Ecological character displacement in the face of gene flow: evidence from two species of nightingales

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Common Nightingale (*Luscinia megarhynchos*)

- wider habitat niche
- looser in interspecific competition
- no song changes between sympatry and allopatry

Thrush Nightingale (*Luscinia luscinia*)

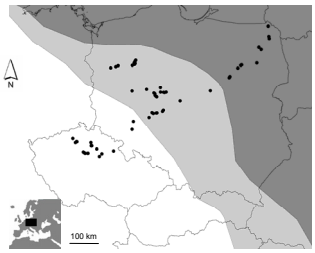
- narrower habitat niche
- winner in interspecific competition
- often sings *L. megarhynchos* song in sympatry

Introduction

Evolution of reproductive barriers is a complex process that can be facilitated by some interspecific interactions, while others lead to barriers' weakening and species fusion. Here we studied how interactions between two hybridizing bird species, the Thrush Nightingale (*Luscinia luscinia*) and the Common Nightingale (*Luscinia megarhynchos*), affect their morphological evolution and speciation.

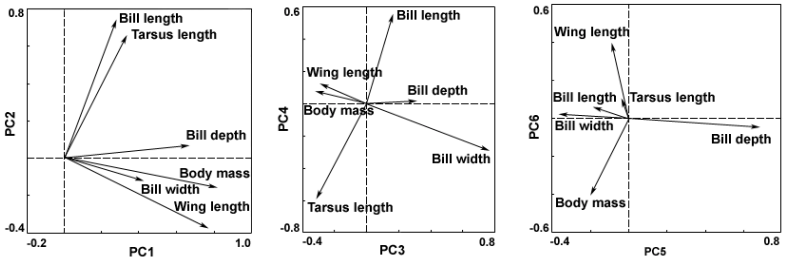
Sampling

We captured 173 males. Three of them were hybrids and were excluded from further morphological analyses.



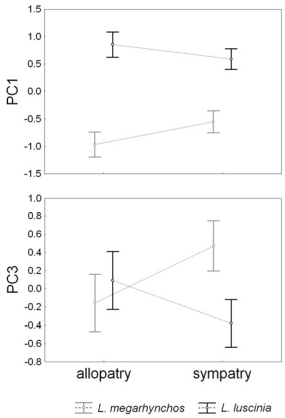
- allopatry, *L. luscinia* (35 individuals)
- sympatry, *L. luscinia* (52 individuals)
- sympatry, *L. megarhynchos* (47 individuals)
- allopatry, *L. megarhynchos* (36 individuals)

Principal component (PC) analysis of morphological traits

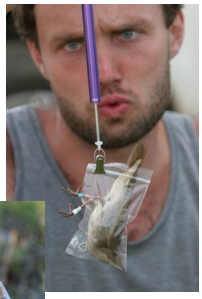


Results

1. Nightingales converged in overall body size (PC1) and diverged in relative bill size (PC3) in sympatry.



Two-way factorial ANOVA, species*region interaction p=0.002 for PC1, p<0.001 for PC3

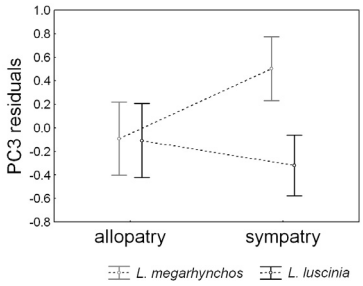


2. Convergence in body size (PC1) can be attributed largely to increasing body size with increasing latitude. The divergence in relative bill size (PC3) is better explained by interspecific interactions than by geographical gradients.

General linear models testing species*region interaction and controlling for the effects of latitude and longitude.

	latitude		longitude		species		region		species*region	
	F	p	F	p	F	p	F	p	F	p
PC1	128.6	**<0.001**	6.64	**0.011**	55.44	**<0.001**	0.14	0.713	0.3	0.585
PC3	0.83	0.364	9.1	**0.003**	12.52	**<0.001**	6.55	**0.011**	5.53	**0.02**

3. Divergence in bill size (PC3) was asymmetric and was caused mainly by increased bill size in *L. megarhynchos* in sympatry.



Analysis of contrasts, p < 0.001 for *L. megarhynchos* p = 0.306 for *L. luscinia*

Conclusion

We found that interspecific interactions in nightingales lead to divergence in relative beak size (PC3) in sympatry. This divergence could be caused either by selection against hybridization (reproductive character displacement) or selection for reduced interspecific competition (ecological character displacement). We argue that the first explanation is unlikely regarding the converge of male song in sympatry. More likely, bill size divergence reflects the starting segregation of feeding niches between the species in sympatry. **Our results are consistent with the idea that ecological character displacement could facilitate species divergence even in the face of ongoing hybridization and may therefore contribute to speciation.**

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