

labeled neurons in the presence of significant numbers of labeled motoneurons. Finally, we found no evidence in the literature for primary cardiac afferent connections to DMV or nucleus ambiguus neurons.

Amelia Standish

Central Research and Development,
E. I. Dupont de Nemours & Co.,
Wilmington, DE 19880-0323, USA

Lynn W. Enquist

Department of Molecular Biology,
Princeton University,
Princeton, NJ 08544, USA

James S. Schwaber
Central Research and Development,
E. I. Dupont de Nemours & Co.

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Hybrid Zones and Sexual Selection

The potential of hybrid zones to provide insight in the area of sexual selection has received only limited attention (1). T. J. Parsons *et al.* find (2) that secondary sexual plumage traits in manakins show unidirectional spread across a hybrid zone as a result of intersexual selection. The observations presented in their report, however, are not sufficient to justify this conclusion.

Parsons *et al.* begin by stating that selection against hybrids is expected to produce "concordant shifts in diagnostic characters." This is an oversimplification: tension zones are expected to show clines for different characters centered in the same place (coincident), but these are unlikely to be the same width (concordant) (3). Cline width is determined by the selection acting, directly or indirectly, on the loci that influence a character; wider clines indicate weaker selection per locus. Width is expected to differ among phenotypic characters, and variation in width is commonly observed (4).

Parsons *et al.* show that the beard and tail characters, and the molecular markers, that separate *Manacus candei* (white-collared manakin) from *M. vitellinus* (golden-collared manakin) have clines less than 20 km wide centered somewhere between localities 7 and 8 [figure 2 of (2)]. These clines are at least approximately, and may be precisely, coincident and concordant. The simplest interpretation of the clines in collar width and underparts color is that they are much wider (about 60 km), but are centered in approximately the same position, close to locality 7. The center of the underparts color cline may be shifted toward *candei*, but this shift would be less than one cline width. The shift could be the result of dominance for the *vitellinus* trait or of a nonlinear color scale, with the underlying allele-frequency clines being coincident. The same arguments apply to the throat color cline on which Parsons *et al.* place most emphasis: it is a broad cline

coincident with the other clines, the only difficulty being the apparent "step" at the Río Changuinola. This step could be an artifact of the color scale used or of the relationship between the color scale and the genetic determination of color, or it could be a result of restricted gene exchange across the river, as Parsons *et al.* suggest. In any case, two-thirds of the change in throat color occurs more or less smoothly between localities 4 and 10, so that it appears incorrect to interpret this pattern as a cline displaced "some 40 km to the west . . ." (2, p. 1645) of the clines for other characters.

Broad clines are suggestive of weak selection if they are maintained by selection against hybrids. However, Parsons *et al.* suggest that the main selection pressure on these male plumage traits is through female preferences. Two possibilities exist: either *candei* females have preferences for *candei* male plumage traits and *vitellinus* females for *vitellinus* traits [the "preexisting preference" hypothesis (5)]. There is no good reason to assume preexisting preference for golden throat color, because out of four species in the genus, two have white throats, one golden, one orange, and their phylogenetic relationships are unknown. If such a preference existed in *candei* it would predict a rapid spread of golden throats into *candei* after contact with *vitellinus*. The advancing wave would be narrow, which is not the pattern observed. Alternatively, a sharp cline is expected where two populations meet that differ in both male traits and preferences, as rare migrants are at a disadvantage relative to local males. Finally, throat color may be irrelevant to sexual selection. In this case a broad cline is expected, the width being dependent only on dispersal rate and time since contact (6). Physical barriers to gene exchange may impede the spread of such neutral characters producing stepped clines, and chance events may cause the cline centers to move apart.

The best interpretation of the data presented by Parsons *et al.* seems to be that male plumage is irrelevant to male mating success (7). Perhaps this is the interesting message that this hybrid zone has for us about sexual selection. The male display behavior which is so highly conserved in the genus may be the key trait for intersexual selection, while the highly variable plumage may diverge purely by chance.

Roger K. Butlin

Rachel M. Neems

Department of Genetics,
University of Leeds,
Leeds LS2 9JT, United Kingdom

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Response: Our report (1) documented the differential introgression of male plumage traits (2) across a hybrid zone. We have proposed sexual selection as a plausible mechanism to explain this phenomenon and are pursuing observational and experimental means of testing this hypothesis. We have not ruled out other mechanisms, nor have we said that sexual selection, if it occurs, need be intersexual; intrasexual mechanisms are also plausible [note 17 in (1)]. Nor did we state that selection against hybrids in tension zones will always produce clines of the same width. Butlin and Neems favor a hypothesis of neutral diffusion to explain the differential introgression of male secondary sexual plumage traits. While the actual processes involved can only be demonstrated by additional data, we will attempt to explain why our original hypothesis of sexual selection seems more plausible.

Butlin and Neems are correct that we place the greatest emphasis on throat color, and it is certainly true that the color scale values we employed are nonlinear. We arbitrarily assigned to white throats a score of 6, while scores from 5 to 1 represent subtly different shades of bright yellow. On this scale, the jump from 5 to 6 represents a

major quantitative and qualitative leap, while the change from 5 to 4 is as subtle a shift as can be detected visually. Thus, it is not the case that "two-thirds of the change in throat color occurs . . . between localities 4 and 10." In the region spanning localities 4 through 7, all males have brilliant yellow throats, collars, and beards; in addition to the 45 we collected, scores more were observed, many in the vicinity of locality 4. Throat and collar color varies little in this region, although an average trend to more orangish yellow is discernible in populations nearer to parental *vitellinus*. Despite their bright yellow throats and collars, birds from localities 4 through 7 are morphometrically and genetically indistinguishable from *M. candei*, the "white-collared manakin," and across the Río Changuinola at locality 3 all males have pure white throats, collars, and beards (1). The primary phenotypic change in throat color occurs between localities 3 and 4, and there is a profound asymmetry of throat and collar color introgression relative to the primary genetic and morphometric transition that occurs between localities 7 and 8 (3).

It is conceivable that this phenotypic asymmetry could reflect tails of introgression of *vitellinus* throat color alleles, with yellow being dominant. However, if the frequencies of *vitellinus* plumage alleles are similar to those of the *vitellinus* genetic markers we measured in localities 4 through 7, this would have to be an extreme effect involving many loci (4). It is more likely that the asymmetry results from frequencies of *vitellinus* plumage alleles that are substantially higher than those of the other *vitellinus* genetic markers.

Cline widths in tension zones can vary in response to the levels of selection a particular character experiences. In many zones, however, clines in numerous characters are often similar in both position and width (5). For example, *Bombina* toads have clines virtually identical in position and width for mitochondrial DNA, multiple "neutral" enzyme markers, call frequency, and morphology (6, 7). There is strong evidence indicating that this is a result of many loci spread throughout the genome that are negatively selected in hybrids, giving rise through linkage

disequilibrium to coincident, abruptly stepped clines. Such stepped clines are thought to result from a barrier to neutral gene flow that can be expressed as a value acting on the genome as a whole. Stepped clines are seen in *Ranidella*, *Uroderma*, *Caledia*, *Mus*, and *Podisma* hybrid zones (8). In the manakin zone, the shifts in tail length, beard length, mitochondrial DNA, and two anonymous nuclear DNA markers that occur between localities 7 and 8 are suggestive of such a barrier to neutral gene flow. The DNA markers themselves are likely to be selectively neutral (9). Butlin and Neems propose that the male plumage traits introgress farther because they experience less selection than these DNA markers. For this to be true, the DNA markers would have to be independently linked to loci under selection, suggesting that such loci are common and widespread. This is a situation that is likely to give rise to an overall barrier to neutral gene flow, which would extend to plumage characteristics as well.

The only diagnostic characters we have examined that do not change between localities 7 and 8 are male secondary sexual traits; it is unlikely that this is a result of chance alone, and sexual selection favoring *vitellinus* traits would be a mechanism in common to account for the asymmetric introgression. No plausibility argument can substitute for direct evidence for or against sexual selection, which we are pursuing. The situation may prove to be more complex than we have hypothesized; however, we doubt that what sets the plumage characters apart is that they are the only ones that are neutral (10).

Thomas J. Parsons

Department of Plant Pathology,
University of Nebraska,
Lincoln, NE 68583-0722, USA

Storrs L. Olson

Department of Vertebrate Zoology,
Smithsonian Institution,
Washington, DC 20560, USA

Michael J. Braun

Laboratory of Molecular Systematics and
Department of Vertebrate Zoology,
Smithsonian Institution,
Washington, DC 20560, USA

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2. A photograph of birds from localities 3, 4, and 10 (per our report) is in a paper by N. H. Barton [*Curr. Biol.* 3, 797 (1993)].
3. We recognize that collar width and underparts color show a more gradual and complete transition between localities 3 and 7. Under our hypothesis of sexual selection favoring yellow throats and collars, it may be that these additional male traits experience lower levels of selection or are neutral and linked to the determinants of throat and collar color; thus, they may have gradually become dissociated from the yellow throat and collar alleles as these spread throughout the region.
4. A minimum of 35 males with the bright yellow phenotype (and none with white collars and throats) were observed at locality 4. We have not detected introgression of *vitellinus* genetic markers at localities 4 through 7, but since the two *candei* nuclear markers are not fixed in parental *candei*, low-frequency introgression might escape detection. To explain the observed plumage patterns by dominance of *vitellinus* alleles, let us generously imagine a frequency of 20% for all *vitellinus* alleles at locality 4. Even if a single *vitellinus* allele at any color determination locus were sufficient to confer the bright yellow phenotype, approximately seven (or more) loci would have to be involved in order for white-collared birds to be so rare (observed frequency of white birds is less than $1/35 = 0.028$; for seven unlinked loci, expected frequency of homozygous white at all loci is $[(0.8)^2]^7 = 0.044$). Fieldwork conducted in 1994 has raised the number of adult males observed between localities 4 and 8 to over 100, and one white-collared male (not a typical *M. candei*) was discovered; hence, estimated frequency of white-collared males is <0.01 . Unexpectedly, this bird was found near the center of the morphometric and genetic cline shifts between localities 7 and 8, at the only locality where tail and beard lengths are intermediate between those of *M. candei* and *M. vitellinus* ($n = 20$). The occurrence of a white-collared bird in this region of presumed genetic admixture does not support the dominance hypothesis. Under this hypothesis, white-collared birds would be more likely to occur in locality 4, near the source of *candei* alleles.
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7. ——— and N. H. Barton, *Evolution* 45, 237 (1991).
8. N. H. Barton and K. S. Gale in (6), pp. 13-45.
9. M. Kimura, *The Neutral Theory of Molecular Evolution* (Cambridge Univ. Press, Cambridge, United Kingdom, 1983).
10. The example that Butlin and Neems cite [W. S. Moore, *Evolution* 41, 539 (1987)], where male plumage is irrelevant to male mating success, concerns a territorial pair-bonding woodpecker with only slight sexual dimorphism. This example is probably not relevant to these lek-breeding, highly dimorphic manakins.

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