overcome. This result is especially intriguing since it could mean that flies drink despite an aversive reaction to the ethanol-containing solution. To test this possibility more directly, Devineni and Heberlein [6] presented flies with quinine, an aversive tasting compound. Flies avoid drinking quinine-containing food (Figure 1B), and the authors found that, indeed, when quinine was added to ethanol-containing food, they initially avoided the cocktail. Over the next four days, though, they started preferring the ethanol/quinine food over regular food, while still avoiding quinine food versus regular food (Figure 1C). These findings indicate that over time flies are willing to 'suffer' adverse consequences, or at least taste, in order to drink ethanol.

After showing that flies escalate their drinking, and are willing to overcome adversity for it, Devineni and Heberlein [6] set out to test whether flies would show relapse behavior. Relapse is defined as the reinstatement of drug-taking behavior after a period of (forced) abstinence in a previously addicted individual. To do this, flies were fed ethanol to establish a strong preference, and then they were fed sugar-containing food only for one, or three days. After this forced abstinence, when they were given a choice again between sucrose/yeast solution with or without ethanol, they immediately returned to strong ethanol-preference, and did not show the low preference typical for naïve flies. Thus, flies show escalating drinking behavior, are willing to overcome adverse taste to drink, and show relapse-like behavior after forced abstinence.

Repeated drug-taking results in tolerance — more drug needs to be consumed in order to attain the same subjective and physiological responses. Tolerance is one of the diagnostic criteria for addiction, and since it reflects a nervous system adaptation, is believed to play a role in the development of addiction. Flies develop tolerance to repeat ethanol administration [9,10], and a collection of *Drosophila* learning and memory mutants showed a high incidence of ethanol tolerance defects [11]. Of the 27 sensitivity and tolerance mutants Devineni and Heberlein [6] then tested for ethanol preference, one, *krasavietz*, showed a preference defect. It is surprising that only one of these mutants would have an ethanol preference defect, given that many mouse mutants with altered naïve ethanol responses show changes in drinking behavior too [4]. Nevertheless, the data show that ethanol-drinking in flies is a genetically tractable behavior, and it will be interesting to see in the future whether pathways that are important in naïve alcohol sensitivity and in the development of tolerance play a vital role in determining whether flies like to drink. The new study [6] will certainly help us on the way towards understanding the molecular and genetic underpinnings of why flies, and some of us humans, like to drink and may become addicted.

**References**
1. American Psychiatric Association (1994). Diagnostic and Statistical Manual of Mental Disorders (Washington, DC: American Psychiatric Association).
2. Goldman, D., Oroszi, G., and Ducci, F. (2005). The genetics of addictions: uncovering the genes. Nat. Rev. Genet. *6*, 521–532.
3. Schuckit, M.A. (1994). Low level of response to alcohol as a predictor of future alcoholism. Am. J. Psych. *151*, 184–189.
4. Crabbe, J.C., Phillips, T.J., Harris, R.A., Arends, M.A., and Koob, G.F. (2006). Alcohol-related genes: contributions from studies with genetically engineered mice. Addic. Biol. *11*, 195–269.
5. Cadieu, N., Cadieu, J.-C., El Ghadraoui, L., Grimal, A., and Lambœuf, Y. (1999). Conditioning to ethanol in the fruit fly — a study using an inhibitor of ADH. J. Insect Physiol. *45*, 579–586.
6. Devineni, A.V., and Heberlein, U. (2009). Preferential ethanol consumption in *Drosophila* models features of addiction. Curr. Biol. *19*, 2126–2132.
7. Cami, J., and Farre, M. (2003). Drug addiction. New Engl. J. Med. *349*, 975–986.
8. Ja, W., Carvalho, G., Mak, E., De La Rosa, N., Fang, A., Liong, J., Brummel, T., and Benzer, S. (2007). Prandiology of Drosophila and the CAFE assay. Proc. Natl. Acad. Sci. USA *104*, 8253–8256.
9. Scholz, H., Ramond, J., Singh, C.M., and Heberlein, U. (2000). Functional ethanol tolerance in Drosophila. Neuron *28*, 261–271.
10. Atkinson, N.S. (2009). Tolerance in Drosophila. J. Neurogenet. *23*, 293–302.
11. Berger, K., Kong, E.C., Dubnau, J., Tully, T., Moore, M.S., and Heberlein, U. (2008). Ethanol sensitivity and tolerance in long-term memory mutants of Drosophila melanogaster. Alcohol. Clin. Exp. Res. *32*, 895–908.

University of Texas Southwestern Medical Center, Department of Psychiatry and Program in Neuroscience, 5323 Harry Hines Blvd., Dallas, TX 75390-9127, USA.
E-mail: adrian.rothenfluh@utsouthwestern.edu

DOI: 10.1016/j.cub.2009.10.057

---

# Speciation: New Migratory Direction Provides Route toward Divergence

**Biogeographic patterns suggest that divergent migratory behaviors can drive the evolution of new species. New research on warblers reveals that a novel migratory direction has resulted in genetic and phenotypic divergence.**

**Darren E. Irwin**

Two species can evolve from one as a result of adaptation into two distinct ecological niches [1]. Ernst Mayr argued that such shifts into new ecological niches are "almost without exception initiated by a change in behavior" [2]. One behavior that is of crucial importance to many organisms is seasonal migration [3]; this allows organisms to survive periods of low resources in their breeding habitats. An intriguing question is whether divergent shifts in migratory behavior might often initiate speciation.

Blackcap warblers (*Sylvia atricapilla*) provide a fascinating system for the study of migration. Decades of research [4–8] have revealed at least three distinct migratory behaviors (Figure 1): blackcaps breeding in western Europe tend to migrate southwestward in the autumn into Spain and then south toward west Africa, whereas those breeding in eastern Europe tend to migrate southeastward. During the past half-century, a somewhat counterintuitive third behavior has emerged: some blackcaps breeding in central Europe now migrate northwestward and winter in the United Kingdom, apparently a result of the increasing number of bird feeders in the country. Remarkably, orientation

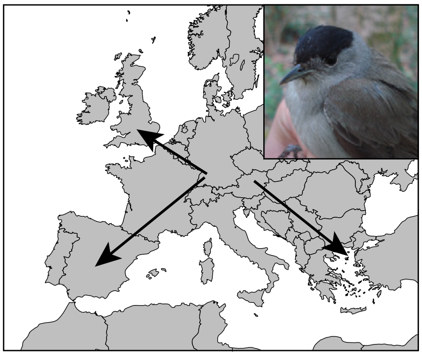


Figure 1. The three major autumn migratory directions taken by breeding blackcap warblers in central Europe.

In western Germany, most blackcaps migrate southwestward, while a small but growing portion of the population migrates northwestward into the UK. In Austria and much of eastern Europe, blackcaps orient southeastward. A male blackcap is shown at upper right (photo: Gregor Rolshausen).

experiments using lab-reared birds have shown that these migratory directions are genetically encoded, and that hybrids display instinctive orientations that are intermediate to the parental groups [4,7].

Two recent studies [9,10] have examined whether this novel northwestward migration is contributing to population differentiation and speciation. Both examined birds breeding in central Europe and inferred wintering location from stable isotopes in claws of breeding birds. Bearhop *et al.* [9] concluded that there is assortative mating based on wintering location, possibly due to differences in the timing of breeding. In this issue, Rolshausen *et al.* [10] report exciting new evidence that the northwest-migrating blackcaps are diverging genetically and phenotypically from those that migrate southwest.

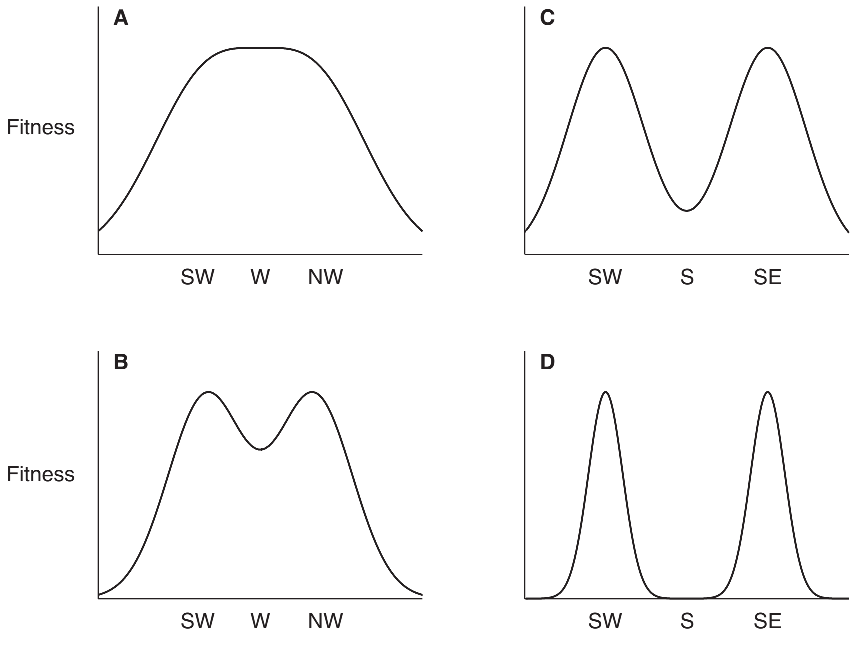
Rolshausen *et al.* [10] show that the two groups have diverged in molecular markers (microsatellites), wing pointedness, beak shape, and beak and plumage colors. While the amount of genetic divergence is small ($F_{ST}$ = 0.008), it is statistically significant and greater than that between two southwest-migrating populations separated by distance. Divergence in the phenotypic traits is also small but significant: wings are on average rounder in the northwestern migrants, apparently due to the shorter migratory route to Britain. Beaks are pointier in the northwestern migrants, which the authors attribute to a shift in winter food from fruits for southwest migrants to seeds and fat (in bird feeders) for northwest migrants. The browner beaks and plumage among northwest migrants is more mysterious; Rolshausen *et al.* [10] suggest that they may be brought on by differing environmental conditions. Altogether, these results indicate that the novel migratory route has resulted in divergence in a variety of traits after a relatively short period of time (roughly half a century). These changes are particularly notable because the two migratory groups breed in the same region, as there is little evidence for sympatric speciation in birds [11].

The literature on bird migration is filled with two seemingly contradictory ideas: that migration is highly labile [10,12], and that migration is highly conserved [13–15]. The rapid growth in northwestward migration in blackcaps has been used as a prime example of how easily migratory routes can change [12]. But broad biogeographic patterns have led to the conclusion that migratory routes can be highly constrained. Migratory species, somewhat counterintuitively, tend to have smaller breeding ranges than nonmigratory species [13,14], possibly due to constraints on range expansion; expanding into new breeding ranges requires changes to the migratory program. This may explain why some major groups of migratory birds in the Northern Hemisphere are confined either to Eurasia or North America (for example, New World *versus* Old World warblers, which are distinct evolutionary clades) [15].

How can we reconcile these competing ideas of lability and constraint of migratory behavior? I suggest the heuristic tool of adaptive landscapes, in which fitness is plotted as a function of trait value (Figure 2). We can visualize a population as being located on an adaptive peak corresponding to its current migratory behavior [15], with an alternative potentially good migratory behavior as a second adaptive peak. What determines whether part of the population shifts to the new adaptive peak? First, the distance between the peaks compared to the current variation in the population determines the size of mutational changes that are needed; if the mutational changes required are too large, they will be unlikely to occur. Second, the shallowness of the fitness valley between the two peaks determines how easily the population can move from one peak to the other. If the valley is shallow, the population can easily move by gradual change to the new peak; if the valley is deep, only a major mutation can move an individual to the new peak, but breeding between that individual and one on the original peak would likely produce offspring that fall in the fitness valley. Thus, some shifts in migratory behavior can evolve easily, while others may be so difficult that they do not occur. For example, expansion of a warbler species between Eurasia and North America would apparently require too big a change in migratory behavior.

Adaptive landscapes can also be used to visualize the process of speciation. Speciation is most likely to occur when there is a deep valley between two adaptive peaks. In the case of the blackcaps, an important unanswered question is whether there is selection against intermediates; demonstrating assortative mating (for example, [9]) is not equivalent to showing divergent adaptive peaks. Maps of blackcap wintering distributions (for example, [16]) show a continuous distribution from the southwestern to northwestern sides of Europe, raising the possibility that there is not strong selection against birds with intermediate orientation between southwest and northwest. The isotopic signatures also show a full range of values [9,10,17], suggesting that birds may not be divided into discrete areas in the winter. It should also be noted that the amount of divergence in molecular markers and morphological traits is still rather small, certainly nowhere near the usual level of differentiation between distinct species. In a companion paper, Rolshausen *et al.* [17] note that the amount of reproductive isolation based on timing of breeding is rather small.

Another migratory divide within blackcaps, that between southwest and southeast migrants, is associated with much more divergence and apparently greater selection against hybrids [4,5,8,10]. In an orientation



Current Biology

Figure 2. Possible adaptive surfaces representing the fitness of birds in relation to their instinctive autumn migratory direction.

In blackcaps, the situation in western Germany is most likely well represented by either (A), in which there is no selection against intermediates, but rather a broad range of migratory orientations from southwest to northwest is of roughly constant fitness, or (B), in which there is some selection against intermediates. The situation in southeastern Germany and Austria is most likely well represented by (C), in which there is strong selection again intermediates, due to the challenges of crossing the Alps, the Mediterranean, and possibly the Sahara Desert. Migratory divides in central Siberia [15] may be best represented by (D), in which there is a deep and wide fitness valley between peaks. In the latter case, evolution from one peak to the other is nearly impossible; if there are populations on both peaks, hybridization is strongly selected against.

experiment using captive birds, Helbig [4] showed that hybrids between these groups orient directly south, a direction that would take them over the Alps and into the Mediterranean at its widest point. Presumably such a route would be of low fitness, possibly promoting further reproductive isolation between these groups [4]. This migratory divide is reminiscent of others in Europe, such as in willow warblers in Sweden [18,19], as well as those in Siberia [15] and North America [20]. In particular, patterns of species diversification in Siberia appear strongly associated with alternative migratory routes around the Tibetan Plateau [15]. In these cases, there appear to be large fitness valleys between two adaptive peaks for differing migratory behavior. The populations arrived on divergent peaks not by evolving directly from one peak to the other, but rather by way of gradual evolution of more divergent migratory routes during their time in glacial refugia [15].

Overall, the genetic and morphological divergence revealed by Rolshausen *et al.* [10] demonstrates an important prediction of the hypothesis that divergent migratory routes may be contributing to the evolution of reproductive isolation. Perhaps future work can test another important prediction: that blackcaps with intermediate migratory orientation are selected against. Blackcaps provide a wonderful model system for the evolution and ecology of migration, the impacts of humans on the evolutionary trajectories of wild species, and the role of migratory behavior in speciation.

## References

1. Schluter, D. (2009). Evidence for ecological speciation and its alternative. Science *323*, 737–741.
2. Mayr, E. (1963). Animal Species and Evolution (Cambridge, MA: Harvard University Press).
3. Dingle, H. (1996). Migration: The Biology of Life on the Move (Oxford: Oxford University Press).
4. Helbig, A.J. (1991). Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). Behav. Ecol. Sociobiol. *28*, 9–12.
5. Helbig, A.J. (1991). SE- and SW-migrating Blackcap (*Sylvia atricapilla*) populations in Central Europe: Orientation of birds in the contact zone. J. Evol. Biol. *4*, 657–670.
6. Berthold, P., Helbig, A.J., Mohr, G., and Querner, U. (1992). Rapid microevolution of migratory behaviour in a wild bird species. Nature *360*, 668–670.
7. Helbig, A.J., Berthold, P., Mohr, G., and Querner, U. (1994). Inheritance of a novel migratory direction in central European blackcaps. Naturwissenschaften *81*, 184–186.
8. Pérez-Tris, J., Bensch, S., Carbonell, R., Helbig, A.J., and Tellería, J.L. (2004). Historical diversification of migration patterns in a passerine bird. Evolution *58*, 1819–1832.
9. Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P., and Farnsworth, K. (2005). Assortative mating as a mechanism for rapid evolution of a migratory divide. Science *310*, 502–504.
10. Rolshausen, G., Segelbacher, G., Hobson, K.A., and Schaefer, H.M. (2009). Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. Curr. Biol. *19*, 2097–2101.
11. Price, T. (2008). Speciation in Birds (Greenwood Village, Colorado: Roberts & Co. Publishers).
12. Pulido, F. (2007). The genetics and evolution of avian migration. BioScience *57*, 165–174.
13. Böhning-Gaese, K., González-Guzmán, L.I., and Brown, J.H. (1998). Constraints on dispersal and the evolution of the avifauna of the Northern Hemisphere. Evol. Ecol. *12*, 767–783.
14. Bensch, S. (1999). Is the range size of migratory birds constrained by their migratory program? J. Biogeogr. *26*, 1225–1235.
15. Irwin, D.E., and Irwin, J.H. (2005). Siberian migratory divides: the role of seasonal migration in speciation. In Birds of Two Worlds: The Ecology and Evolution of Migration, R. Greenberg and P.P. Marra, eds. (Baltimore, Maryland: Johns Hopkins University Press), pp. 27–40.
16. Aymí, R., and Gargallo, G. (2006). Blackcap: *Sylvia atricapilla*. In Handbook of the Birds of the World. Vol. 11. Old World Flycatchers to Old World Warblers, J. del Hoyo, A. Elliott, and D.A. Christie, eds. (Barcelona: Lynx Edicions), pp. 693–694.
17. Rolshausen, G., Hobson, K.A., and Schaefer, H.M. (2009). Spring arrival along a migratory divide of sympatric blackcaps (*Sylvia atricapilla*). Oecologia Online First doi: 10.1007/s00442-009-1445-3.
18. Bensch, S., Grahn, M., Müller, N., Gay, L., and Åkesson, S. (2009). Genetic, morphological, and feather isotope variation of migratory willow warblers show gradual divergence in a ring. Mol. Ecol. *18*, 3087–3096.
19. Irwin, D.E. (2009). Perspective: Incipient ring speciation revealed by a migratory divide. Mol. Ecol. *18*, 2923–2925.
20. Ruegg, K. (2007). Genetic, morphological, and ecological characterization of a hybrid zone that spans a migratory divide. Evolution *62*, 452–466.

Biodiversity Research Centre, and Department of Zoology, University of British Columbia, 6270 University Blvd., Vancouver, BC, V6T 1Z4, Canada.
E-mail: irwin@zoology.ubc.ca

DOI: 10.1016/j.cub.2009.11.011