SHORT COMMUNICATION

Heterospecific female mimicry in *Ficedula* flycatchers

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Abstract

Mimicry is a widespread phenomenon. Vertebrate visual mimicry often operates in an intraspecific sexual context, with some males resembling conspecific females. Pied flycatcher (*Ficedula hypoleuca*) dorsal plumage varies from the ancestral black to female-like brown. Experimental studies have shown that conspecific and heterospecific (collared flycatcher, *F. albicollis*) individuals of both sexes respond, at least initially, to brown individuals as if they were female. We quantified the perceptual and biochemical differences between brown feathers and found that brown pied flycatcher males are indistinguishable from heterospecific, but not from conspecific, females in both aspects. To our knowledge, this is the first evidence of a visual mimetic signalling system in a sexual context where the model is heterospecific to the mimic. By only mimicking heterospecific females, brown pied flycatcher males can establish territories next to the more dominant collared flycatcher in sympatry, suffer less aggression by darker conspecifics in allopatry and preserve within-species sexual recognition throughout the breeding range. A closer look at the evolutionary history and ecology of these two species illustrates how such a mimetic system can evolve. Although likely rare, this phenomenon might not be unique to *Ficedula* flycatchers.

Introduction

In nature, there are several examples where organisms (or their parts) resemble other living organisms (mimicry) or their ecological background (crypsis). Mimicry can be defined as the cases where 'an organism (the mimic) simulates the signal properties of a second living organism (the model) which are perceived as signals of interest by a third living organism (the operator), such that the mimic gains in fitness as a result of the operator [incorrectly] identifying it as an example of the model' (Vane-Wright, 1980). It is assumed that all three elements of a mimicry system are under selection,
whereas crypsis systems entail no selection acting on the (nonliving) model (Endler, 1981). Three factors determine the type of mimetic relationship (Vane-Wright, 1976): (i) the mode of interaction (e.g. warning, defensive, aggressive), (ii) the effect of a mimic's presence to the model (beneficial or detrimental), and (iii) the taxonomic relationships within the tripartite signalling system (interspecific, intraspecific or bipolar). For example, invertebrate mimicry often refers to interspecific predator–prey interactions, based on aposematic visual signals that (deceptively or not) signal nonpalatability (Ruxton *et al.*, 2004) or lure male prey (Lloyd, 1975). Although similar phenomena occur in vertebrates (Greene & McDiarmid, 1981), visual mimicry in birds is largely restricted to intraspecific sexual contexts, where female mimicry has a defensive function, and can be a permanent male alternative reproductive strategy (Jukema & Piersma, 2006; Sternalski *et al.*, 2012) or a temporary phenotype in some first-year breeding

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males (i.e. delayed plumage maturation; Rohwer *et al.*, 1980; Hawkins *et al.*, 2012).

Pied flycatcher (*Ficedula hypoleuca*) males show a continuous variation in dorsal plumage, from conspicuous black to a brown-grey resembling (breeding) females (Lundberg & Alatalo, 1992). This trait is heritable (Slagsvold & Lifjeld, 1992; Alatalo *et al.*, 1994; Lehtonen *et al.*, 2009a) and consistent across years (Dale *et al.*, 2002; Ivankina *et al.*, 2007; Potti & Montalvo, 2008; Galván & Moreno, 2009), in contrast to delayed plumage maturation phenomena. Instead, it has been suggested that brown plumage in male pied flycatchers, a derived trait, forms the ancestral dark male phenotype of *Ficedula* flycatchers (Sætre *et al.*, 1997b), which originated due to secondary contact with collared flycatchers (*F. albicollis*) in central Europe after the last ice age (Qvarnström *et al.*, 2010; Sætre & Saether, 2010). In sympatry, brown plumage is an advantageous trait in interspecific male–male competition with the more dominant collared flycatchers (Gustafsson & Pärt, 1991; Sætre *et al.*, 1993; Alatalo *et al.*, 1994), and favoured by conspecific female mate choice to reduce costly hybridization (Sætre *et al.*, 1997b). Therefore, the incidence of brown pied flycatcher males in a population is higher the closer it is to the (older) central European sympatric area (Røskaft *et al.*, 1986; Lehtonen *et al.*, 2009a).

Sætre and colleagues (Slagsvold & Sætre, 1991; Sætre & Slagsvold, 1992; Sætre *et al.*, 1993) conducted several 'territorial intrusion' field experiments in the 1990s, where a caged live individual is placed near a defended nest box. These experiments have been conducted in both allopatric and sympatric populations and have shown that both sexes of both species behave towards (natural or manipulated) brown 'intruders' as if they were female: at least initially, males entice and females behave aggressively. Therefore, this is a potentially complex female mimicry system, with a single mimic (brown pied flycatcher males), two potential models (collared and pied flycatcher females) and four possible operators (collared flycatcher males and females and pied flycatcher males and females).

In this study, we use feather melanin composition analysis and spectrophotometry to quantify the differences between dorsal feathers collected from brown pied flycatcher males, from conspecific (pied flycatcher) females and from heterospecific (collared flycatcher) females. Our aim was to determine which (if any) of the two female types, brown pied flycatcher males resemble both perceptually and biochemically (i.e. the likely model in this mimicry system).

Materials and methods

Feather collection and analyses

Five to ten feathers (*c.* 6 mg, 0.25-cm^2 area of skin exposed) were cut from the centre of the dorsal area of pied flycatchers held temporarily in captivity in 2008 and 2011, in Ruissalo Botanical Gardens, Turku, Finland. Note that because sympatric and allopatric northern European populations are phenotypically and genetically nondifferentiated (Lehtonen *et al.*, 2009a), sampling from an allopatric population should not bias the results. We subdivided the continuous variation in dorsal darkness into two discrete variants based on the relative percentage of black and brown feathers (Drost, 1936): males were considered brown when they showed ≤40% of dorsal darkness (Drost scores > 5); males were considered black when they showed ≥60% of dorsal darkness (Drost scores ≤ 3). Collared flycatchers feathers were obtained from preserved specimens kept in a −20°C freezer for < 10 years in Hungary and the Czech Republic. These storage conditions should provide reliable comparisons with 'fresh' samples possible (K. Wakamatsu, pers. comm.). Note that only brown individuals are used in the current analyses: pied flycatcher brown males, pied flycatcher females and collared flycatcher females. Nonetheless, Table S1 provides the median values for all feather traits measured also from darker conspecific and heterospecific males as a reference.

Melanin is a common avian feather pigment which comes in two main forms that differ in granule size and shape, in chemical composition and in colour (Mcgraw, 2006). Eumelanin and pheomelanin, responsible for dark/grey and buff/chestnut coloration, respectively, tend to coexist and their ratio reflects the variation in shades and hues both across and within species (Ito & Wakamatsu, 2003; Mcgraw *et al.*, 2005; Mcgraw, 2006). Feather melanin concentrations were assessed following the well-established methods described in Wakamatsu *et al.* (2002) and Ito *et al.* (2011). Briefly, using 3–5 mg of feathers, eumelanin and pheomelanin were specifically measured as the markers pyrrole-2,3,5-tricarboxylic acid (PTCA) after alkaline hydrogen peroxide oxidation and 4-amino-3-hydroxyphenylalanine (4-AHP) after hydroiodic acid hydrolysis, respectively. To convert to contents of eumelanin and pheomelanin, contents of PTCA and 4-AHP were multiplied by factors of 25 and 9, respectively. Because the relative proportion of the two types of melanin has been suggested to confer more information (Mcgraw, 2006) than total melanin content, we have calculated the ratio of eumelanin to pheomelanin concentrations. The role of structural coloration such as the ultraviolet (UV) component in bird plumage signals is well established (Bennett *et al.*, 1994; Badyaev & Hill, 2003; Bennett & Thery, 2007), and the absorption spectra of eumelanin and pheomelanin differ at all wavelengths, including the ultraviolet region (Mcgraw, 2006). Work by Siitari and colleagues (Siitari & Huhta, 2002; Siitari *et al.*, 2002) suggested that UV reflectance in the same plumage areas that define dark-brown continuum is involved in visual signalling in pied flycatchers and under female choice. Most importantly, this trait varied

independently of the dark-brown classification (Siitari & Huhta, 2002). The same spectrophotometry equipment (EG & G Gamma Scientific) and general methodology of Siitari *et al.* (2002, 2007) were used in the current study. Briefly, three to five superimposed feathers were placed on a dark velvet background (low reflectance at all wavelengths). Although this might seem a small number (Quesada & Senar, 2006), it was sufficient to make sure that the superposition of the pigmented area at the distal end of the feathers was equivalent to the natural feather arrangement, while simultaneously providing an opaque surface to measure. The spectra were recorded three times per sample over the 320- to 700-nm range and relative to a 99% white standard (WS-2). The sample was illuminated at 55 degrees to the surface from the proximal end, with recording done at 90 degrees (35 degrees to illumination) and 17 mm distance. All measurements were taken in a dark room. We used Avicol v.6 (Gomez, 2006) to analyse the averaged reflectance spectra for each individual. Spectra were corrected by (i) removing an artificial equipment peak (15 nm local smoothing between 640 and 660 nm) and (ii) performing a whole spectra triangular smoothing (20 nm distance). Brightness was normalized at fifty per cent prior to the two calculations of chroma to avoid intrinsic methodology-based sources of error when measuring dark feathers (R. Montgomerie, pers. comm.). Ultraviolet chroma was computed for the wavelength interval between 320 and 400 nm (i.e. the proportion of reflectance from the total measured between 320 and 700 nm). Because the colour 'brown' is difficult to determine in terms of a wavelength interval and because absorption differences between the two types of melanin include the red wavelengths (Mcgraw, 2006), we adapted Avicol's in-built 'brown chroma' option to include red wavelengths. Thus, our variable red-brown chroma corresponds to the 500- to 700-nm interval.

Statistical analyses

A nonparametric version of the independent-sample *t*-test was chosen to run pairwise comparisons between groups, because our inherent small sample sizes (*c.* 15 per group) failed to meet its statistical assumptions. For instance, within-group distribution of the (transformed) dependent variables was often not normal, and the variances between groups differed. We therefore conducted Wilcoxon rank sum tests for two independent samples in R (v 2.13.2; R Core Development Team, 2012). We used the 'wilcox_test' function available from the package 'coin' (Hothorn *et al.*, 2008). Its output provides a Z-statistic and calculates P-values using Monte Carlo simulations ($n = 10\,000$ repeats in the present study). Effect size 'd' and its 95% confidence levels (CL) were obtained using Nakagawa and Cuthill's (2007) R script (the statistic 'Z' was used in the place of '*t*' in equation 10; S. Nakagawa, pers. comm.)

Results & discussion

We found that brown pied flycatcher males are more likely sexual mimics of heterospecific (collared flycatcher) than of conspecific females. In fact, male brown pied flycatcher and female collared flycatcher dorsal feathers are statistically indistinguishable in all three major traits: melanin composition (eumelanin-to-pheomelanin ratio) and both ultraviolet and red-brown chromas (Fig. 1; Table 1). In contrast, brown male and female pied flycatchers differ in melanin composition and ultraviolet reflectance, with a nonsignificant but considerable difference in red-brown chroma (Fig. 1; Table 1). Unfortunately, the threshold for red-brown chroma discrimination ability is currently unavailable for this species, because we lack the detailed information needed to compute colour contrasts using physiological models of avian colour vision (Bennett & Thery, 2007). However, we believe that the observed 4% difference in ultraviolet chroma between brown male and female pied flycatchers (Fig. 1c; Table S1) is biologically meaningful and that all operators in this mimetic system are able to detect it. Previous experimental work has shown that female pied flycatchers can detect a 2% difference in male dorsal plumage ultraviolet chroma (Siitari *et al.*, 2002).

All previously reported cases of female mimicry in sexually dichromatic birds pertain to contexts where the (temporary or permanent) resemblance of the (young) male mimic to duller conspecific females functions as a defensive mechanism to minimize sexual recognition (Wiens, 2001; Hawkins *et al.*, 2012). Therefore, all members of these mimetic systems (mimic, model and operator) belong to the same species. Our results suggest that the model and the (main) operator in this mimicry system are heterospecific to the mimic. Because the expression of dichromatism in birds is determined by both past and current contexts (i.e. function, ecology and selection patterns; reviewed in Badyaev & Hill, 2003), a closer look at the evolutionary interactions between the two species involved in this mimetic system can highlight the particular conditions necessary for such phenomena to occur.

Rainey and Grether (2007) have put forward that a mimicry interaction where the evolutionary benefit to a mimic is expressed as a competitive advantage in the access to a defended resource or its control should be viewed as a case competitive mimicry (cf. defensive *sensu* Vane-Wright, 1976). Behavioural experiments have shown that brown male pied flycatchers have such a competitive advantage, both in intra- and interspecific male–male interactions (Gustafsson & Pärt, 1991; Slagsvold & Sætre, 1991; Sætre *et al.*, 1993; Alatalo *et al.*, 1994): in sympatry, they suffer reduced aggression and therefore can establish breeding territories closer to more social dominant collared flycatcher males; in allopatry, the same advantage applies to interactions with darker
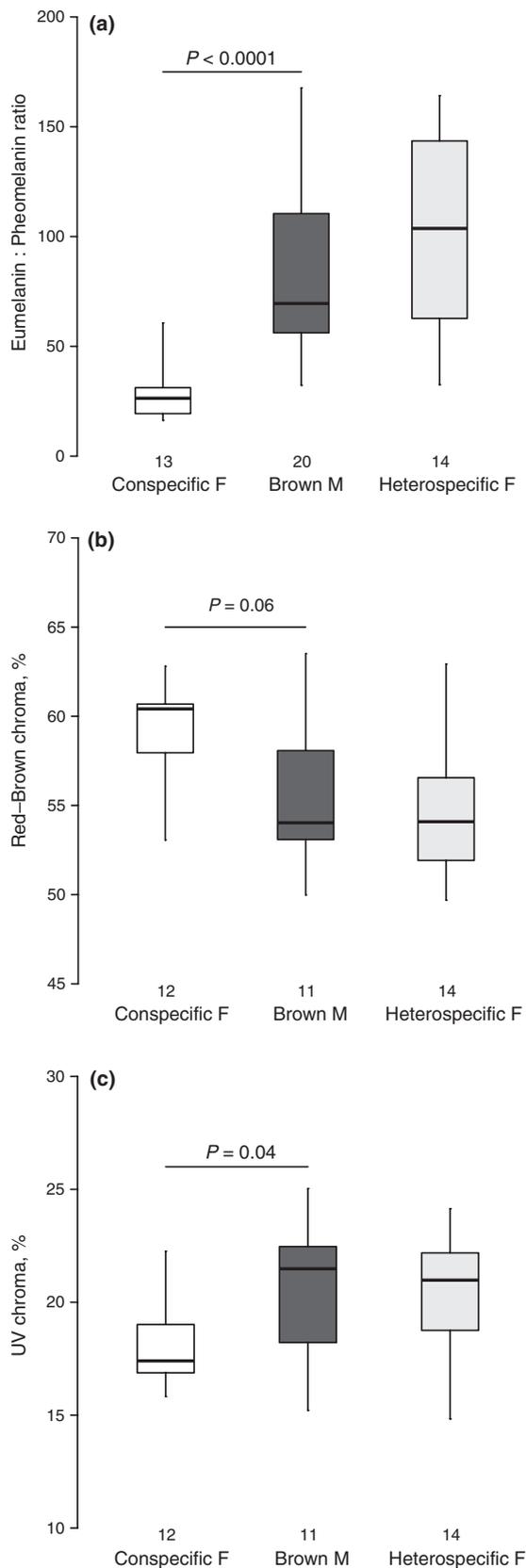
Fig. 1 Median feather trait values in the brown pied flycatcher (*Ficedula hypoleuca*) males, that is, the mimic, and the two potential models in the mimetic system: conspecific and heterospecific (collared flycatcher, *F. albicollis*) females. Boxes refer to interquantile ranges, and whiskers extend to minimum and maximum datapoints. (a) Ratio between eumelanin and pheomelanin concentrations. (b) Brightness-normalized red-brown (500–700 nm) chroma. (c) Brightness-normalized ultraviolet (UV) (320–400 nm) chroma. Lines show significant differences (or marginal nonsignificance with large effect size) between groups (see Table 1 for detailed statistical analyses). Numbers at the *x*-axis denote sample sizes.

Table 1 Pairwise comparison of dorsal feather traits between brown pied flycatcher (*Ficedula hypoleuca*) males and the two types of females: conspecific and heterospecific (*F. albicollis*). *Z*-statistic from Wilcoson rank sum test is provided together with the Monte Carlo-simulated *P*-value and a corresponding effect size d with 95% confidence limits. Melanin trait *n* = 20 (male), *n* = 13 (conspecific female) and *n* = 14 (heterospecific female). Chroma traits *n* = 11 (male), *n* = 12 (conspecific female) and *n* = 14 (heterospecific female).

	z	P	Effect size d (95% CL)
Vs. Conspecific females			
Eumelanin/pheomelanin ratio	−4.46	< 0.0001	−1.55 (−2.35, −0.75)
Eumelanin (ng/g)	−1.47	0.145	−0.51 (−1.22, 0.20)
Pheomelanin (ng/g)	4.27	< 0.0001	1.48 (0.69, 2.27)
Red-brown chroma (%)	1.90	0.061	0.80 (−0.10, 1.71)
UV chroma (%)	−2.09	0.035	−0.88 (−1.79, 0.03)
Vs. Heterospecific females			
Eumelanin/pheomelanin ratio	−1.47	0.147	−0.51 (−1.22, 0.20)
Eumelanin (ng/g)	3.09	0.003	1.08 (0.32, 1.83)
Pheomelanin (ng/g)	2.94	0.003	1.02 (0.27. 1.77)
Red-brown chroma (%)	0.88	0.408	0.35 (−0.48, 1.20)
UV chroma (%)	< 0.001	> 0.999	0.00 (−0.83, 0.83)

conspecifics. In addition, there is strong female choice for browner pied flycatcher males in sympatry, which reduces the occurrence of costly hybridization (Sætre *et al.*, 1997b). However, in both allopatric and sympatric populations, brown pied flycatcher males must still be both species recognizable and sexually recognizable to conspecific females. Although the latter can be easily disclosed behaviourally (e.g. through species-specific song and displays), sex-specific behavioural suppression is often a key addition for a successful morphology-based concealment of sex (e.g. Langmore & Bennett, 1999). Therefore, it would be interesting to investigate how brown males initially behave when inspecting or being inspected by darker (i.e. more dominant) neighbours of either species.

Remarkably, males of neither flycatcher species follow species assortative pairing patterns when given a

choice (Sætre *et al.*, 1997a), despite the fact that perceptually the two female plumages are (statistically) different (Table S2). This suggests that at least in males, there is no ability to, or there is no selection for, distinguishing between female types nor, by proxy, brown males from females. The high cost of erroneously displaying aggression towards a potential mate might explain the latter. Note that the potential for error is considerable, as trait distributions overlap considerably between the sexes and between species (Fig. 1). Therefore, there might be (temporal) variation in (conspecific) sexual recognition ability by males. In pied flycatcher females, this ability is also unclear, although one can assume that there is selection pressure to correctly identifying the sex of a brown individual, because nesting female pied flycatchers (but not female collared flycatchers) are rather aggressive towards brown 'intruders' (Slagsvold & Sætre, 1991; Sætre *et al.*, 1993).

Sexual dichromatism is the ancestral state in *Ficedula* flycatchers (Sætre *et al.*, 1997b), but there are currently no data on the specific mechanism behind dichromatism in this family (Kimball & Ligon, 1999). Dimorphism-to-monomorphism transitions are more common than the reverse in avian plumage evolution (Price & Birch, 1996). Although the latter are more often the result of changes in female cf. male plumage (Badyaev & Hill, 2003), a phylogenetic study of (recent) speciation events in passerine birds suggests that phenotypic divergence in phenotypes between species is largely restricted to male traits under strong sexual selection, namely those used in mate choice and species recognition (Seddon *et al.*, 2013). We propose that the abundance in sympatry of brown pied flycatcher males might represent a ongoing but spatially localized shift from dichromatism (or greater phenotypic variation) towards an apparent 'monochromatism' (or reduced phenotypic variation), which is favoured by a combination of strong agonistic (i.e. interspecific competition; Gustafsson & Pärt, 1991; Sætre *et al.*, 1993; Alatalo *et al.*, 1994) and reproductive (female choice; Sætre *et al.*, 1997b) character displacement. It is common that these two types of character displacement mechanisms co-occur (reviewed in Grether *et al.*, 2009). Rice and Pfennig (2007) proposed two (nonmutually exclusive) general routes for the evolution of character displacement. According to one route, male brown coloration in pied flycatchers would be a trait that first appeared in sympatry (a truly derived character; Sætre *et al.*, 1997b); according to the alternative route, brown plumage was already present as part of phenotypic variation in pied flycatchers before secondary contact occurred. Because there is genetic variation in this trait, no genetic segregation between sympatric and allopatric populations (Lehtonen *et al.*, 2009a) and no evidence for consistent selection against this trait in allopatry (see below), the second route can better explain heterospecific mimicry in *Ficedula*. Selection on melanin-based plumage differs considerably in the absence of collared flycatchers, and it promotes male phenotypic diversity. For instance, fluctuating selection can explain (yearly) variation in mean dorsal coloration within and across allopatric populations (Sirkiä *et al.*, 2010): the relative fitness of darker and browner pied flycatcher males is influenced by environmental conditions such as temperature during breeding. Moreover, female choice in allopatric populations (for pair and/or extra-pair mates) is largely independent of dorsal darkness (e.g. Alatalo *et al.*, 1986; Lehtonen *et al.*, 2009b; Sirkiä & Laaksonen, 2009; Moreno *et al.*, 2010). Therefore, by only mimicking collared flycatcher females, brown pied flycatcher males suffer lower intrasexual aggression (by both heterospecific and conspecific rival males), while insuring within-species sexual recognition in both sympatry and allopatry.

The currently observed unique mimetic system in *Ficedula* flycatchers probably results from a series of evolutionary conditions, each of which is not unique: ancestral sexual dichromatism, a (partial) secondary contact zone between closely related (e.g. congeneric) species, aggressive defence of (ecologically overlapping) breeding territories, dominance asymmetry in interspecific interactions, existing (or potential for) variation in traits in the subordinate species that are involved in competitor (mis)identification (see Grether *et al.*, 2009 for examples of the latter two points). Therefore, a detailed look at both female and male plumage traits in species that fit (some) the latter criteria might uncover other examples of heterospecific sexual mimicry in birds.

Acknowledgments

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Median trait values for all measured dorsal feather traits in both sexes of the two flycatcher species.

Table S2 Pairwise comparison of dorsal feather traits between pied flycatcher and collared flycatcher females.