus, whereas the response of the thrush nightingale did not differ between stimuli.

The first pattern confirms the presence of interspecific aggression between nightingale species in sympatry already described by Sorjonen (1986). Individuals of both species were apparently excited by heterospecific playbacks and all tested birds approached the dummy in response to the playback. Moreover, physical attacks on the dummy were observed in heterospecific playback experiments in both nightingale species, although not in all individuals. This character of behavioural responses to simulated playback observed in nightingales is comparable to reactions observed in other passerines defending their territories such as *Phoenicurus* redstarts (Sedláček, Fuchs, & Exnerová, 2004) or *Acrocephalus* warblers (Catchpole, 1978). Moreover, the nightingales' congener, the bluethroat, which also boasts a highly complex song, showed similar levels of aggressive behaviour in response to playbacks of its different subspecies (Turčoková et al., 2011). Our demonstration of

Table 2
The effects of the type of stimulus, order of stimuli and species identity on the strength of aggressive response of the common nightingale and the thrush nightingale during playback experiments

Predictor variable	PC1			PC2			Minimum distance		
	df	F	P	df	F	P	df	F	P
Order	1,27	5.53	0.026	1,27	0.10	0.759	1,27	0.93	0.342
Species	1,28	5.12	0.032	1,28	0.90	0.350	1,28	0.99	0.329
Stimulus	1,27	1.33	0.259	1,27	1.46	0.237	1,27	1.57	0.221
Species∗stimulus	1,27	4.52	0.043	1,27	0.09	0.771	1,27	0.71	0.407

The strength of aggressive response was expressed by three different response variables: PC1, PC2 and minimum distance. PC1 quantifies the increasing level of aggressiveness from approach with signs of interest to an attack on the taxidermic dummy during the experiment (see Table 1). PC2 quantifies the increasing amount of time devoted to singing during the experiment (see Table 1). Minimum distance is the minimum distance of the tested individual to the dummy during the experiment. The type of stimulus is represented by the predictor variable 'stimulus' (conspecific versus heterospecific), the order of stimuli by the predictor variable 'order' (first versus second) and species identity by the predictor variable 'species' (the common nightingale versus the thrush nightingale). The effects of particular predictor variables were estimated by linear mixed-effects models run separately for each response variable.
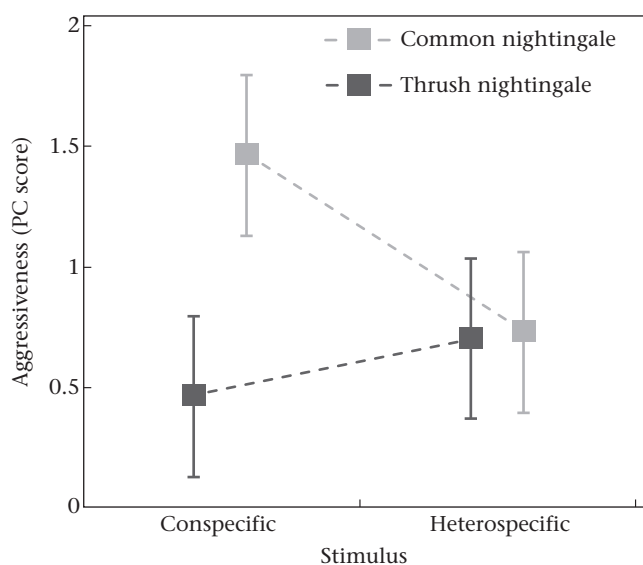
Figure 1. Aggressiveness of the behavioural response of nightingale males estimated by a linear mixed-effects model with the type stimulus (conspecific versus heterospecific) and species (the common nightingale versus the thrush nightingale) as predictors. Aggressiveness was quantified using scores along the first principal component (PC) axis revealed by PCA on six variables describing the behavioural response (see Table 1). Least-square means ± SE are depicted.

interspecific aggression is also consistent with the observation of interspecific territoriality on sites of co-occurrence (Ranoszek, 2001; Sorjonen, 1986) and implies the existence of interference competition between the two nightingale species in sympatry.

The previous study of Sorjonen (1986) suggested that males of the thrush nightingale, which is the larger and presumably competitively dominant species, are more aggressive in heterospecific reactions than common nightingale males. However, this finding could be a methodological artefact arising from the fact that stimuli were always presented in the same order (the thrush nightingale first, followed by the common nightingale) and the pause between stimuli was only 3 min in Sorjonen's study. Responses thus cannot be treated as independent; it seems likely that the reaction of tested thrush nightingale males to heterospecific stimuli was enhanced by the preceding conspecific playback (e.g. Lovell & Lein, 2004; Petrusková et al., 2008). We have not observed any such carryover effect in our study (which provided a sufficiently long, 1-day, break between the two stimuli). In fact, stronger reaction to the first playback stimuli resulted in a weak order effect, which was accounted for in the statistical analysis.

When we avoided the bias caused by the fixed order of stimuli in the playback experiments and quantified the level of males' response, we found that the smaller species, the common nightingale, was generally more aggressive. However, its higher aggressiveness was solely due to its stronger response to conspecific stimuli. When exposed to the heterospecific stimulus, the response of the common nightingale was much weaker, and did not differ significantly from that of the thrush nightingale. Interestingly, Stadie (1991) also suggested the common nightingale was more aggressive based on his observations of birds breeding in captivity. Our results suggest that competitive dominance of the larger thrush nightingale is not accompanied by increased aggressiveness. Similar examples have been described also in other avian and reptile species, although these typically involve distantly related taxa and not sister species (Martin & Ghalambor, 2014; Vanhooydonck, Van Damme, & Aerts, 2000).

A similar level of aggressiveness in the response of the thrush nightingale to both conspecific and heterospecific stimuli is unusual. Typically, territorial males react only to intrusions by conspecifics (Catchpole & Slater, 2008), and if heterospecific territoriality is observed, the reaction to conspecifics is usually stronger (e.g. Gil, 1997; Toms, 2013) as observed in the common nightingale. In the thrush nightingale, the asymmetry in interspecific copying of songs seems to be responsible for the observed pattern. Most males of the thrush nightingale in sympatry include parts of the common nightingale song in their repertoires, while such mixed singing does not occur in the common nightingale in sympatry (Becker, 2007; Vokurková et al., 2013) or is extremely rare (Lille, 1988). Furthermore, repertoires of some of these thrush nightingale mixed singers are actually dominated by the common nightingale song types (Vokurková et al., 2013). This copying could have an effect on the intensity of response of the thrush nightingale to the common nightingale song. Even a 'pure' common nightingale song recorded from allopatry presented in our experiment might be perceived by the focal thrush nightingale male as a song sung by a conspecific 'mixed singer'. In contrast, the common nightingale male would not mistake the heterospecific song presented in the experiment for the song of its own species, because we used recordings of the thrush nightingale from allopatry where the mixed singing was not detected (Vokurková et al., 2013).

Mixed singing in closely related bird species is usually considered to be maladaptive, resulting from erroneous learning (Helb et al., 1985). For example, in collared flycatchers, *Ficedula albicollis*, and pied flycatchers, *Ficedula hypoleuca*, mixed singing increases the rate of interspecific hybridization in sympatry and its frequency declines with the time since secondary contact (Haavie et al., 2004). As discussed in Vokurková et al. (2013), however, song convergence does not seem to substantially increase the rate of hybridization between nightingales. Vokurková et al. (2013) proposed two mechanisms by which the mixed singing in nightingales may have an adaptive value: (1) intraspecific female choice with preference for more complex songs resulting in increased fitness of the mixed singing thrush nightingale males in sympatry; and (2) territorial interactions between males of the two competing species. This latter alternative is supported by results from our playback experiments. We suggest that mixed singing in the thrush nightingale could be an adaptive response to interspecific competition. More similar heterospecific song may result in better competitor recognition and thus distinction of territory boundaries between the two species (Cody, 1969; Tobias et al., 2014). A similar relationship between song similarity and the intensity of male territorial response of co-occurring species has already been observed in *Hypocnemis* antbirds (Tobias & Seddon, 2009) and crested larks, *Galerida cristata*, and thekla larks, *Galerida theklae* (Laiolo, 2012). Together with our results, these studies show how interference competition may drive phenotypic convergence, which is a more common outcome of interspecific interactions than previously assumed (Tobias et al., 2014).

Further studies are needed, however, to provide more direct evidence on the possible role of song convergence in male–male aggressive interactions and its adaptive value in nightingales. We suggest that it can be tested by exposing individual males of both species to the sympatric songs with different levels of interspecific copying and/or different types of copied song. Furthermore, experiments investigating whether a tendency to mixed singing has a genetic basis should be performed (Grether et al., 2009).

Acknowledgments

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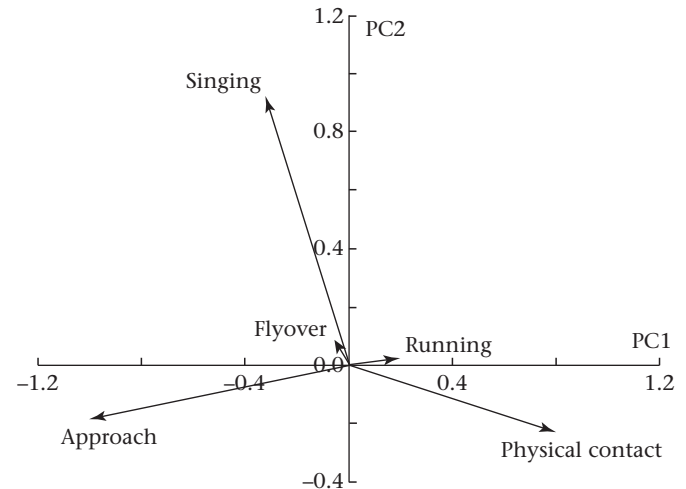
Appendix

Figure A1. Relationships between particular types of behavioural response of males of the common nightingale and the thrush nightingale during playback experiments and first two principal component axes (PC1 and PC2) revealed by PCA. Note that the response type 'flight-attack' is not depicted owing to the absence of correlation with any of the axes.