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Distinguishing between male and territory quality: females choose multiple traits in the pied flycatcher

Päivi Maria Sirkiä [a,*], Toni Laaksonen [a,b]

[a] *Section of Ecology, Department of Biology, University of Turku*
[b] *Finnish Museum of Natural History, University of Helsinki*

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To understand how sexual selection works, it is important to distinguish between the mechanisms underlying mating success. One of the basic questions is to differentiate between the importance of territory-related resources (gained through male–male competition) and male quality in female choice. Few studies, however, have tried to separate these two often intercorrelated variables. We randomized territory quality among male pied flycatchers, *Ficedula hypoleuca*, and studied which male traits were associated with their success in female mate choice. Females appeared to choose multiple male traits in the wild when the males were not allowed to choose territories before female choice for males. Males with a long tarsus, large white wing patch and versatile song were favoured by females. In addition, the contrast of ultraviolet (UV) reflectance in the white wing patch relative to its background, that is, the dorsal brown-black coloration of the males, appeared to be an important mate choice cue. The UV reflectance had a stronger effect on pairing success in dark males than in brown ones. An experimental manipulation of the UV reflectance revealed that the UV coloration of the males appeared to be used in female choice early but not late in the pairing season, which suggests time-dependent plasticity in female choice. Our study thus exemplifies the complexity of mate choice; it is both temporally constrained and dependent on multiple ornaments.

Sexual ornaments, such as complex song or bright coloration of males, are thought to have evolved through the process of sexual selection (Darwin 1871; Andersson 1994). Sexual selection can arise through two different mechanisms: competition for access to mates or mate choice (Darwin 1871; Andersson 1994). Distinguishing between these two mechanisms in driving the evolution of sexual traits is an important but often neglected aspect needed for understanding how sexual selection works (Kotiaho & Puurtinen 2007).

Identifying the targets of mate preferences is a necessary first step for understanding the sexual selection process (Chenoweth & Blows 2006). There are several reasons why this may not always be easy. First, there are multiple ornaments or display components in many sexually signalling species (Møller & Pomiankowski 1993; Johnstone 1995; Brooks 2002; Candolin 2003; Badyaev 2004). Different traits may convey information for different receivers: for instance one trait may be a signal for the opposite sex whereas another signal may be used in intrasexual competition (Andersson et al. 2002). Second, another layer of complexity is added by the growing evidence that ecological, social and temporal variation may create context-dependent flexibility in mate choice; a trait can be sexually selected for in one situation but not in another (e.g. Qvarnström et al. 2000; Alonzo & Sinervo 2001; Oh & Badyaev 2006; Chaine & Lyon 2008). Third, it is essential but demanding to examine the relative strength of inter- and intrasexual selection which can interact with each other in several ways (see e.g. Forsgren et al. 1996; reviewed in Qvarnström & Forsgren 1998; Wong & Candolin 2005; Kotiaho & Puurtinen 2007; Hunt et al. 2008; DuVal & Kempenaers 2008).

In many species in which males compete for resources necessary for attracting females (e.g. suitable breeding sites), dominant males monopolize high-quality resources and consequently gain mating advantages (Andersson 1994). Good-quality individuals are furthermore likely also to have good-quality territories and discrimination between choice of territory versus mate is often difficult. It might appear that females choose some male traits, but it may be that the males carrying these traits are holding the best resources and their success is thus actually based on success in male–male competition (Griffith & Pryke 2006). The distinction between the importance of territory-related resources and that of phenotypic indicators of individual quality is often ignored. In nonexperimental studies the two variables can hardly be separated at all and it is also challenging to conduct field

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* Correspondence: P. M. Sirkiä, Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland.
E-mail address: pmsirk@utu.fi (P.M. Sirkiä).

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experiments in which it is possible to distinguish between them. Despite numerous studies on sexual selection and mate choice cues (reviewed in e.g. Andersson 1994; Candolin 2003; Griffith & Pryke 2006; Hill 2006), few studies have successfully separated individual quality from resources in mate choice in the wild (Alatalo et al. 1986; Slagsvold 1986; Eckerle & Thompson 2006; but see e.g. Lehtonen et al. 2007; Dijkstra et al. 2008 for captivity studies aiming to separate the effects of male traits and nest size on female choice in fishes).

One of the few experiments aiming to distinguish between territory and individual quality in the wild was conducted by Alatalo et al. (1986) on the pied flycatcher, *Ficedula hypoleuca*. In this classic study, the males were directed to randomly allocated territories in their order of arrival at the breeding grounds. The males were given a choice of only one territory (with two nestboxes) at a time and a new territory was set up only after the previous one was occupied. Once a group of males had territories, the already arrived females were removed. Thus the newly arriving females (the first choice group) could choose from a complete set of males that were of different phenotypes but on random territories. In some of the territories the females were removed another time and the order of choices in a second arrival group of females (the second choice group) was recorded. Alatalo et al. found that there was a good correlation between the orders in which the males were chosen by the two groups of females. From this they concluded that females primarily chose the territory, since any of the traits that they measured from the males (dorsal coloration, size or song characteristics of the males) did not explain the order in which the males were chosen.

Despite its merits, there are at least two critical enhancements that can be added to the design presented above. First, only those male traits that were measured may be excluded as explanations for the order of female choice. Mate choice cues that were not studied include ultraviolet (UV) coloration and forehead patch size, which have since been shown to affect female mate choice in the pied flycatcher (Potti & Montalvo 1991; Siitari & Huhta 2002; Siitari et al. 2002). The second limitation in the design is that even if a correlation between a male trait and female choice were detected, it could be that this trait is not the cause of female choice but that it is just correlated with another trait that is the target of female choice. Only an experimental manipulation of the particular male trait could reveal causality.

We continued the investigation of mate choice cues along the path of Alatalo et al. (1986) and conducted experiments aiming to separate male quality from territory quality in the pied flycatcher. The pied flycatcher is sexually dimorphic in plumage coloration during the breeding season, with males bearing multiple ornaments (Lundberg & Alatalo 1992). The melanin-based dorsal coloration (head and back) of the males varies from completely brown to black (Drost 1936; Lundberg & Alatalo 1992). In an aviary study dorsal plumage colour functioned as a cue for mate choice (Sætre et al. 1994), but in other studies no relationship has been observed (Alatalo et al. 1986; Dale & Slagsvold 1990; Lundberg & Alatalo 1992; Lampe & Espmark 2003). Males have a conspicuous white forehead patch (Lundberg & Alatalo 1992), which is a sexually selected trait at least in a Spanish population (Potti & Montalvo 1991). Males also have large white wing patches and white areas in the outer tail feathers (hereafter called tail patches) that vary in size and shape. Also, song is a secondary sexual character that appears to be important in mate choice; in aviary experiments females preferred more complex songs (Eriksson 1991; Lampe & Sætre 1995) and in a field study males with more elaborate songs had a greater chance of becoming paired (Lampe & Espmark 2003).

A significant breakthrough in avian mate choice studies after the work of Alatalo et al. (1986) was the realization that most birds can also detect near-ultraviolet light (UV-A; 320–400 nm; see Cuthill et al. 2000; Hart 2001; Eaton 2005). The UV reflectance of male plumage traits affects mate choice in many species (e.g. Bennett & Cuthill 1996; Andersson & Amundsen 1997; Bennett et al. 1997; Andersson et al. 1998; Hunt et al. 1998; Johnsen et al. 1998; Sheldon et al. 1999; Siitari et al. 2002; Delhey et al. 2003, 2006). The sexually dimorphic UV component of coloration seems to signal individual quality in the pied flycatcher, since early arriving and old males have a higher proportional UV reflectance than later arriving or young ones (Siitari & Huhta 2002). The male's UV reflectance affected female mate choice in pied flycatchers in aviary experiments (Siitari et al. 2002), but no studies have been conducted on this topic in free-living populations. In our study population, males with lower UV reflectance are more likely to be cuckolded (to lose paternity) than males with high reflectance values, while other male plumage traits do not appear to be important in this respect (Lehtonen et al. 2009).

We designed and conducted two experiments. The first one, the random territory experiment, was based on randomizing territory

Table 1
Experimental treatments

Experiment	Methods	Analyses
Random territory experiment		
Male settlement	Males were directed to randomly allocated territories; they could not choose between territories when they arrived	
First selection period	Females were allowed to choose between males (first choice group)	Pairing rank of males was correlated against male original (natural) UV chroma
UV manipulation	The first choice group of females was removed and UV reflectance of males was manipulated	A repeated measures model was performed to analyse (1) whether UV manipulation changed the pairing rank of males between the first and second female choice groups, (2) whether other male traits were associated with their pairing rank, and (3) whether there were time effects in how these traits were associated with pairing rank (comparison between the two selection trials)
Second selection period	Second female choice group was allowed to choose between the males	
Early season UV manipulation experiment	Males had a choice of territory. They were captured soon after arrival and their plumage UV reflectance was manipulated. Pairing time of males was monitored.	Male pairing time was compared between UV-reduced and control groups
Combination of random territories and early season UV manipulation experiments	The data from the two UV manipulations were combined for the analysis of seasonal change in female choice for experimentally manipulated UV reflectance	The essential test was whether the effect of UV manipulation on pairing time changed during the season (interaction between the treatment and the date of manipulation)

Early season UV manipulation could be conducted early in the mating season, while the plumage manipulation in the random territory experiment was conducted relatively late in the pairing season of the population. The combination of the two experiments thus allowed us to examine temporal plasticity in how UV reflectance is used in mate choice.