

unlikely to be as dramatic as is often presupposed. The evolution of the mammalian olfactory processing system and its connections with hypothalamic and other regions controlling reproductive physiology and behavior have resulted in a far more flexible and integrated system than that for processing pheromones in invertebrates. We are unlikely, therefore, to discover mammalian pheromones which drive an inevitable and unconscious behavioral or physiological reaction such as that portrayed, for example, in Roald Dahl's celebrated short story *Bitch* [20] which features a fictional odourant cocktail capable of driving men to exhibit unconscious intense and insatiable sexual responses to women.

References

1. Karlson, P., and Lüscher, M. (1959). 'Pheromones': a new term for a class of biologically active substances. *Nature* 183, 55–56.
2. Baxi, K.N., Dorries, K.M., and Eisthen, H.L. (2006). Is the vomeronasal system really specialized for detecting pheromones. *Trends Neurosci.* 29, 1–7.
3. Baum, M.J., and Bakker, J. (2013). Roles of sex and gonadal steroids in mammalian pheromonal communication. *Front. Neuroendocrinol.* 34, 268–284.
4. Novotny, M.V., Ma, W., Wiesler, D., and Židek, L. (1999). Positive identification of the puberty-accelerating pheromone of the house mouse: the volatile ligands associating with the major urinary protein. *Proc. Roy. Soc. Lond. B* 266, 2017–2022.
5. Haga, S., Hattori, T., Sato, T., Sato, K., Matsuda, S., Kobayakawa, R., Sakano, H., Yoshihara, Y., Kikusui, T., and Touhara, K. (2010). The male mouse pheromone ESP1 enhances female sexual receptive behavior through a specific vomeronasal receptor. *Nature* 466, 118–122.
6. Singer, A.G., Agosta, W.C., Clancy, A.N., and Macrides, F. (1987). The chemistry of vomeronasally detected pheromones: characterization of an aphrodisiac protein. *Ann. NY. Acad. Sci.* 519, 287–298.
7. Booth, W.D. (1982). Steroid hormone and pheromone binding proteins in submaxillary gland and saliva of pig. In *Olfaction and Endocrine Regulation*, W. Breipol, ed. (London: IRL Press), pp. 353–356.
8. Delgado, J.A., Gelez, H., Ungerfeld, R., Hawken, P.A.R., and Martin, G.B. (2009). The 'male effect' in sheep and goats – revisiting the dogmas. *Behav. Brain Res.* 200, 304–314.
9. Murata, K., Tamogami, S., Itou, M., Ohkubo, Y., Wakabayashi, Y., Watanabe, H., Okamura, H., Takeuchi, Y., and Mori, Y. (2014). Identification of an olfactory signal molecule that activates the central regulator of reproduction in goats. *Curr. Biol.* 24, 681–686.
10. Murata, K., Wakabayashi, Y., Sakamoto, K., Tanaka, T., Takeuchi, Y., Mori, Y., and Okamura, H. (2011). Effects of brief exposure of male pheromone on multiple-unit activity at close proximity to kisspeptin neurons in the goat arcuate nucleus. *J. Reprod. Dev.* 57, 197–202.
11. Sakamoto, K., Wakabayashi, Y., Yamamura, T., Tanaka, T., Takeuchi, Y., Mori, Y., and Okamura, H. (2013). A population of kisspeptin/neurokinin B neurons in the arcuate nucleus may be the central target of the male effect phenomenon in goats. *PLoS One* 8, e81017.
12. Brennan, P.A., and Kendrick, K.M. (2006). Mammalian social odours: attraction and individual recognition. *Phil. Trans. Roy. Soc. B.* 361, 2061–2078.
13. Dulac, C., and Torello, A.T. (2003). Molecular detection of pheromone signals in mammals: from genes to behaviour. *Nat. Rev. Neurosci.* 4, 551–562.
14. Kang, N., Baum, M.J., and Cherry, J.A. (2011). Different profiles of main and accessory olfactory bulb mitral/tufted cell projections revealed in mice using an anterograde tracer and whole mount, flattened cortex preparation. *Chem. Senses* 36, 251–260.
15. Jouhanneau, M., Szymanski, L., Martini, M., Ella, A., and Keller, M. (2013). Kisspeptin: a new neuronal target of primer pheromones in the control of reproductive function in mammals. *Gen. Comp. Endocrinol.* 188, 3–8.
16. Boehm, U., Zou, Z., and Buck, L.B. (2005). Feedback loops link odor and pheromone signaling with reproduction. *Cell* 123, 683–695.
17. Preti, G., Wysocki, C.J., Barnhart, C.J., Sondheimer, S.J., and Leyden, J.J. (2003). Male axillary extracts contain pheromones that affect pulsatile secretion of luteinizing hormone and mood in women recipients. *Biol. Reprod.* 68, 2107–2113.
18. Stern, K., and McClintock, M.K. (1998). Regulation of ovulation by human pheromones. *Nature* 392, 177–179.
19. Frasnelli, J., Lundström, J.N., Boyle, J.A., Katsarkas, A., and Jones-Gotman, M. (2011). The vomeronasal organ is not involved in the perception of endogenous odors. *Hum. Brain Mapp.* 32, 450–460.
20. Dahl, R. (1976). *Switch Bitch* (London: Penguin Books).

Key Laboratory for Neuroinformation,
University of Electronic Science and
Technology of China, Chengdu 610054,
China.
E-mail: k.kendrick.uestc@gmail.com

<http://dx.doi.org/10.1016/j.cub.2014.02.019>

Climate Change: A Hybrid Zone Moves North

A shifting zone of hybridization between two chickadee species helps us understand the proximate mechanisms driving species responses to climate change.

Bettina Harr¹ and Trevor Price^{2,*}

In association with climate change, the northern range limits of northern species are moving northward [1]. These species southern range limits also appear to be moving northward, albeit at a slower rate and with greater heterogeneity between species [2,3]. While the ultimate reason may well be climate change, the more proximate mechanisms are difficult to determine. How much can range shifts be attributed to changes in the available resources (such as a longer growing season or different kinds of food) plus competition for these resources [4]?

One reason why it is so difficult to determine the role of competition is that when resource quality or quantity gradually varies over space, theory predicts that the species will show a large overlap in their geographical range. One species may be superior at one end of the gradient and the other at the other end so that the two species mutually set each other's range limit, but over an extensive area, each species can persist alongside the other by consuming a different portion of the available resources [5] (Figure 1). The gradual spatial turnover from one species to the other makes it difficult to empirically demonstrate competition

as the ultimate cause of the range limits of each species. It should make it even more difficult to assess drivers of range expansions and contractions under climate change.

Hybridization between species changes this dynamic. A small amount of cross-mating between a pair of species can considerably narrow the overlap between them [5] (Figure 1). This is essentially because any individual that hybridizes leaves no offspring, and hence has zero fitness. The result is a steep cline across which the two species regularly interact, making it easier to directly evaluate species interactions in range movements. Further, in a hybrid zone, the southern limit of one species is tied to the northern limit of the other, so the two boundaries move at the same rate. This coordinated change in range movements, plus the close proximity of the parental forms, implies studies on moving hybrid zones have much to offer to our understanding of species

responses to climate change. A number of bird hybrid zones are moving along a south–north axis [6], and one particular hybrid zone is the focus of a new paper by Taylor and colleagues [7] in this issue of *Current Biology*.

Taylor *et al.* [7] used genomic methods to study a classic moving bird hybrid zone, that between the black-capped chickadee (*Poecile atricapillus*, to the north) and Carolina chickadee (*P. carolinensis*, lying to the south) in eastern North America (Figure 2). Based on songs and morphology the zone is considered to be about 30 km wide. It stretches >1,500 km from Kansas to New York state, although not everywhere along this transect do the species actually come into contact. The hybrid zone has been moving north at a rate of ~1 km per year for more than 100 years [8,9]. Even though northward movement commenced long before the current global warming trend, climate is strongly implicated as a determinant of zone position, because it tracks present-day winter temperatures well [7]. For example, the zone dips south 300 km along the trace of the Smoky mountains in Tennessee and North Carolina [7].

Taylor *et al.* [7] performed genetic analysis of the hybrid zone in eastern Pennsylvania. Taking advantage of a new high-throughput method called genotyping by sequencing (GBS), they were able to identify and genotype 1,425 single nucleotide polymorphisms (SNPs) in 167 individuals across the hybrid zone. Seventy-five SNP loci showed clinal geographic variation, with cline widths less than 100 km (average 31 km). These are the loci that can be used to study the temporal dynamics of the hybrid zone at a truly genome-wide level. When comparing the samples taken from the same hybrid zone 10 years apart, 71 out of the 75 loci showed cline centers displaced northwards in the more recent sample, by an average of 9 km. Ten of the 167 individuals studied were clearly F1 hybrids between the two species, but there are no obvious early generation backcrosses. The genomes of both species as a whole appear to be moving north, with very little, if any, introgression between the species.

The classic conception of a hybrid zone is that of a ‘tension zone’ in which the parental forms mate randomly, and hybrids have low fitness. The zone is

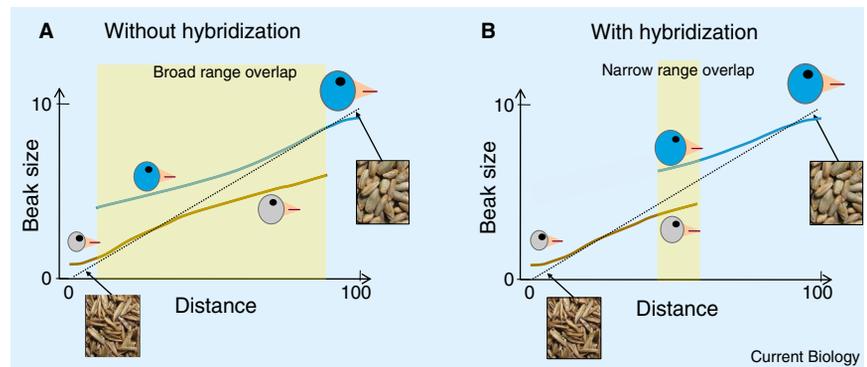


Figure 1. How competition and hybridization between species affects range limits.

The blue and grey lines depict mean values of a trait (e.g., beak size) across space for two species competing for a resource (seeds, whose mean size varies geographically, dotted line). (A) Model in which females always mate with males of their own species. (B) Same as (A), but conspecific preferences are imperfect, such that when males of the two species are in equal frequency, 1% of the time the females mate with a heterospecific male. Model after [5].

maintained by a balance of dispersal of members of the parental species into the zone and selection against the hybrids [10]. Most hybrid zones differ from this ideal, however. For example, nonrandom mating is common in hybrid zones, with individuals more often pairing with members of their own species than would be expected by chance. This includes some of the best-known hybrid zones, such as that between the Townsend’s warbler (*Setophaga townsendi*), and hermit warbler (*Setophaga occidentalis*), in the Pacific northwest, about which we will have more to say below. Also in contradiction to the classic conception, parental forms often suffer reduced fitness when on the wrong side of the zone. For example, resources may differ across the zone (Figure 1), or males of one species when surrounded by the other may be subject to aggression [6,11]. In birds, it is the chickadee hybrid zone that comes closest to the notion of a tension zone [6]. Based on mitochondrial DNA differences, the two species may be separated by as much as 4 million years [6]. This long separation time would be expected to lead to low fertility in the hybrids, as has been confirmed in field studies of the chickadees [9] and is supported by the apparent absence of recent generation backcrosses in the genomic analysis. As far as we know, mating is random, i.e., conspecific pairs in a particular locality do not appear to be more frequent than expected based on the frequency of the parental types in that place. Most pair formation apparently occurs

well before the breeding season commences and exactly how the heterospecific pairs form remains to be determined [12], but the species do look very similar (Figure 2), which may be one reason why cross-pairing is common.

Low hybrid fitness and random mating should make for a narrow hybrid zone, but these factors are not expected to drive zone movement in any particular direction. Instead, interactions between the parental species are likely to be the main reason for directional movement. In several moving bird hybrid zones, the dominant species is displacing the subordinate one [6]. This is a curious finding, because if the dominant has an inherent advantage, it raises the question of why subordinates should ever persist in nature [13]. We suggest that in the case of moving zones, behavioral dominance is a flexible trait, reflecting response to current conditions. Thus, in a warmer and shorter winter, the southern species (Carolina chickadee) may be better suited to build up the resources that enable it to displace the northern species. This and other narrow hybrid zones provide excellent systems in which to investigate competitive interactions between parental types in response to climate change.

Moving hybrid zones have many implications for the process of speciation, as well as determinants of range limits. Providing at least one fertile backcross is produced, genes can leak from one taxon to the other, thereby slowing divergence, but



Figure 2. Birds in the zone. Black-capped chickadee (left) and Carolina chickadee (right). Painting copyright David Sibley, reproduced with permission.

perhaps only at certain regions of the genome. Some parts of the genome may move with the zone and others get left behind, but the extent to which this happens does depend on the fitness of hybrids. The black-capped/Carolina chickadee zone apparently results in hybrids of very low fitness and introgression of genes from one side of the zone should be rare. Other studies based on small molecular datasets have found some evidence for introgression [14,15], which may be ancient. However, alternatives, such as shared ancestral polymorphism, have been hard to rule out.

Limited, or no, introgression may be contrasted with the findings from other moving zones, in which the species involved are younger and gene exchange more frequent. Rohwer *et al.* [16] found that the hybrid zone in Washington State between southern hermit warblers and northern Townsend's warblers was likely to be moving south. This was inferred from the presence of hermit warbler mitochondrial DNA in Alaskan Townsend's warblers, 2,000 km to the north of the present zone. Dominance of Townsend's males is implicated in zone movement, and the discordance between plumage and mtDNA could be explained if male plumage and associated dominance traits moved south but the females disperse more or less at random. Hybrid zones between recently separated groups such as these are calling out for genomic

analyses along the lines pioneered by Taylor *et al.* [7]: climate change not only affects range limits, but also the potential for hybridization and introgression during a protracted speciation process.

References

1. Parmesan, C., and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
2. Thomas, C.D., and Lennon, J.J. (1999). Birds extend their ranges northwards. *Nature* 399, 213–213.
3. Sunday, J.M., Bates, A.E., and Dulvy, N.K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change* 2, 686–690.
4. Post, E. (2013). *Ecology of Climate Change: the Importance of Biotic Interactions* (Princeton University Press).

5. Goldberg, E.E., and Lande, R. (2006). Ecological and reproductive character displacement on an environmental gradient. *Evolution* 60, 1344–1357.
6. Price, T. (2008). *Speciation in Birds* (Boulder, CO: Roberts and Co.).
7. Taylor, S.A., White, T.A., Hochachka, W.M., Ferretti, V., Curry, R.L., and Lovette, I. (2014). Climate-mediated movement of an avian hybrid zone. *Curr. Biol.* 24, 671–676.
8. Brewer, R. (1963). Ecological and reproductive relationships of black-capped and Carolina chickadees. *Auk* 80, 9–47.
9. Bronson, C.L., Grubb, T.C., and Braun, M.J. (2003). A test of the endogenous and exogenous selection hypotheses for the maintenance of a narrow avian hybrid zone. *Evolution* 57, 630–637.
10. Barton, N.H., and Hewitt, G.M. (1989). Adaptation, speciation and hybrid zones. *Nature* 341, 497–503.
11. Stein, A.C., and Uy, J.A.C. (2006). Unidirectional introgression of a sexually selected trait across an avian hybrid zone: a role for female choice? *Evolution* 60, 1476–1485.
12. Curry, R.L., Rossano, L.M., and Reudink, M.W. (2007). Behavioral aspects of chickadee hybridization. In *Ecology and Behavior of Chickadees and Titmice: an Integrative Approach*, K. Otter, ed. (Oxford: Oxford University Press), pp. 95–110.
13. Rohwer, S., and Ewald, P.W. (1981). The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* 35, 441–454.
14. Sattler, G.D., and Braun, M.J. (2000). Morphometric variation as an indicator of genetic interactions between black-capped and Carolina chickadees at a contact zone in the Appalachian Mountains. *Auk* 117, 427–444.
15. Davidson, B.S., Sattler, G.D., Via, S., and Braun, M.J. (2013). Reproductive isolation and cryptic introgression in a sky island enclave of Appalachian birds. *Ecol. Evol.* 3, 2485–2496.
16. Rohwer, S., Bermingham, E., and Wood, C. (2001). Plumage and mitochondrial DNA haplotype variation across a moving hybrid zone. *Evolution* 55, 405–422.

¹Max-Planck Institute of Evolutionary Biology, 24304 Plön, Germany. ²Department of Ecology and Evolution, University of Chicago, Chicago, IL 60637, USA.
*E-mail: pricet@uchicago.edu

<http://dx.doi.org/10.1016/j.cub.2014.02.023>

Hearing Damage and Deafness: A Role for the Circadian Clock

Severe noise can cause permanent hearing damage. A recent study now shows that the capacity to recover from noise damage varies with time of day, driven by circadian clock control of a nerve growth factor (BDNF) in the inner ear.

Andrew S.I. Loudon

We are all familiar with the effects of loud noise on our hearing. These include 'ringing in the ear' and temporary deafness, but for severe noise trauma, these effects can be permanent. The cause of these

problems resides in the spiral cochlea of the inner ear, specifically involving damage to the delicate hairs of the inner ear, which are tuned to specific frequencies, and also importantly the dendrites of the auditory nerve.

The circadian clock is known to be regulated by environmental stimuli, of