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A sexually selected character displacement in flycatchers reinforces premating isolation

Glenn-Peter Sætre*, **Truls Moum**†,
Stanislav Bureš‡, **Miroslav Král**§,
Martin Adamjan‖ & **Juan Moreno**¶

* Department of Biology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway
† Department of Molecular Cell Biology, Institute of Medical Biology, University of Tromsø, N-9037 Tromsø, Norway
‡ Palacký University, Laboratory of Ornithology, Tr. Svobody 26, 771 46 Olomouc, Czech Republic
§ Forestry Commission, 783 86 Dlouhá Loučka, Czech Republic
‖ Zoological Museum, P/Sevaka 7, Jerevan 44, Armenia
¶ Museo Nacional de Ciencias Naturales, J. Guiterrez Abascal 2, 28006 Madrid, Spain

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Theory suggests that natural selection against the production of unfit hybrids may reinforce barriers to gene flow, eventually leading to reproductive isolation of differentiated populations[1-4]. This mode of speciation may be achieved by female choice selecting for a divergence in male secondary sexual traits that facilitates species recognition. Although intuitively appealing, conclusive evidence for such reinforcement is generally lacking[5-8], and serious doubts have been raised about its validity[9-11]. We have tested key predictions of the reinforcement hypothesis on the European, black-and-white, *Ficedula* flycatchers, using molecular techniques, field observations and mate choice experiments. In populations where two species coexist, we show that female choice selects for a divergence in male plumage colour and that the resulting character displacement reduces the frequency of hybridization.

The current geographical distribution of European *Ficedula* flycatcher forms has led researchers to suggest that a sympatric divergence in secondary sexual characters has occurred[12-14]. In a large area in Central and Eastern Europe the breeding distribution overlaps for two clearly differentiated flycatchers, the brown form of
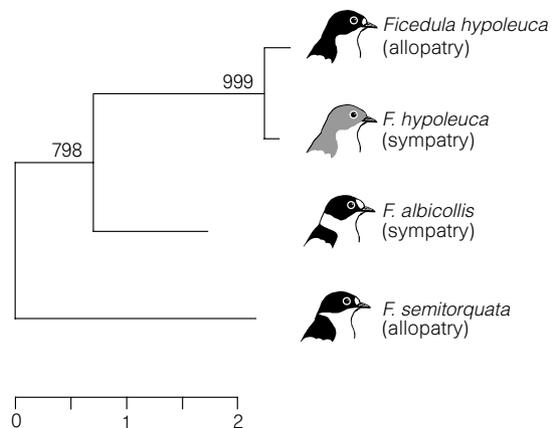

Figure 1 Phylogenetic relationships among sympatric and allopatric flycatchers based on mitochondrial DNA sequences. A neighbour-joining tree is presented with genetic distances drawn to scale. The scale refers to Kimura 2-parameter distances (%). Values at the nodes represent bootstrap replication scores based on 1,000 resamplings. The phylogenetic reconstruction suggests that the plumage characters in sympatry are derived traits, supporting the argument of a sympatric character divergence.
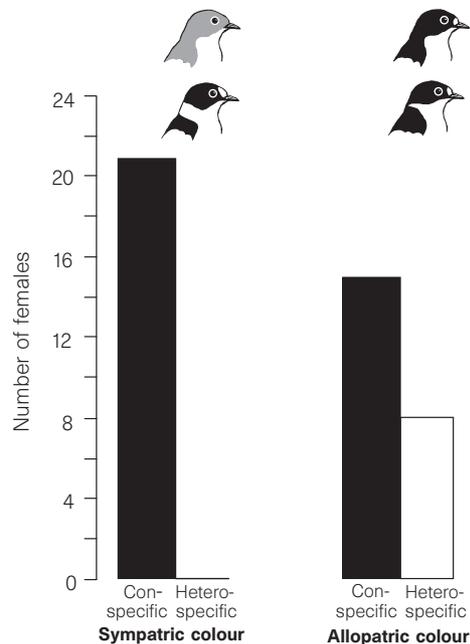
Figure 2 Species recognition by female pied and collared flycatchers from sympatric populations. Species assortative mating was significantly reduced when males of the two species had plumage characteristics typical of allopatric populations (small difference) compared to when the males had plumage characteristics typical of sympatric populations (large difference: $\chi^2 = 6.7$, d.f. $= 1$, $P = 0.009$). In the case of allopatric colours, 5 out of 12 female pied flycatchers and 3 out of 11 female collared flycatchers chose the heterospecific male.

Figure 3 Mate preferences of female flycatchers. Left, female collared flycatchers preferred male conspecifics with large patches of white to those with reduced patch sizes ($\chi^2 = 7.4$, d.f. $= 1$, $P = 0.007$). Centre, sympatric female pied flycatchers preferred brown coloured male conspecifics to black-and-white ones ($\chi^2 = 5.3$, d.f. $= 1$, $P = 0.027$). Right, allopatric female pied flycatchers (previously published data[26]) preferred black-and-white coloured male conspecifics to brown ones ($\chi^2 = 5.4$, d.f. $= 1$, $P = 0.020$). Mate preferences of sympatric female pied flycatchers were opposite to those of allopatric ones ($\chi^2 = 8.1$, d.f. $= 1$, $P = 0.005$).

the pied flycatcher (*Ficedula hypoleuca*) and the black-and-white collared flycatcher (*Ficedula albicollis*). These two forms are restricted to the zone of overlap and adjoining areas[12,13]. The distributions of allopatric flycatchers encircle the area of sympatry[12]. Different allopatric flycatchers resemble each other and are intermediate to the sympatric ones in plumage characteristics. The majority of males are black-and-white but with smaller patches of white on the forehead, neck and primaries than those of a typical collared flycatcher. Hypotheses on evolutionary history based on geographical distributions have been problematic because the phylogenetic relations between the various allopatric and sympatric forms have remained unresolved. Accordingly, it has been difficult to assess whether the colours of the sympatric forms represent the derived character states[12]. Using mitochondrial DNA analysis, we found that one of the phenotypically intermediate allopatric forms, the semicollared flycatcher (*Ficedula semitorquata*, here given the status of species), is the most genetically divergent form (Fig. 1). Allopatric pied flycatchers resemble semicollared flycatchers phenotypically, but are only distantly related to that species (Fig. 1). These results indicate that the coloration occurring in allopatry might represent the ancestral state, whereas the colorations occurring in sympatry are derived traits. Hence, the phylogenetic relations suggest that a sympatric divergence in plumage characteristics has occurred.

Reinforcement can be considered an evolutionary response to maladaptive mating behaviour. Selection may favour assortative mating when hybridization is detrimental to fitness[15]. Breeding records and fitness data were collected from sympatric populations in the Czech Republic and Slovakia[16]. According to the reinforcement hypothesis we expected to find negative fitness consequences from hybridization and a bias towards species-assortative mating, reflecting a history of selection against hybridization. A total of 2,348 mating events occurring in temporal and spatial sympatry
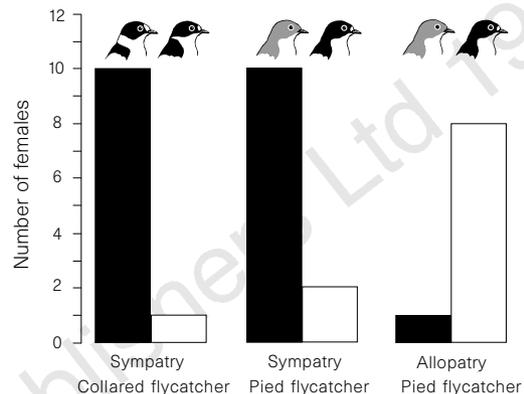
were analysed. Of these, 2,226 (94.8%) were species assortative, 61 (2.6%) were heterospecific and 61 (2.6%) involved one hybrid[16]. If mating had been random we would have expected a frequency of 13.8% heterospecific matings based on temporal and spatial availability of potential mates. The observed frequency deviates significantly from the expected one ($\chi^2 = 235.3$, d.f. $= 1$, $P < 0.0001$). Hence, mating is strongly skewed towards species assortative ones. Hybrids had very low fertility. In pure and mixed-species pairs ($n = 332$) only 4.9% of the eggs failed to hatch, compared to 74.1% in pairs with a hybrid ($n = 60$; $t = -25.1$, d.f. $= 391$, $P < 0.0001$). Hence, there is a substantial selection potential against hybridization.

Male plumage characteristics that resemble those of allopatric flycatchers are found at low frequencies among sympatric pied and collared flycatchers[12-14]. Therefore, the degree of interspecific divergence in plumage colour varies. The existence of such variation makes it possible to investigate whether selection for sympatric character divergence is currently operating.

According to the reinforcement hypothesis the ultimate explanation for a sympatric character divergence is that it reduces the probability of hybridization. Two experiments were designed to investigate whether divergence in plumage colour facilitates species recognition. In aviary trials, females of both species from sympatric populations could choose between one male of each species. First, females of both species were allowed to choose between males with divergent plumage characteristics, typical of sympatric populations. All females responding by building a nest chose the conspecific male (Fig. 2). Second, the females were allowed to choose between males with more similar colours, typical of allopatric flycatchers. A high proportion of the females then built their nest in the nest-box advertised by the heterospecific male (Fig. 2). Hence, divergence in plumage characteristics helps species recognition.

In most models of the reinforcement hypothesis it has been

assumed that an eventual development of assortative mating is caused by the action of natural selection on an assortative mating locus[10,17–19]. However, sexual selection in the form of female preferences for male traits may enhance the reinforcement process[4,20]. When hybridization is detrimental to fitness, female choice for divergent male characteristics in sympatry would parallel the 'choice of good genes process' of sexual selection[21–23]. We tested whether the observed character divergence of the flycatchers was related to a female preference for divergent male characteristics. In one experiment, female collared flycatchers could choose between a male conspecific with large patches of white (forehead, neck and primaries) and a conspecific with reduced white patches, resembling an allopatric flycatcher. The females preferred the one with the larger white patches (Fig. 3). In another experiment, female pied flycatchers from the same mixed populations could choose between one dull, brown and one black-and-white conspecific male. The females preferred the dull, brown male (Fig. 3). Hence, in sympatry, females of the two species show preference for divergent male characteristics.

In allopatry, a black-and-white colour of a male pied flycatcher indicates a high viability of the carrier[24,25] and females prefer such males to dull, female-like brown ones[26] (Fig. 3). In sympatry with collared flycatchers, mate preferences of female pied flycatchers are opposite to those in allopatry (Fig. 3). To our knowledge, the present study is the first on mate choice in any species to demonstrate a female preference for the least conspicuous male traits[27]. By choosing dull, brown males, female pied flycatchers increase the probability of obtaining a conspecific mate. Hence, in the case of this species it appears that selection against hybridization in sympatry with the collared flycatcher overrides the general trend of sexual selection for elaborate traits.

In conclusion, female choice selects for a character displacement of male plumage traits in sympatric flycatchers that helps species recognition. Character displacement and assortative mating are adaptive, because heterospecific matings result in hybrid offspring with very low fertility. As would be expected from a history of selection against hybridization there was a strong bias towards species-assortative mating in sympatric populations. Hence, there is evidence for ongoing speciation by reinforcement of premating isolation in sympatric pied and collared flycatchers enhanced by a sexually selected character divergence in male plumage colour. □

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Methods

Sequencing and phylogenetic analysis. Genomic DNA was isolated from blood samples of sympatric Czech pied (*F. hypoleuca*; $n = 8$) and collared flycatchers (*F. albicollis*; $n = 10$), and from allopatric Spanish pied flycatchers ($n = 10$). DNA from the semicollared flycatcher (*F. semitorquata*) was isolated from a museum specimen of Armenian origin. We used bluethroat (*Luscinia svecica*) for outgroup-rooting. The mitochondrial NADH dehydrogenase subunit 6 gene (ND6) was enzymatically amplified using conserved primers in the control region (5′-GGTTCTCGTGAGAAACACGAT-3′) and the tRNA^Pro gene (5′-TCCATCTCCAGCTCCCAAAGC-3′). Several sequencing primers were used (data available on request). The complete ND6 sequence (519 base pairs) was collected in all specimens using the Ampltaq Cycle sequencing kit (Perkin Elmer) and Thermo Sequenase radiolabelled terminator cycle sequencing kit (Amersham). The average genetic distance from the outgroup, *L. svecica*, to the flycatcher species was 18.2%. Intraspecific variation was low, with a maximum of two steps in all pairwise comparisons. With reference to the most common genotype in each species, substitutions were present at six nucleotide positions that were consequently omitted from the phylogenetic analysis. Kimura 2-parameter distances with a transition/transversion ratio set at 20 and the neighbour-joining method were used for phylogeny reconstruction[28]. Sequences have been deposited in the EMBL database (accession numbers Y10215; Y10308–Y10311).

Hybrid fitness and mating pattern. Data on hatching success and frequency of hybridization were collected from 14 mixed-species populations in the Czech Republic and Slovakia[16]. Classification of hybrids versus pure individuals is based on several species-specific morphological traits and vocalizations that are intermediate in hybrids[12,16]. Estimates of expected and observed frequencies of hybridization are based on years in which individuals of both species were found breeding within the same locality (temporal and spatial sympatry).

Mate choice and species recognition. Experiments in four outdoor aviaries ($3 \times 3 \times 1.9\,\text{m}$)[29] were conducted during spring 1995 and 1996 at Dlouhá Loučka, Czech Republic. The aviaries contained one female compartment and two male compartments. The males advertised separate nest-boxes. The females could see both males but the males could not see each other, and nylon netting prevented the birds from entering other compartments. Food and water were freely available and dried grass and leaves served as nesting material for females. Birds were captured from different nest-box areas 0–30 km away from the aviaries, and birds within each trial were captured at different sites to avoid previous experience. Males were habituated to aviaries for 24 h whereafter females were introduced. The chosen male was regarded as the one advertising the nest-box in which the female built her nest. To avoid possible correlates of plumage colour we used colour manipulations[26] to produce differences. Previous studies show that pied and collared flycatchers respond similarly to colour manipulated and naturally coloured birds[14,26]. In the species recognition experiments (Fig. 2) each pair of males ($n = 30$ pairs) was used to test the response of one female of each species. In the case of sympatric colours, 11 female collared and 10 female pied flycatchers responded by building a nest, and in the case of allopatric colours, 11 female collared and 12 female pied flycatchers responded. We used a balanced design with respect to relative position of the males in the aviaries and order of presentation. In the mate choice experiments of sympatric populations (Fig. 3, left and centre) each pair of males (collared flycatcher, $n = 15$ pairs; pied flycatcher: $n = 13$ pairs) was used to test the response of one conspecific female. Pairs of males were selected on basis of similarity in age, size and initial plumage colour (using birds with typical sympatric colours only). One randomly chosen male within each pair was colour-manipulated using Nyanzol[26] to resemble black-and-white, allopatric male flycatchers. We used a balanced design with respect to relative position of the painted and the unpainted males in the aviaries. Similar methods were used for mate choice of allopatric pied flycatchers (Fig. 3, right)[26]. The birds used in experiments were captured at different localities, though from a geographically restricted area (30 km radius). Field data (mating order of colour types) from other flycatcher populations[12,30] are consistent with the experimental results obtained, suggesting that the observed differences in mate choice apply to allopatric and sympatric populations in general. Nevertheless, note that these characteristics may vary among localities and future efforts should be made to conduct similar tests in sympatric and allopatric populations throughout the species range.

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Dissociating types of mental computation

William D. Marslen-Wilson* & Lorraine K. Tyler*

Centre for Speech and Language, Birkbeck College, University of London, Malet Street, London WC1E 7HY, UK
* Both authors contributed equally to this work.

A fundamental issue in the study of cognition and the brain is the nature of mental computation. How far does this depend on internally represented systems of rules, expressed as strings of symbols with a syntax, as opposed to more distributed neural systems, operating subsymbolically and without syntax? The mental representation of the regular and irregular past tense of the English verb has become a crucial test case for this debate. Single-mechanism approaches argue that current multilayer connectionist networks can account for the learning and representation both of regular and of irregular forms[1,2]. Dual-mechanism approaches, although accepting connectionist accounts for the irregular forms, argue that a symbolic, rule-based system is required to explain the properties of the regular past tense and, by extension, the properties of language and cognition in general[3–5]. We show here that the regular and irregular past tense are supported by different neural systems, which can become dissociated by damage to the brain[6,7]. This is evidence for functional and neurological distinctions in the types of mental computation that support these different aspects of linguistic and cognitive performance.

This research brings new evidence to bear on the mental representation of the regular and irregular past tense in English, by examining the performance of aphasic patients with acquired neurological damage. If regular and irregular forms are mentally represented and processed in fundamentally the same way, then both should be affected in similar ways by damage to the brain that disrupts morphological processing systems. If there are two separate underlying systems engaged, respectively, by the regular and irregular morphology, then it should be possible to find dissociations in performance between these two morphological domains.

We selected two aphasic patients (J.G. and D.E.) with well documented difficulties in the comprehension and production of inflected forms in English[8]. Both patients have typical 'agrammatic' speech, which is hesitant and rarely contains inflected words[8–10]. In tests of their ability to interpret morphologically complex words, they can access the stems of such words, but have consistent difficulties in interpreting the combination of the stem with an
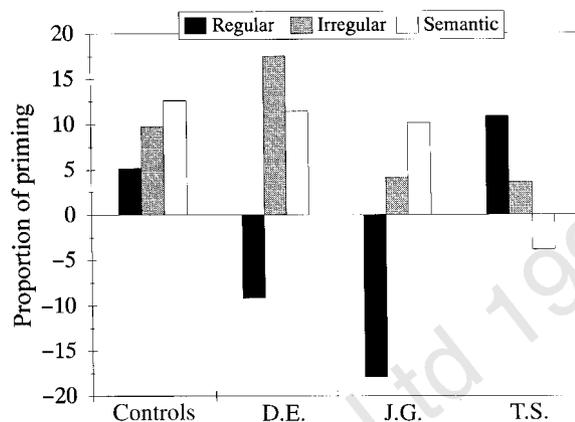

Figure 1 Priming effects across patients (D.E., J.G., T.S.) and control subjects for regular and irregular past tense primes and for semantic primes. Effects are expressed as response proportions (mean priming effect for each condition as a proportion of mean control reaction-time for that condition) to normalize for differences in base reaction-time between subjects.

inflectional affix: as in forms such as 'jumps' or 'smiling' (decomposable into {jump} + {−s} and {smile} + {−ing})[8,9]. Such patients should also have problems in the access and interpretation of regular past tense forms such as 'jumped' or 'smiled' which again involve the combination of a stem with a regular inflectional affix. The crucial question is whether they will show the same deficit for irregular forms such as 'gave' or 'taught', where the morphological relationship between prime and target does not involve the same types of combinatorial operation.

To test this required appropriate experimental tasks, using auditory rather than visual materials, and avoiding spoken responses, because both patients have difficulty in reading text and in producing speech[11,12]. Instead, we used an auditory priming task, where a spoken target word is immediately preceded by a spoken prime word, and the listener makes a timed lexical decision response to the target ('is this a word or not?'). For unimpaired subjects, responses to a target word speed up when it is preceded by a morphologically related prime (as in the prime/target sequence 'jumped/jump' or by a semantically related prime (as in 'swan/goose'), but not when the relationship is purely phonological (as in 'gravy/grave'). Earlier studies confirmed that these patients could perform this task and that they showed normal levels of semantic priming[9,10,13].

The two patients and six age-matched normal controls were tested in an auditory priming experiment that contrasted priming effects for regular and irregular past tenses (Table 1). For the regular past tense condition, the target word (for example 'jump') shares its stem morpheme with the prime, always a regular inflected past tense form (for example 'jumped'), and would normally show priming relative to a control prime (for example 'locked') that has no morphological or semantic relation with the target. Similarly, for the irregular past tense conditions, the target (such as 'give') shares an underlying morpheme with the prime, always an irregular inflected form (such as 'gave'), and this should also produce priming relative to an unrelated prime (such as 'shows'). In each case, we assume that priming reflects the repeated activation, by the prime and the target, of the same underlying lexical representations.

For comparison, we included a semantic priming condition (Table 1), where the prime word (such as 'swan') is preceded by a semantically (but not associatively) related prime word ('goose'), which should elicit priming for both controls and patients, and a phonological condition where the prime and target were only phonologically related (as in pairs such as 'gravy/grave').

Control subjects, consistent with results from other groups of