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Geographic variation in behaviour: an introduction

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INTRODUCTION

Environments vary across space and time, and behavioural divergence among populations is commonplace. Differences in behaviour may represent genetic divergence or phenotypic plasticity, and arise from abiotic or biotic factors. In turn, such differences in behaviour may promote reproductive isolation and speciation, and they may also influence how traits such as mating displays relate to fitness. With these realizations there has been an enormous increase in the number of studies and techniques used to study geographic variation in behaviour, especially since the publication of Foster and Endler's (1999) book, *Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms*. The new body of work makes important contributions to our understanding of the patterns, processes, and consequences of geographic variation in behaviour. This work remains to be incorporated into mainstream evolutionary theory. For example, researchers still too often characterize species with single populations, and even in comparative studies researchers often use a single estimate for an entire species.

This special collection originated from the symposium '*Geographic Variation in Behaviour*' at the 2011 Annual Animal Behavior Society meeting in Bloomington, Indiana. Caitlin R. Gabor and Andrea S. Aspbury organized the symposium. As organizers of the symposium, and together with Rafael L. Rodríguez as editors of this special volume, our goal was to attract the best possible set of papers. All the contributed papers emphasize the connection between geographic variation and speciation, and provide empirical insights into this connection. The contributed papers also represent varied approaches to understanding animal behaviour – the different authors use diverse techniques and perspectives, and do so at varying taxonomic scales. With this collection we wish to understand how research on geographic variation in behaviour is shaping our understanding of the mechanisms that result in geographic variation and its contributions to reproductive isolation and speciation.

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EVOLUTIONARY PROCESSES AND SPECIATION

By focusing on geographic variation in the conditions that a species faces across its geographic range, and the influence of this variation on behaviour, we can gain a better understanding of evolutionary process. For example, within a species, similar phenotypes may be expressed by the same or different genetic variants via the same or different combinations of plasticity and genetic change (West-Eberhard, 2005). However, populations are often connected, and gene flow can reduce behavioural variation across a species' geographic range. If the spatial scale of the variation in selection across populations is less than that of the spatial scale of variation in gene flow, then populations may evolve adaptive phenotypic plasticity (Thompson, 2005). Within a species, similar phenotypes may be expressed by the same or different genetic variants via the same or different combinations of plasticity and genetic change. Studies of geographic variation in behaviour also provide insight into the speciation process, such as investigations of incipient species, interactions between closely related sympatric species, and co-evolving populations (Thompson *et al.*, 2002; Chek *et al.*, 2003; Hoskin and Higgie, 2010). Finally, studies focusing on geographic variation in response to current rapid environmental change will provide further insight into the speciation process (Hanifin *et al.*, 2008).

Gerhardt (2013) discusses geographic variation in acoustic communication, focusing on case studies of reproductive character displacement and assessing when such patterns of geographic variation are more or less likely to occur in nature. Gerhardt also evaluates how reproductive character displacement may promote cascades of speciation in which assortative mating occurs on the basis of differences in the signals of displaced and non-displaced populations. Gerhardt's paper ties in nicely with the paper by Langerhans and Makowicz (2013), which relates patterns of sexual selection and divergence in mate preferences to ecological causes of divergence. In Langerhans and Makowicz's paper the pattern is a result of the presence or absence of predators, whereas in Gerhardt's paper the pattern involves the presence of closely related species.

Variation in interspecific interactions across populations may also contribute to variation in assortative mating across populations (Hoskin and Higgie, 2010; Gerhardt, 2013). In addition, these relationships can change over time due to length of co-existence and thus it is important to examine not just variation across a species' geographic range, but also variation in behaviour across time (Gabor *et al.*, 2013). Along these lines, Pröhl *et al.* (2013) address patterns of geographic variation and genetic distance related to divergence in mating calls and in coloration traits that vary in the strength of selection stemming from predators and from mate choice. Pröhl *et al.* focus on linking differences in both behavioural and body coloration traits to genetic population structure in two widely distributed species. They point out the need to link the mechanisms of sexual and natural selection during speciation, especially in broadly distributed species.

Nosil *et al.* (2013) and Foster (2013) each consider how environmental variation affects behavioural variation, and what the effects of this variation are. Nosil *et al.* integrate examination of climatic variation across the landscape occupied by populations of stick insects with prior studies of host-plant use, reinforcement, and patterns of gene flow, to better understand geographic variation in mating and feeding behaviour in this system. Similarly, Foster evaluates the additional impact of response to rapid environmental change on geographic variation in behaviour along with how rapid environmental change can affect evolutionary rescue and extinction probabilities. Finally, Rodríguez (2013) addresses some

mechanisms that can sustain genetic variation in phenotypically plastic traits within and across sites and over time.

DISCUSSION

What have we learned?

The papers presented in this issue provide examples of studies that consider geographic variation in behaviour in appropriate contexts and suggest new directions to consider for those who are examining geographic variation. Langerhans and Makowicz (2013) argue that more studies should directly address the mechanistic role of sexual selection during speciation to complement comparative studies. Such an approach should lead to a richer understanding of the role of mating behaviours in speciation. Furthermore, research should focus on tying together more closely studies of reproductive character displacement and ecological speciation (Gerhardt, 2013). In many cases, they are thought of separately but ecological speciation may drive reproductive character displacement. Langerhans and Makowicz (2013) propose important ways to reveal if these two factors act in unison. Both Gerhardt (2013) and Gabor *et al.* (2013) explore the causes and consequences of reproductive character displacement in their study systems but have not directly tested whether the divergence in assortative mating is linked to natural or sexual selection. Testing these hypotheses in systems that show geographic variation in behaviour is a fruitful avenue to explore.

Rodríguez (2013) suggests that researchers should examine geographic variation not only in traits but also in phenotypic plasticity of those traits by comparing patterns among sites and over time. By comparing reaction norms between environments, it may be possible to understand the developmental and selective factors that shape patterns of geographic variation, predict likely responses to future environmental change, and evaluate how far the speciation process has progressed. Indeed, Nosil *et al.* (2013) point out the need to study direct environmental effects of climate on behavioural changes such as mating and feeding preferences. Future studies need to address this by first examining the genetic basis to the traits of focus and then considering novel rearing systems to examine the reaction norms of the species. Another fruitful approach will be to design studies that allow us to determine which factors sustain genetic variation in plasticity under selection across geographic ranges of species.

Similarly, the discussion by Nosil *et al.* (2013) of the effects of climate on host preference links with the discussion of Foster (2013) on rapid environmental change. Many species and species interactions are facing the effects of rapid environmental change. It is therefore important to study the same populations over time, as such studies may provide more insight into how – or if – rapid environmental change is affecting populations. Indeed, this is what has been found in sticklebacks as an outcome of the long-term studies on the same populations (Behm *et al.*, 2010).

We hope that this special issue will inspire informed research into the causes and consequences of geographic variation in behaviour. Although much has been learned since Foster and Endler (1999), it is evident that much more is still to be discovered.

REFERENCES

Behm, J.E., Ives, A.R. and Boughman, J.W. 2010. Breakdown in postmating isolation and the collapse of a species pair through hybridization. *Am. Nat.*, **175**: 11–26.

Chek, A.A., Bogart, J.P. and Lougheed, S.C. 2003. Mating signal partitioning in multi-species assemblages: a null model test using frogs. *Ecol. Lett.*, **6**: 235–247.

Foster, S.A. 2013. Evolutionary insights from behavioural geography: plasticity, evolution and responses to rapid environmental change. *Evol. Ecol. Res.*, **15**: 705–731.

Foster, S.A. and Endler, J.A. 1999. *Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms.* New York: Oxford University Press.

Gabor, C.R., Alberici da Barbiano, L. and Aspbury, A.S. 2013. Geographic variation in male mate choice in a gynogenetic species complex: evaluating long-term data across mating contexts. *Evol. Ecol. Res.*, **15**: 653–666.

Gerhardt, H.C. 2013. Geographic variation in acoustic communication: reproductive character displacement and speciation. *Evol. Ecol. Res.*, **15**: 605–632.

Hanifin, C.T., Brodie, E.D., Jr. and Brodie, E.D., III. 2008. Phenotypic mismatches reveal escape from arms-race coevolution. *PLoS Biol.*, **6**: 471–482.

Hoskin, C.J. and Higgie, M. 2010. Speciation via species interactions: the divergence of mating traits within species. *Ecol. Lett.*, **13**: 409–420.

Langerhans, R.B. and Makowicz, A.M. 2013. Sexual selection paves the road to sexual isolation during ecological speciation. *Evol. Ecol. Res.*, **15**: 633–651.

Nosil, P., Riesch, R. and Muschick, M. 2013. Climate affects geographic variation in host-plant but not mating preferences of *Timema cristinae* stick-insect populations. *Evol. Ecol. Res.*, **15**: 689–704.

Pröhl, H., Willink, B. and Hauswaldt, S. 2013. Geographic variation in sexual signals and behaviour in two species of poison frogs. *Evol. Ecol. Res.*, **15**: 667–687.

Rodríguez, R.L. 2013. Causes of variation in genotype × environment interaction. *Evol. Ecol. Res.*, **15**: 733–746.

Thompson, J.N. 2005. *The Geographic Mosaic of Coevolution*. Chicago, IL: University of Chicago Press.

Thompson, J.N., Nuismer, S.L. and Gomulkiewicz, R. 2002. Coevolution and maladaptation. *Integr. Comp. Biol.*, **42**: 381–387.

West-Eberhard, M.J. 2005. Developmental plasticity and the origin of species differences. *Proc. Natl. Acad. Sci. USA*, **102**: 6543–6549.