Fecundity selection does not vary along a large geographical cline of trait means in a passerine bird

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Local environmental and ecological conditions are commonly expected to result in local adaptation, although there are few examples of variation in phenotypic selection across continent-wide spatial scales. We collected standardized data on selection with respect to the highly variable plumage coloration of pied flycatcher (*Ficedula hypoleuca* Pall.) males from 17 populations across the species' breeding range. The observed selection on multiple male coloration traits via the annual number of fledged young was generally relatively weak. The main aim of the present study, however, was to examine whether the current directional selection estimates are associated with distance to the sympatric area with the collared flycatcher (*Ficedula albicollis* Temminck), a sister species with which the pied flycatcher is showing character displacement. This pattern was expected because plumage traits

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in male pied flycatchers are changing with the distance to these areas of sympatry. However, we did not find such a pattern in current selection on coloration. There were no associations between current directional selection on ornamentation and latitude or longitude either. Interestingly, current selection on coloration traits was not associated with the observed mean plumage traits of the populations. Thus, there do not appear to be geographical gradients in current directional fecundity selection on male plumage ornamentation. The results of the present study do not support the idea that constant patterns in directional fecundity selection would play a major role in the maintenance of coloration among populations in this species. By contrast, the tendency for relatively weak mosaic-like variation in selection among populations could reflect just a snapshot of temporally variable, potentially environment-dependent, selection, as suggested by other studies in this system. Such fine-grained variable selection coupled with gene flow could maintain extensive phenotypic variation across populations. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **114**, 808–827.

INTRODUCTION

Population differentiation in phenotypic traits is expected to reflect a balance between the diversifying effect of local, spatially variable selection and the homogenizing effect of gene flow (Endler, 1980; Kirkpatrick & Barton, 1997). Differentiation between populations is considered to be elevated by spatial variation in sexual selection regimes and rapid divergence is predicted in male traits that are targets of female choice (Lande, 1982). Classical models of natural and sexual selection predict that selective regimes change smoothly along a cline over a species' distributional range (Endler, 1980; Lande, 1982). However, intra- or interspecific biotic interactions or environmental heterogeneity may lead to smaller-scaled spatial variation in selection regimes (Brodie & Ridenhour, 2002; Svensson & Sinervo, 2004; Gosden & Svensson, 2008; Cornwallis & Uller, 2010). Understanding whether selection varies along clines or in a mosaic-like fashion has important implications for patterns of adaptive evolution (Siepielski *et al*., 2013).

Studies investigating spatial variation in phenotypic selection across large geographical scales are still scarce, and the understanding of patterns of selection and of the selective agents behind phenotypic patterns remains poor. Such studies have been conducted in relation to behavioural traits (Soler *et al*., 1999, 2001), morphology (Blanckenhorn *et al*., 1999; Svensson & Sinervo, 2004; Møller *et al*., 2006; Gosden & Svensson, 2008) and other phenotypic traits, including animal coloration (Calsbeek, Bonvini & Cox, 2010; Weese *et al*., 2010; Svensson & Waller, 2013). However, few studies have assessed geographical variation in contemporary selection on sexually selected colour ornaments. This is surprising, not least given the importance of sexual selection in animal coloration in many different taxonomic groups (Andersson, 1994; Hill, 2006).

We investigated current selection pressure on the plumage ornaments of male pied flycatchers across a continent-wide spatial scale. The pied flycatcher is a small hole-nesting passerine bird that has sexually dimorphic plumage coloration, with males displaying multiple apparent ornaments, such as a white forehead patch and conspicuous white wing and tail patches (Lundberg & Alatalo, 1992). Despite the fact that sexual selection in this species has been extensively studied across much of their breeding range for decades (Alatalo, Lundberg & Stahlbrandt, 1984; von Haartman, 1985; Slagsvold & Lifjeld, 1988), the patterns of selection on male ornaments still remain largely unknown.

The most conspicuous coloration trait in male pied flycatchers is the melanin-based dorsal coloration that varies from completely brown to black (Drost, 1936; Lundberg & Alatalo, 1992). Melanin coloration is often linked with reproduction (Meunier *et al*., 2011), stress sensitivity (Almasi *et al*., 2012), parasite resistance (Lei *et al*., 2013), and the costs of parasite infections (Karell *et al*., 2011a). Several studies have found context-dependent selection on melanin-based coloration (Roulin *et al*., 2008; Dreiss *et al*., 2010; Karell *et al*., 2011b; Dreiss *et al*., 2012). This is the case also in an allopatric population of the pied flycatcher where the breeding success of different melanin phenotypes has been found to be dependent on current weather conditions (Sirkiä, Virolainen & Laaksonen, 2010; Sirkiä *et al*., 2013). Melanin-based coloration typically shows high heritability in birds (Roulin & Ducrest, 2013); also in the pied flycatcher, black–brown melanin-based coloration has been shown to be highly heritable in different populations (reported h^2 values in the range 0.6–0.9) (Alatalo, Gustafsson & Lundberg, 1994; Grinkov, 2000; Lehtonen *et al*., 2009a). There is much more phenotypic variation in the dorsal black–brown coloration of pied flycatchers among populations than is predicted by neutral genetic variation (Lehtonen *et al*., 2009a), which is similar to the heritable melanin coloration of barn owls (*Tyto alba*) (Antoniazza *et al*., 2010). Such patterns are commonly interpreted as indirect signals

of divergent selection on a trait (Leinonen *et al.*, 2008).

The distributions of the pied flycatcher and the closely related collared flycatcher overlap in Central and Eastern Europe (Fig. 2). In areas of sympatry, male pied flycatchers are mostly brown, probably as a result of the avoidance of interspecific competition and hybridization with the black-and-white collared flycatcher (Král, Järvi & Bičík, 1988; Lundberg & Alatalo, 1992; Sætre *et al.*, 1997; Qvarnström, Rice & Ellegren, 2010; Sætre & Sæther, 2010). There is selection for brown dorsal coloration in males in the sympatric area (Sætre *et al.*, 1997). In allopatric areas, both colour types occur, although the frequency of darker males (and thus the level of sexual dichromatism) appears to increase with distance from the Central European breeding areas (Røskaft *et al.*, 1986; Lundberg & Alatalo, 1992; Lehtonen *et al.*, 2009a). This has often been assumed to be associated with sexual selection for conspicuous coloration, whereas gene flow from sympatric and nearby areas is expected to be the main factor maintaining variation in male phenotype in allopatric areas. Some studies have found sexual selection for black male coloration in allopatric areas (Røskaft & Järvi, 1983; Sætre, Dale & Slagsvold, 1994; Dale & Slagsvold, 1996; Sætre *et al.*, 1997). However, there are also several studies conducted in single allopatric populations that have not found any clear benefits for black males in mate choice (Alatalo, Lundberg & Glynn, 1986; Alatalo, Lundberg & Sundberg, 1990; Potti & Montalvo, 1991a; Sirkiä & Laaksonen, 2009; Lehtonen, Primmer & Laaksonen, 2009b) or breeding success (Røskaft & Järvi, 1983) and there have been no attempts to analyze selection acting on plumage coloration in multiple populations. In addition, selection on male dorsal coloration has been found to be context-dependent, depending on current temperatures (Sirkiä *et al.*, 2010). In the light of current evidence, there is no consensus that black coloration *per se* is sexually or naturally selected in the allopatric area in all contexts. Spatial pattern of selection on melanin coloration thus remains unknown in allopatry.

Another aspect of avian plumage coloration is reflectance at near-ultraviolet (UV) light wavelengths (UV-A; 320–400 nm), which is visible to birds (Cuthill *et al.*, 2000). The UV reflectance is sexually selected for in the pied flycatcher, at least in some allopatric populations (Siitari *et al.*, 2002; Sirkiä & Laaksonen, 2009; Lehtonen *et al.*, 2009b), although spatial variation in selection on the trait is unknown. The remaining plumage traits studied are conspicuous white ornamental patches in the forehead, wing, and tail, which all vary greatly in size and shape. Most males have a white forehead patch, the size of which has a heritable component (Potti & Canal, 2011; but see also Dale *et al.*, 1999). Sexual selection has been found to act on forehead patch size in some allopatric populations (Potti & Montalvo, 1991a; Sirkiä *et al.*, 2010; Canal, Potti & Dávila, 2011; Järvistö, Laaksonen & Calhim, 2013). Sexual selection has also been indicated to act on wing patch size (Sirkiä & Laaksonen, 2009; Sirkiä *et al.*, 2010) but not on tail patch size (Sirkiä & Laaksonen, 2009), which has received little study. Spatial variation in selection on wing and tail patches remains unknown. Common for all the plumage ornamentation traits, mean conspicuousness increases with the distance from the sympatric area (Sirkiä, 2011; T. Laaksonen, P.M. Sirkiä, S. Calhim, P. Adamík, A.V. Artemyev, E. Belskii, C. Both, S. Bureš, M. Burgess, B. Doligez, J.T. Forsman, V. Grinkov, U. Hoffmann, E. Ivankina, M. Král, I. Krams, H.M. Lampe, J. Moreno, M. Mägi, A. Nord, J. Potti, P-A. Ravussin, L. Sokolov, unpubl. data). Although selection on male plumage ornaments has been widely studied in the pied flycatcher, most studies have concentrated on only one or few phenotypic traits at a time and no study has compared selection acting on plumage traits across populations. When studying ornamentation, it is important to examine multiple attributes simultaneously (Candolin, 2003; Laczi *et al.*, 2011). We analyzed selection on five different plumage traits that cover the main axis of male colour variation in this species. Because the coloration traits under investigation are correlated (see Supporting information, Table S1; Ivankina *et al.*, 2007; Sirkiä & Laaksonen, 2009; but see also Moreno *et al.*, 2011), we were particularly interested in comparing the roles of indirect and direct selection because indirect selection on correlated traits may potentially drive the evolution of some of the studied traits.

We estimated selection on plumage traits of male pied flycatchers via fecundity (defined as the number of fledglings produced). Males gain fitness benefits through producing a higher number of fledglings. This may occur as a result of pairing with a female in good condition (Fisher, 1930) or indirectly if female investment in the clutch is dependent on the attractiveness or quality of the male (Burley, 1986; Sheldon, 2000). Selection can also be differentially acting on male phenotype during the nestling period (Sirkiä *et al.*, 2010). The intensity of selection caused by annual fecundity can be investigated by comparing the standardized number of fledged young with the standardized male plumage trait.

On the basis of the previous evidence, it can be hypothesized that there should be an association between ongoing directional selection on the plumage traits of the pied flycatcher and the distance to the sympatric area with the collared flycatcher. In allopatric areas, selection is often expected to be towards black plumage coloration and for large
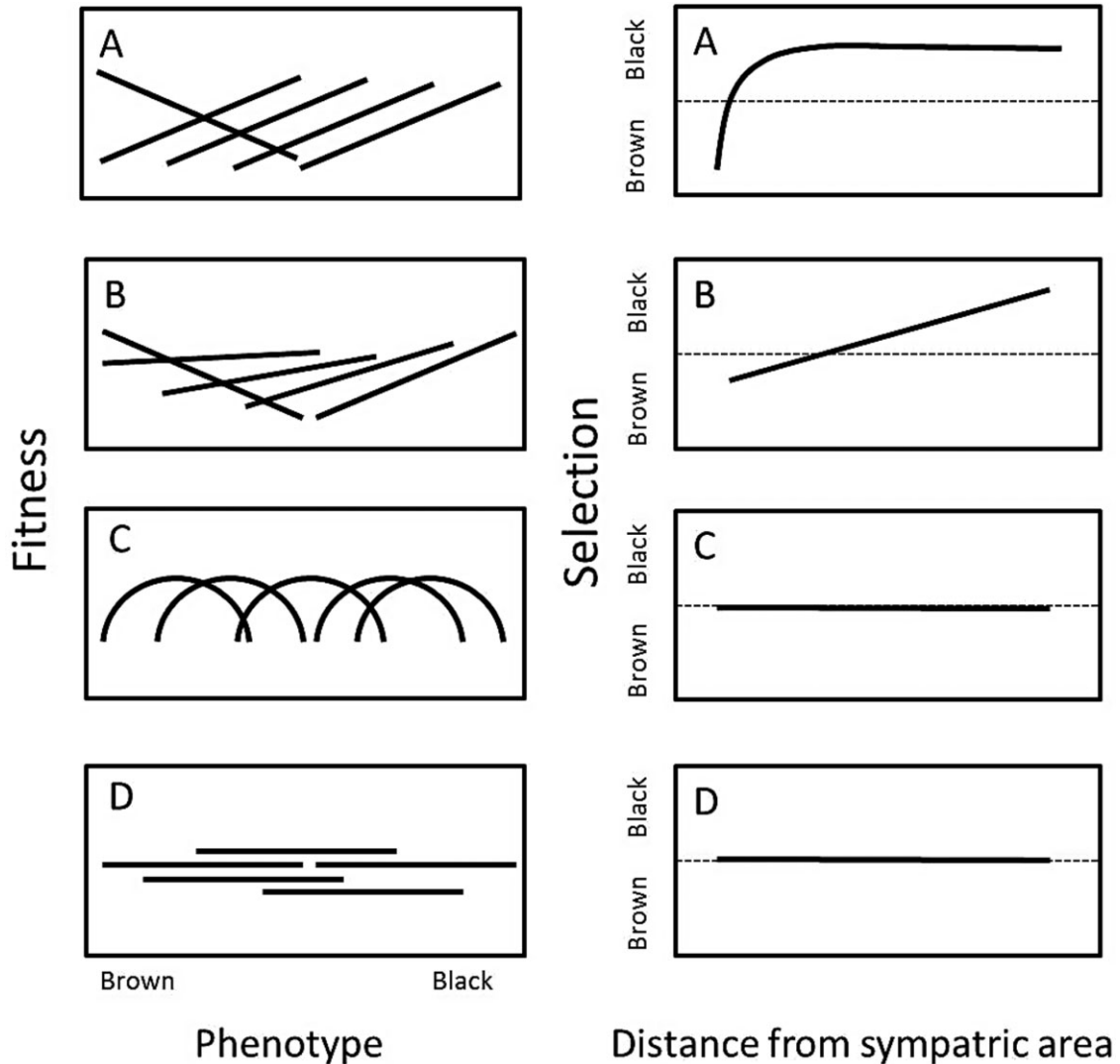
Figure 1. Conceptual illustration of four different hypotheses concerning the association between selection on male phenotype and distance from sympatric area. On the left, different lines represent associations between fitness and male phenotype in different populations. On the right, the predicted relationship between selection on male trait among populations in relation to the distance from sympatric area is shown. Male black–brown coloration is used as an example of the phenotypic traits studied. Note that ranges of ornamentation among populations may be variable among populations but are not presented here. A, there is selection on brown male coloration and small ornaments in mostly brown populations close to sympatric areas with the collared flycatcher whereas in allopatric areas selection is towards black plumage coloration and for large ornaments. B, there is ongoing directional selection on phenotype. The direction of selection on male phenotype in relation to distance from sympatric area is smooth and gradient-like: selection for conspicuous coloration can be expected to become stronger with an increasing distance from the sympatric area. C, different populations are locally adapted and there is no association between current selection and distance from the sympatric area. D, fitness is not related to phenotype in any of the populations and there is no association between selection and distance from sympatric area.

ornaments, whereas gene flow from sympatric areas can be expected to be the main factor maintaining phenotypic variation in allopatry (Fig. 1A). In this case, wide variation in male phenotype in allopatric populations would be maintained mainly by gene flow from sympatric populations. On the other hand, selec-

tion for conspicuous coloration can be expected to become stronger with an increasing distance from the sympatric area (Fig. 1B). Alternatively, populations can be primarily locally adapted and selection landscape can thus be more variable. In this case, selection is expected to be balanced within populations and

no association is expected between selection and distance to the sympatric area (Fig. 1C). One alternative for such fine-scaled and spatially variable selection is that selection on coloration is context-dependent (Sirkiä *et al.*, 2010, 2013) and variation in male coloration represents colour polymorphism in which different male types may eventually gain same fitness via different routes. A fourth option is that there is no selection operating on male ornamentation; in this case, no association between selection and distance to the sympatric area can be expected either (Fig. 1D). However, in the case of no selection on male phenotype, variation between populations should decrease with time, which is not supported by the wide geographical variation among populations and earlier studies observing selection on male colour phenotype.

The present study aimed to examine spatial variation in fecundity selection pressure on plumage coloration of male pied flycatchers. We used data from 17 different study populations that were well distributed across the species breeding distribution to calculate standardized linear fecundity selection coefficients. We were particularly interested in determining whether selection on conspicuous male plumage coloration strengthens with distance from the sympatric area with the collared flycatcher. In addition, to determine whether there are other large scale geographical patterns in selection, we tested whether the latitude or longitude of the sampled populations affects selection patterns on male plumage coloration. We further determined the relationship between selection acting on the phenotype and the observed mean phenotypes among populations. Overall, we aimed to increase our understanding of the mechanisms that maintain phenotypic variation at large spatial scales.

MATERIAL AND METHODS

STUDY AREAS

Data were collected from 17 populations that constitute a considerable coverage of the breeding range (Fig. 2, Table 1). The data were collected in 2007–2010, with most populations providing data from 2 years (Table 1). Altogether, we collected data for 2818 breeding attempts of males with known plumage traits. The data were collected mainly from males that were captured when feeding nestlings.

The distance from each study area to the closest edge of the Central and Eastern European breeding range of the collared flycatcher was estimated on the basis of the map in the Birds of the Western Palearctic (Cramp & Simmons, 2006) and complemented with more local information from the authors (P. Adamík, S. Bureš, A.V. Bushuev, D. Hoffmann, M. Král, I. Krams, P-A. Ravussin, L. Sokolov). We neglected the popula-

tions of the collared flycatcher on the Swedish islands Gotland and Öland in this respect because the recent expansion of collared flycatchers to these islands is of limited area and as yet without apparent effect on pied flycatcher coloration even on the islands themselves (Qvarnström *et al.*, 2009, 2010). In addition, the frequency of the pied flycatchers on these islands has decreased strongly, which limits the potential gene flow from these areas to a very low level. We therefore assume that the occurrence of collared flycatchers or gene flow from these rather small islands has not yet affected selection on male pied flycatcher coloration in the surrounding areas.

PHENOTYPIC MEASUREMENTS

The data were collected by different individuals in each study population but all contributors recorded male plumage traits, took photographs, and collected feather samples in a prescribed way. Feather samples and photographs were sent to P. M. Sirkiä (PMS) who measured the UV reflectance and the sizes of ornamental patches as described below. Detailed description of male phenotypic variation across the breeding distribution will be reported elsewhere (T. Laaksonen, P.M. Sirkiä, S. Calhim, P. Adamík, A.V. Artemyev, E. Belskii, C. Both, S. Bureš, M. Burgess, B. Doligez, J.T. Forsman, V. Grinkov, U. Hoffmann, E. Ivankina, M. Král, I. Krams, H.M. Lampe, J. Moreno, M. Mägi, A. Nord, J. Potti, P-A. Ravussin, L. Sokolov, unpubl. data).

Dorsal coloration

The dorsal coloration of the head and back of males was estimated by Drost scores (Drost, 1936) in the field by the observer. Drost scores I and II represent males with a black head and back, although, in group I, the rump of a male is black, whereas, in group II, it is more or less light. In group VII, males have a completely brown dorsal coloration, thus representing 0% of black (Lundberg & Alatalo, 1992; Glutz von Blotzheim & Bauer, 1993; for a detailed description, see Drost, 1936). Although dorsal coloration was estimated in the field, it was also photographed in most of the sampling sites [not in the Tomsk, Moscow region or Courish spit populations (Russia)]. If Drost scores were not estimated in the field, PMS estimated it based on the photographs [La Hiruela (Spain) and some occasional cases in other populations]. A sample of 20 photographs per sampling site was checked by PMS to confirm the consistency of coloration estimation between different observers in different populations. If the sample of 20 checked males included any disagreement between the coloration score of the observer and PMS, the rest of the photographed individuals were re-examined too. In general, the
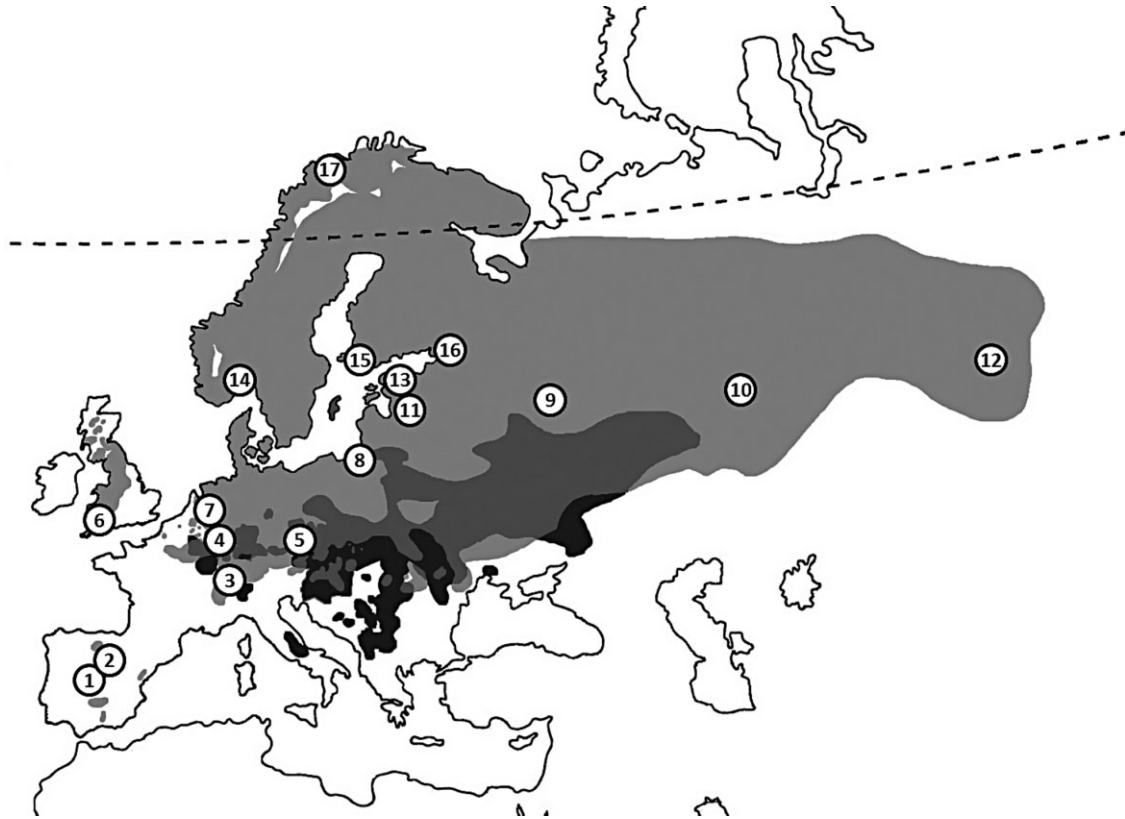
Figure 2. Breeding ranges of pied and collared flycatchers and the locations of the pied flycatcher populations studied. Light grey area illustrates the breeding range of the pied flycatcher in allopatry; the middle grey area illustrates the sympatric breeding area of both pied and collared flycatcher; and the dark grey area illustrates the allopatric breeding area of collared flycatcher. This map is modified from Birds of the Western Palearctic (Cramp & Simmons, 2006) and Flint *et al*. (1984) using local information. The white circles indicate the locations of the study populations: 1, Valsaín-Lozoya (Spain); 2, La Hiruela (Spain); 3, Vaud (Switzerland); 4, Harthausen (Germany); 5, Moravia and Jeseníky (Czech Republic); 6, East Dartmoor (United Kingdom); 7, Drenthe (the Netherlands); 8, Courish spit (Russia); 9, Moscow region (Russia); 10, Middle Urals (Russia); 11, Kraslava (Latvia); 12, Tomsk (Russia); 13, Kilingi-Nõmme (Estonia); 14, Oslo (Norway); 15, Ruissalo (Finland); 16, Karelia (Russia); 17, Skibotn (Norway).

coloration estimation between observers was very consistent because corrections were made to only 3% of all colour estimations. Differences in estimations between populations do not affect the calculation of selection estimates because male traits were standardized within populations (see below).

UV measurements of white wing patch
The second tertial feathers (from the three tertial feathers on each wing) were collected for UV reflectance measurements. Measurements were taken from the white area of the feather, which forms part of the white wing patch (Sirkiä & Laaksonen, 2009). UV reflectance was measured from the tertial feather because white feathers typically have higher UV reflectance than dark ones (Eaton & Lanyon, 2003) and tertials have a rigid feather structure, unlike the soft plumaceous structure of dark or brown body feathers. Measurements from collected feathers are congruent with measurements from wing patches in live birds (Sirkiä & Laaksonen, 2009). Measurements were conducted in a laboratory using a 2048 element spectrophotometer with a DH-S deuterium halogen light source (Avantes). Measurements were taken perpendicularly to the feather surface and a mean of three measurements per feather was used as an explanatory variable in the analyses. UV measurements were carried out by two persons (PMS and an assistant). To measure reflectance in the ultraviolet part of the spectrum, the proportion of the ultraviolet light from total reflectance was calculated (relative UV reflectance or UV chroma; $R_{320–400\,nm}$ /$R_{320–700\,nm}$).

The repeatability of measurements from the same feather samples, which was measured as an intraclass correlation (Lessells & Boag, 1987), was $r = 0.89$ ($N = 30$, $F_{9,20} = 25.83$, $P < 0.0001$). Samples from one population per study year were measured mainly at the same measuring bout. However, if the samples

Table 1. Details of the study populations, including coordinates, distance (km) from the sympatric area with the collared flycatcher, and years of population sampling

Population	Country	Coordinates	Distance (km)	Years
Valsaín-Lozoya	Spain	40°55′N, 3°54′W	1309	2008–2009
La Hiruela	Spain	41°4′N, 3°27′W	1280	2008–2009
Vaud	Switzerland	46°49′N, 6°38′E	130	2008–2009
Harthausen	Germany	49°30′N, 8°36′E	50	2010
Moravia-Jeseníky	Czech Republic	49°56′N, 17°23′E	0	2008–2010
East Dartmoor	United Kingdom	50°36′N, 3°44′W	540	2009–2010
Drenthe	The Netherlands	52°52′N, 6°17′E	380	2008–2009
Courish spit*	Russia	55°5′N, 20°44′E	110	2009
Moscow region*	Russia	55°44′N, 36°51′E	150	2008
Middle Urals†	Russia	56°49′N, 59°39′E	490	2008–2009
Kraslava‡	Latvia	55°53′N, 27°11′E	310	2008–2009
Tomsk§	Russia	56°20′N, 84°56′E	2000	2008–2009
Kilingi-Nõmme	Estonia	58°7′N, 25°05′E	360	2008–2009
Oslo¶	Norway	58°7′N, 10°38′E	900	2009–2010
Ruissalo	Finland	60°26′N, 22°10′E	600	2007–2009
Karelia	Russia	60°46′N, 32°48′E	640	2008–2009
Skibotn	Norway	69°20′N, 20°21′E	1600	2007–2009

*Data on ornamental patch sizes missing, †In 2007, data only on dorsal coloration, ‡Data on ultraviolet (UV) reflectance in 2009. §Data on wing and tail patch sizes missing. ¶Data on UV reflectance in 2009.
If the study was conducted in several sub-areas, the mean coordinates are given.

were measured during two measuring sessions, we checked that the calibration of the equipment did not cause differences between measuring occasions ($P > 0.10$). The UV reflectance measurements were conducted during 2008–2010 and there were minor differences between some of the measuring sessions as a result of differences in calibration of the equipment. These differences do not influence selection estimates because the male traits were standardized within populations (see below). However, to be able to compare mean UV reflectance values between sampled populations, ten samples (individuals) of each set of samples measured at a time (i.e. ten samples per population and year) were re-measured in one session. The mean difference between the first measurements and the re-measurements conducted in one session were used to correct the differences between measuring bouts in the original values. The corrected values were used when looking at variation in phenotypic traits among populations and when comparing selection estimates to the mean reflectance values among populations. It is known that structural coloration may erode over time (Delhey *et al.*, 2010). Feather samples were collected mainly during the nestling period; however, in the Oslo population (Norway), samples were mainly collected during pairing at the beginning of the breeding season. This difference does not affect the analyses of our study because the measurements were standardized within populations for calculation of selection estimates (see

below). However, when analyzing the amount of variation in UV reflectance among populations and when comparing selection estimates to the mean observed UV reflectance of white wing patch, the analyses were conducted with and without the population of Oslo.

Nonpigmented ornament patches
Forehead, wing, and tail patches were photographed in the field. A ruler was held at the same distance from the camera as the target ornamental patch. The area of white was later measured from the photographs using IMAGEJ (Abramoff, Magelhaes & Ram, 2004). The forehead patch was photographed directly from the front, and the wing patch directly from the side when the wing was in resting position. If the forehead patch consisted of two separate patches, the area of both patches was summed and this value was used as a variable in the analyses. In the Tomsk population (Russia), the size of the forehead patch was measured with a calliper in the field according to a long-term protocol of the study. In the Valsaín-Lozoya population (Spain), the wing patch was photographed from a slightly different angle than in other populations. These differences do not affect the selection analyses of the present study because the measurements were standardized within populations (see below). However, when analyzing variation in plumage traits among populations and comparing between selection coefficients and mean observed phenotype of a population, analyses were conducted with

and without the Tomsk and Valsaín-Lozoya populations with respect to forehead patch size and wing patch size, respectively. Tail feathers were photographed with the outermost feathers on one side of the tail fanned from each other; thus, the total area of white was visible. Tail patch area was calculated as a sum of these white areas.

REPRODUCTIVE VARIABLES

All populations used nest boxes for breeding in and were checked at least weekly to determine laying date, clutch size, and the number of nestlings and fledglings. Fecundity was defined as the number of fledged young per male in one year. The number of fledged young is affected by several factors including, for example, timing of breeding, clutch size, and nestling mortality, although the effect of different components on fecundity was not separated in the present study.

All nests involved in experiments that could have affected breeding date or the number of fledglings were excluded from the analysis (443 nests in six populations). Males may also gain higher fecundity by being polygynous or by fertilizing extra-pair females, although selection acting via polygyny (Huk & Winkel, 2006) and via extra-pair copulations appears to be weak in the pied flycatcher (see below). In general, polygyny occurs in the pied flycatcher at a low rate. However, in many of the populations, no polygamous males were reported, mainly because it is usually difficult to identify polygamous males without detailed observations during the pairing and nestling phases. In a fraction of populations, some of the males were known to be polygamous and the second nests of the polygamous males were omitted from the analyses (74 nests in ten populations). Because information on polygamous males was available only in a small fraction of populations, it was not possible to take polygamy into account when considering patterns of selection among populations. Furthermore, it was not possible to obtain information on possible extra-pair paternity as a result of the amount of work required for sampling and genotyping the number of broods included in the study. However, the frequency of extra-pair paternity (percentage of offspring) in the pied flycatcher is low in most of the populations (Finland 4.4% (Lehtonen *et al*., 2009b); Germany 5.1% (Lubjuhn *et al*., 2000); Norway 4–7% (Lifjeld, Slagsvold & Lampe, 1991; Ellegren *et al*., 1995); Spain 7.5–20% of offspring (Moreno *et al*., 2010, 2013; Canal, Jovani & Potti, 2012). Thus, we consider that a lack of extra-pair information should not greatly influence the results.

SELECTION ANALYSIS

It is important to be able to describe selection in standardized terms and to quantitatively compare selection in different populations (and across studies). In the analysis of selection, we used the approach developed by Lande & Arnold (1983) and Arnold & Wade (1984), in which linear regression models are used to calculate estimates of selection pressure. The dependent variable is a measure of fitness (number of fledged young), which is standardized by dividing by its mean value. Explanatory variables are standardized to a mean of zero and variance of one. The resulting standardized selection coefficients represent proportional change in fitness for a proportional change in the trait in question, which makes it possible to compare selection across different populations and more generally with other studies and species. When there were data for more than a single year, the standardization of both male traits and the fitness variable were conducted separately for each year. Accordingly, we avoid bias caused by possible between-year variation in male traits or fitness variable. However, because the present study aimed to compare variation in selection pressure among populations, the overall selection estimates were calculated from data pooled over years so that a single selection estimate was derived for each population and male coloration trait.

Selection acts rarely on single traits in isolation and correlational selection seems to be common (Phillips & Arnold, 1989; Blows & Brooks, 2003). Selection differentials represent overall selection, which consists of both direct and indirect selection acting via correlated traits. Male coloration traits are correlated in the pied flycatcher (see Supporting infromation, Table S1; Ivankina *et al*., 2007; Sirkiä & Laaksonen, 2009; but see also Moreno *et al*., 2011). To be able to control for indirect selection on a trait as a result of selection on other correlated traits, partial selection coefficients (selection gradients) were calculated. This was achieved using partial selection differentials estimated by multiple linear regression, where the standardized fitness component was the dependent variable and standardized phenotypic traits were the explanatory variables (Lande & Arnold, 1983; Arnold & Wade, 1984). Partial selection coefficients were not calculated for sites where more than one of the male traits was missing (three sites). Calculation of nonlinear selection gradients was considered but, because the magnitude of quadratic selection is often relatively small and large sample sizes are needed to detect it (Kingsolver *et al*., 2001), we considered our data inadequate for revealing any spatial patterns of quadratic selection.

STATISTICAL ANALYSIS

The analyses were performed with SAS, version 9.2 (SAS Institute). The associations between selection

estimates and distance to the sympatric area, latitude, longitude, and trait means were analyzed with linear regressions. Selection coefficients can be heavily influenced by sample size (Kingsolver *et al.*, 2001; Hersch & Phillips, 2004). Very small sample sizes can produce overestimates of selection estimates and therefore only standardized selection differentials and gradients that are based on more than 15 individual observations are reported (Tables 2, 3) and used in analyses. In addition, we used weighted regressions so that sample sizes of each selection coefficient were taken into account when comparing selection estimates with distance to the sympatric area, latitude, longitude, and trait means. Using weighted regression models (results presented) did not change the results compared to the linear regressions without weighted term. We used Morans *I* to check whether there is spatial autocorrelation in our selection estimates. Moran's *I* coefficients were all $P > 0.10$ and thus there is no evidence of spatial autocorrelation.

Male age may confound selection estimates when there are differences in the phenotypes between young and old males. Old males tend to be darker than young ones because a modest (approximatively one Drost score) change occurs between the ages 1 and 2 years (Lundberg & Alatalo, 1992; Gálvan & Moreno, 2009). In addition, the size of the tail patch depends on age at least in a Russian population (Belskii, 2006). Males were aged in some populations as young (1 years) or old (> 1 years) on the basis of several aspects of feather wear (Karlsson, Persson & Walinder, 1986; Lundberg & Alatalo, 1992; Svensson, 1992). However, age determination is not easy in all populations and information on age was therefore missing in several populations; in addition, for some populations, it was mainly based on recapturing ringed birds (a subset of birds). As a result of this large amount of missing data, the effect of age on selection estimates was analyzed separately with the subset of data in which it was possible (see Supporting information, Table S2). The selection coefficients were re-calculated with these data by including age (1 year or older) as an explanatory factor in the regression analyses. To be able to assess the effect of age on the selection estimates, the selection differentials and selection gradients were compared before and after correction for age. Age was found to affect the selection gradients on dorsal coloration and on UV reflectance of wing patch (see Supporting information, Table S2). Taking age into account weakened these selection estimates (see Supporting information, Table S2). Despite the differences, selection coefficients before and after age-correction were strongly positively correlated in all cases (see Supporting information, Table S2). The age-corrected estimates were not available for all populations and, in most of the populations where they were available, correction for age decreased the sample size substantially. However, the subsequent analyses considering selection estimates that changed significantly when taking age into account (see above) were repeated using age-corrected selection coefficients.

Although male traits were standardized among populations, differences in the measurements of UV reflectance, forehead patch size and wing patch size in populations of Oslo, Tomsk, and Valsaín-Lozoya, respectively, were taken into account when analyzing the amount of variation in coloration traits among populations and when comparing selection estimates with the mean of observed traits across populations. Analyses were conducted both with and without these populations but, because the results of both models were similar, we present the results of the models with these populations included.

Our main interests were the possible patterns in selection, rather than any single selection estimate, and thus we have not applied any multiple test correction to the estimates of selection. To gain more understanding on spatial variation in selection, it is important to pay attention to patterns in selection between locations rather than testing whether selection pressure estimates differ from zero in certain locations.

RESULTS

VARIATION IN SELECTION ESTIMATES AMONG POPULATIONS

There was some variation in the directions and magnitudes of both the standardized selection differentials (Table 2) and gradients (Table 3) on all male plumage traits among populations. Standardized selection differentials varied between positive and negative in relatively even frequencies (dorsal coloration: 7/10; UV: 6/11; forehead patch: 11/4; wing patch: 9/5; tail patch: 6/8), as did standardized selection gradients (dorsal coloration: 9/5; UV: 9/5; forehead patch: 6/8; wing patch: 9/5; tail patch: 8/6). Overall, the selection on plumage traits was relatively weak and most of selection estimates did not differ from zero (Tables 2, 3).

The correlations between standardized selection differentials and gradients on a certain male trait were positive with respect to fecundity selection (Table 4). This indicates that, typically, total selection and direct selection on plumage traits were parallel. There are, however, differences between selection differentials and gradients within male traits in single populations (Tables 2, 3), indicating that there is indirect selection acting on the measured traits.

Table 2. Standardized fecundity selection differentials on male coloration

Population	S_{DC}	SE_{DC}	N_{DC}	S_{UV}	SE_{UV}	N_{UV}	S_{FP}	SE_{FP}	N_{FP}	S_{WP}	SE_{WP}	N_{WP}	S_{TP}	SE_{TP}	N_{TP}
Valsaín-Lozoya	−0.029	0.033	57	−0.043	0.031	61	0.00010	0.032	61	0.012	0.034	56	−0.039	0.035	48
La Hiruela	0.016	0.040	66	0.013	0.039	68	−0.051	0.043	67	0.057	0.044	60	0.046	0.039	66
Vaud	0.069	0.066	81	0.057	0.075	56	0.062	0.15	25	0.15	0.10	37	0.049	0.11	35
Harthausen	0.023	0.060	39	0.080	0.057	38	0.057	0.061	36	0.088	0.064	36	0.0092	0.059	32
Moravia-Jeseníky	−0.12	0.072	27	−0.026	0.076	29	**0.19***	0.078	25	**−0.17** *	0.080	23	0.092	0.086	25
East Dartmoor	−0.018	0.039	84	−0.030	0.038	81	−0.025	0.037	78	0.0012	0.042	69	−0.0022	0.055	47
Drenthe	0.026	0.029	130	**−0.090****	0.034	82	−0.045	0.047	30	−0.042	0.043	37	0.053	0.032	37
Courish spit	**−0.049** *	0.023	22	0.011	0.026	21									
Moscow region	−0.11	0.080	28	0.040	0.098	28									
Kraslava	−0.021	0.017	60	0.020	0.019	48	0.0083	0.017	60	0.024	0.017	59	−0.016	0.023	30
Middle Urals	−0.034	0.038	124	−0.056	0.048	94	0.042	0.047	93	**0.13** *	0.049	91	−0.019	0.047	93
Tomsk	−0.016	0.014	371	−0.020	0.026	132	0.0099	0.014	351						
Kilingi-Nõmme	0.050	0.092	40	−0.039	0.091	41	0.0040	0.091	41	−0.13	0.093	39	−0.0077	0.085	33
Oslo	0.026	0.032	53	**−0.057** *	0.023	49	0.023	0.031	32	0.0062	0.035	30	−0.013	0.038	27
Ruissalo	−0.035	0.033	110	−0.018	0.037	103	0.023	0.034	102	0.031	0.033	101	−0.019	0.036	99
Karelia	−0.024	0.042	189	−0.016	0.045	169	−0.061	0.043	178	−0.012	0.063	89	−0.039	0.055	96
Skibotn	0.083	0.056	90	−0.054	0.054	90	0.050	0.057	86	−0.053	0.059	84	0.078	0.065	86
Mean	−0.0096	0.045	92	−0.014	0.048	70	0.019	0.052	84	0.0060	0.054	58	0.012	0.057	54

Male traits referred: DC, dorsal coloration; UV, ultraviolet reflectance of white wing patch; FP, forehead patch size; WP, wing patch size; TP, tail patch size. $+P < 0.10$; $*P < 0.05$; $**P < 0.01$, all $P < 0.10$ marked in bold. N, number of observations used in the analysis. High fecundity is associated with higher fitness and high selection differential values indicate that there is selection for more pronounced trait (larger trait values).

Table 3. Standardized fecundity selection gradients on male coloration

Population	β_{DC}	$\beta_{SE\ DC}$	β_{UV}	$\beta_{SE\ UV}$	β_{FP}	$\beta_{SE\ FP}$	β_{WP}	$\beta_{SE\ WP}$	β_{TP}	$\beta_{SE\ TP}$	N
Valsaín-Lozoya	−0.044	0.038	−0.054	0.035	−0.011	0.037	0.014	0.039	−0.024	0.036	41
La Hiruela	−0.024	0.074	−0.049	0.069	−0.10	0.061	0.074	0.064	0.036	0.056	35
Vaud	0.11	0.24	0.41	0.33	−0.11	0.27	0.17	0.21	0.21	0.22	18
Harthausen	0.11	0.093	0.049	0.064	0.063	0.099	0.08	0.078	0.0084	0.066	29
Moravia-Jeseníky	−0.088	0.081	−0.0044	0.091	0.099	0.081	**−0.19** +	0.088	**0.19** *	0.077	21
East Dartmoor	−0.075	0.075	−0.04	0.069	−0.021	0.061	−0.029	0.069	−0.011	0.066	41
Drenthe	0.064	0.085	0.0025	0.069	0.034	0.084	−0.023	0.076	0.039	0.044	26
Courish spit											
Moscow region											
Kraslava	−0.0078	0.033	0.032	0.031	−0.017	0.032	−0.0086	0.027	−0.0098	0.030	20
Middle Urals	−0.049	0.06	**−0.13** *	0.052	0.027	0.051	**0.15** **	0.052	−0.011	0.051	91
Tomsk											
Kilingi-Nõmme	0.057	0.10	−0.12	0.11	−0.019	0.12	0.11	0.13	−0.051	0.091	30
Oslo	−0.019	0.043	−0.097	0.039	−0.0082	0.042	0.065	0.040	−0.048	0.041	23
Ruissalo	−0.057	0.042	−0.055	0.044	0.032	0.04	0.0023	0.039	0.0060	0.040	89
Karelia	−0.22	0.15	−0.081	0.13	−0.11	0.13	0.068	0.1	0.11	0.12	49
Skibotn	0.076	0.074	0.018	0.07	0.052	0.064	−0.036	0.067	0.091	0.064	81
Mean	−0.012	0.085	−0.0085	0.086	0.00083	0.084	0.032	0.077	0.038	0.072	45

β, slope of the regression model and β_{SE}, standard error of the slope. Male traits referred: DC, dorsal coloration; UV, ultraviolet reflectance of white wing patch; FP, forehead patch size; WP, wing patch size; TP, tail patch size. +$P < 0.10$; *$P < 0.05$; **$P < 0.01$, all $P < 0.10$ marked in bold. N, number of observations used in the analysis. High fecundity is associated with higher fitness and high selection gradient values indicate that there is selection for more pronounced trait (larger trait values).

Distance from the sympatric area, latitude and longitude

All the associations between selection estimates and distance from the sympatric area (all $P > 0.10$) (Fig. 3, Table 5), as well as latitude or longitude (all $P > 0.10$) (Fig. 3; see also Supporting information, Table S3), were nonsignificant. The associations between age-corrected selection gradients (see Material and methods) on male dorsal coloration and UV reflectance of the wing patch were also nonsignificant (all $P > 0.10$) (see Supporting information, Table S4).

Selection in relation to observed patterns of plumage traits

We tested whether current patterns of the observed plumage traits among populations could be accounted for by the current patterns of selection. However, the relationships between mean male plumage traits and selection estimates were nonsignificant (all $P > 0.10$) (Table 6). This was also the case for relationships between age-corrected selection differentials with respect to dorsal coloration (selection gradient: estimate = -0.0079 ± 0.027, $F_{1,7} = 0.08$, $P = 0.78$) and UV reflectance of the white wing patch (selection gradient: estimate = 3.77 ± 3.09, $F_{1,6} = 1.49$, $P = 0.26$).

DISCUSSION

Selection acting on plumage coloration has been studied extensively in the pied flycatcher, one of the

Table 4. Correlations between standardized selection differentials and selection gradients (partial selection differentials) for different male plumage traits in different populations

Variable	r_s	P	N
Dorsal coloration	0.78	0.0009	14
Ultraviolet reflectance	0.51	0.064	14
Forehead patch size	0.51	0.064	14
Wing patch size	0.64	0.013	14
Tail patch size	0.51	0.064	14

r_s, Spearman's correlation coefficient.

Table 5. The associations between distance to sympatric zone with the collared flycatcher and selection differentials (s) and selection gradients (β) on male coloration traits of in the pied flycatcher

Male trait	Selection coefficient	Estimate (SE)	d.f.	F	P	N
Dorsal coloration	s	−0.0085 (0.018)	1,15	0.05	0.83	17
	β	0.000029 (0.00050)	1,12	0.33	0.57	14
Ultraviolet reflectance	s	−0.000015 (0.000016)	1,15	0.89	0.36	17
	β	−0.0000032 (0.000034)	1,12	0.01	0.93	14
Forehead patch size	s	−0.0000021 (0.000018)	1,13	0.01	0.91	15
	β	−0.0000038 (0.000046)	1,12	0.70	0.42	14
Wing patch size	s	−0.00028 (0.000045)	1,12	0.39	0.54	14
	β	0.0000068 (0.000013)	1,12	0.29	0.60	14
Tail patch size	s	0.000025 (0.000025)	1,12	1.03	0.33	14
	β	0.0000078 (0.000039)	1,12	0.04	0.85	14

Table 6. The relationships between male mean plumage traits and selection differentials (s) and selection gradients (β) on male coloration traits

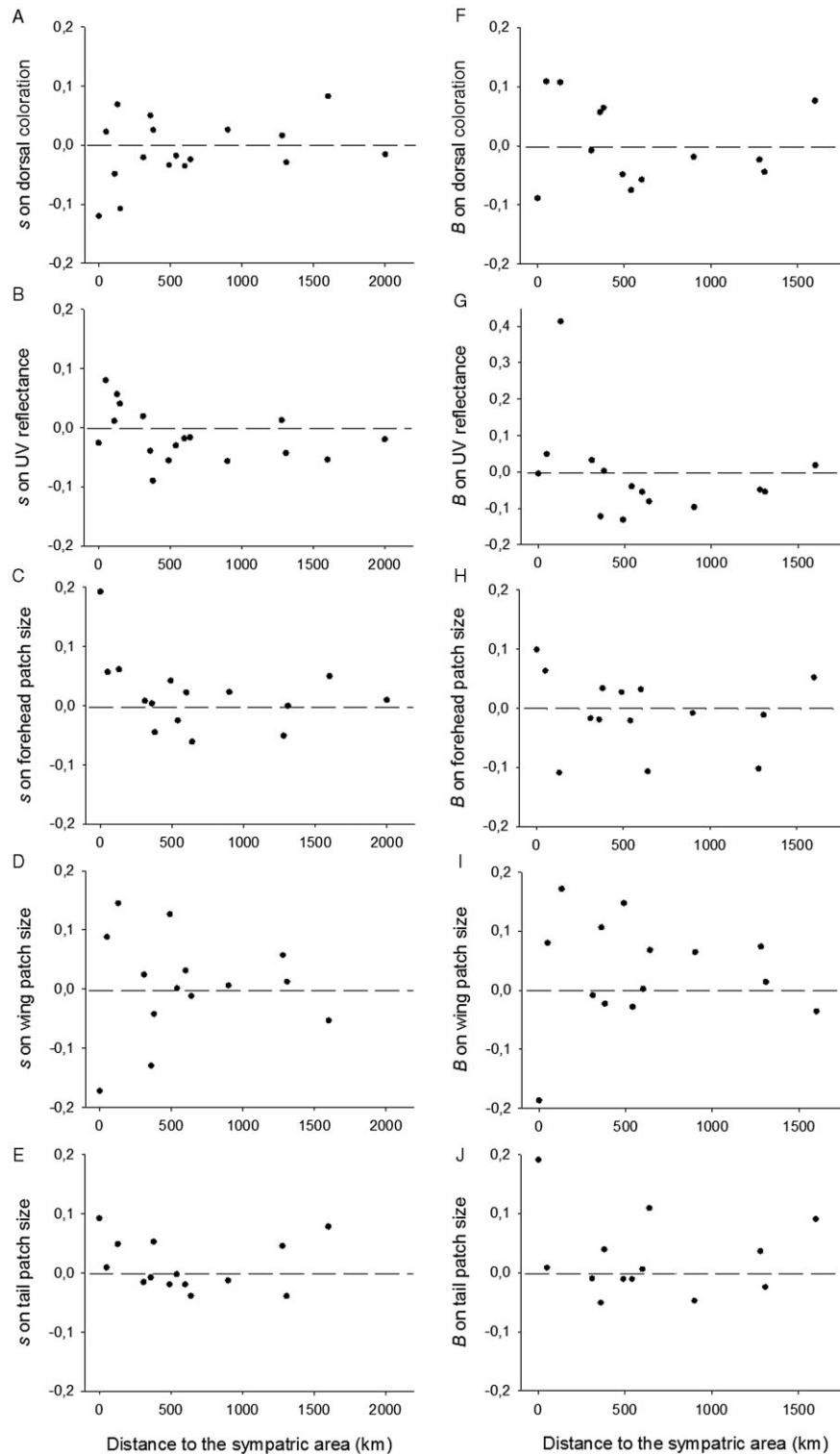| Male trait	Selection coefficient	Estimate (SE)	d.f.	F	P	N
Dorsal coloration	s	−0.0047 (0.010)	1,15	0.23	0.64	17
	β	0.0083 (0.23)	1,12	0.13	0.72	14
Ultraviolet reflectance	s	0.13 (1.44)	1,15	0.01	0.93	17
	β	1.34 (4.37)	1,12	0.09	0.76	14
Forehead patch size	s	−0.0015 (0.0015)	1,12	1.11	0.31	14
	β	−0.0022 (0.0015)	1,12	2.15	0.17	14
Wing patch size	s	−0.000013 (0.00054)	1,12	0.00	0.98	14
	β	−0.00021 (0.00058)	1,12	0.13	0.73	14
Tail patch size	s	0.00010 (0.00038)	1,12	0.07	0.79	14
	β	0.00010 (0.00061)	1,12	0.03	0.86	14

Figure 3. Standardized fecundity selection differentials and gradients on male coloration traits in relation to distance from the sympatric area with the collared flycatcher (km). Selection differentials (*s*) on (A) dorsal coloration, (B) ultraviolet (UV) reflectance, (C) forehead patch size, (D) wing patch size, and (E) tail patch size. Selection gradients (*B*) on (F) dorsal coloration, (G) UV reflectance, (H) forehead patch size, (I) wing patch size, and (J) tail patch size. High fecundity is associated with higher fitness and high selection estimate values indicate that there is selection for more pronounced trait (larger trait values).

model species of evolutionary ecology, although the present study is the first to investigate broad scale spatial patterns of selection on male phenotype in this species. Interestingly, current fecundity selection on male plumage coloration did not vary along clines of phenotypic variation because it was not associated with mean phenotypes, geographical location or the distance from the sympatric area with the sister species collared flycatcher. The results thus suggest that the populations along the plumage colour gradient may be either locally adapted or that the observed spatial pattern of selection is a snapshot of temporal dynamics of selection driven by fluctuating environmental conditions (Sirkiä et al., 2010, 2013). Below, we also discuss the potential role of indirect selection and other selection pathways in the maintenance of plumage colour gradients among populations. However, the factors maintaining the variation remain partly unknown across large geographical scales.

Quantifying patterns between selection and mean phenotypes across populations is informative when trying to understand the strength of selection in an ecological context (Siepielski et al., 2013). Surprisingly, the among-population variation in selection estimates on male pied flycatcher plumage traits was not associated with population mean phenotypes with respect to dorsal black–brown coloration, UV reflectance, forehead patch size, wing patch size or tail patch size. Our results thus suggest that the increase in the level of sexual dichromatism in dorsal coloration with distance from the sympatric area with the collared flycatcher and the parallel gradual changes in other male plumage traits (Sirkiä, 2011; T. Laaksonen, P.M. Sirkiä, S. Calhim, P. Adamík, A.V. Artemyev, E. Belskii, C. Both, S. Bureš, M. Burgess, B. Doligez, J.T. Forsman,V. Grinkov, U. Hoffmann, E. Ivankina, M. Král, I. Krams, H.M. Lampe, J. Moreno, M. Mägi, A. Nord, J. Potti, P-A. Ravussin, L. Sokolov, unpubl. data) are not driven by stable concurrent directional fecundity selection pressure within the gradient. There were no associations between selection and geographical location for the populations.

It is often assumed that clines in phenotypes are products of a smooth change in directional selection acting on the trait (Slatkin, 1973; Lande, 1982). However, regimes of selection have been shown to vary in a relatively fine-grained way, even if the phenotype shows a cline (Svensson & Sinervo, 2004; Gosden & Svensson, 2008). In the pied flycatcher, it has been shown that, in areas of sympatry, character displacement has been driving divergence of male pied flycatcher coloration (Qvarnström et al., 2010) but, in the rest of the breeding range, selection on colour phenotype appears to be relatively weak and tends to vary across populations. Earlier results on

selection on male plumage coloration have been variable both in direction and magnitude (see Introduction). Differences in selection on male plumage traits between populations located in close proximity have also been reported earlier for the pied flycatcher (Gálvan & Moreno, 2009).

Although directional selection for ornamentation is often reported, selection on male plumage coloration may also be stabilizing. If ornamentation is produced at a cost to another important trait, it may be that females should prefer males with medium ornaments to be able to maximize the benefits. The results of the present study show that indirect and total (including indirect) concurrent selection acting on plumage traits of male pied flycatchers is mostly parallel, indicating only a small indirect component of selection. However, even small differences between selection differentials and gradients indicate indirect selection acting on plumage traits and, to some extent, co-evolution of these traits. In the pied flycatcher, environment-dependent selection on male dorsal coloration has been found to be parallel between life-history phases in a Finnish population: the reproductive output of black males is the highest when it is cold during the egg-laying but warm during the nestling period (Sirkiä et al., 2010). To fully understand the role of indirect selection, further investigations and experimental approaches are required. Especially, correlations between melanin coloration and other phenotypic traits, such as behaviour and physiology (Ducrest, Keller & Roulin, 2008; Roulin & Ducrest, 2013), may drive important pathways for indirect selection. Overall, it should be emphasized that maintenance of variation among populations may consist of different combinations of directional and stabilizing selection together with context-dependence and indirect selection. Despite the large data set, we have not been able to fully examine all the possible scenarios and further studies are still needed. It would be especially interesting to be able to focus more on the areas close to the sympatric areas with the collared flycatchers.

The detected current selection on multiple coloration traits in male pied flycatchers is relatively weak compared to the mean reported selection coefficients acting on phenotypic traits (Kingsolver et al., 2001, 2012). Several studies have reported stronger selection estimates on sexual selection acting on coloration traits in, for example, insects (Grether, 1996) and birds (Price & Burley, 1994; Sheldon & Ellegren, 1999; Chaine & Lyon, 2008; but see also Hegyi et al., 2006; Robinson et al., 2012). Power to detect selection coefficients that differ from zero can be influenced by sample size (Kingsolver et al., 2001). We also observed such coefficients with modest sample sizes, whereas there were several cases with relatively large sample

sizes where we did not detect selection that would have differed statistically from zero. This suggests that the sample sizes did not strongly affect the fact that no patterns in the selection coefficients were observed. However, despite applying weighed regressions that take sample size into account, our results may partly suffer from the limited sample size per population. Nevertheless, if selection is consistent over time, a shift in mean phenotype may occur despite weak selection. A meta-analysis on spatial variation of selection suggested that, when selection is weak, there tends to be most variation in the direction of selection (Siepielski *et al.*, 2013), which appears to apply to selection on male pied flycatcher coloration. Relatively weak selection might indicate that the populations are close to selective optima. On the other hand, potential pleiotropic effects may limit the strength of selection if there are antagonistic effects.

In general, any description of spatial patterns of selection is only a snapshot of temporal dynamics of selection (Siepielski, DiBattista & Carlson, 2009; Morrissey & Hadfield, 2012). For example, temporally fluctuating, environment-dependent selection may average to zero across all conditions in time and end up stabilizing selection across years. Thus, temporally variable selection may appear as spatial variation in selection if the time period of observation is not sufficiently long (Siepielski *et al.*, 2013). It may be that different male types in the pied flycatcher may gain the same long-term fitness via different routes. Temporally fluctuating environment-dependent selection has been shown to occur on male pied flycatcher dorsal coloration in a northern allopatric population (Sirkiä *et al.*, 2010, 2013) in a similar way to selection on phenotypic traits in several other species (Chaine & Lyon, 2008; Morris, Rios-Cardenas & Brewer, 2010; Punzalan, Rodd & Rowe, 2010). Environment-dependent, temporally variable selection could also maintain relatively wide among population variation in phenotype and coloration gradient among populations. For example, in the barn owl, potentially environment-dependent variable selection in space and time may account for the maintenance of variation in eumelanic plumage spot size (Roulin, Antoniazza & Burri, 2011). We suggest that understanding the environmental factors affecting selection may be key to understanding fine-scaled spatial structure of selection in our study system. In future studies, it will be essential to bring together the spatio-temporal aspects of selection and environmental factors potentially driving selection.

Ultimately, it is the integration of all fitness components that matters. Although fecundity selection is often stronger than survival selection (Siepielski *et al.*, 2011; Kingsolver *et al.*, 2012), survival has been found to play an important role on selection on a melanin-based coloration in the barn owl (Roulin *et al.*, 2010), in the barn swallow (Saino *et al.*, 2013), and in urban feral pigeons (Récapet *et al.*, 2013). In the light of the existing literature, it us unlikely that there would be strong consistent association between male coloration and survival in the pied flycatcher because several studies have not reported any such associations (Slagsvold & Lifjeld, 1988; Lundberg & Alatalo, 1992; Alatalo *et al.*, 1994; Ivankina, Grinkov & Kerimov, 2001) and those that have found an association have been mixed in their direction (Järvi *et al.*, 1987; Potti & Montalvo, 1991b; Slagsvold, Dale & Kruszewicz, 1995; Belskii & Lyakhov, 2004). In addition, other selection pathways, such as male–male competition, survival, male polygamy, extrapair paternity, and sexually antagonistic selection, could provide new and more accurate views on spatial patterns of selection and on net selection acting on phenotypes. It must also be taken into consideration that our data are to some extent biased towards successful males because we do not have information of those males that do not manage to pair at all and some breeding attempts fail before the male was captured. The knowledge of the proportion of nonbreeding males is very scarce (but see Sternberg, 1989) and may also differ between populations. In addition, if the expression of the traits is changing during the breeding season (Griffith & Sheldon, 2001; Delhey *et al.*, 2010; Adamík & Vaňáková, 2011), the change may to some extent affect the selection estimates. Possible eroding of the plumage ornaments is, however, simultaneous with the progression of the breeding season. Despite these limitations of our selection estimates, we consider that we have been able to increase the understanding on the spatial variation in selection in general.

CONCLUSIONS

Selection regimes have often been shown to vary spatially (Blanckenhorn *et al.*, 1999; Jann, Blanckenhorn & Ward, 2000; Møller *et al.*, 2006; Gosden & Svensson, 2008), although few studies have been able to study patterns of selection across large geographical areas. With the results of the present study, we are able to add to our understanding of spatial variation in selection acting on several phenotypic traits simultaneously. We show that none of the expected patterns were found with respect to current fecundity selection on male pied flycatcher plumage. Current selection was not associated with the distance to areas of sympatry with a sister species where character displacement is taking place, and were not associated with the observed mean plumage traits of the populations. There do not appear to be

geographical gradients in current directional fecundity selection on male plumage ornamentation. Our results thus do not support the idea that constant directional fecundity selection would play a major role in the maintenance of coloration among populations. On the other hand, the tendency for weak, mosaic-like variation in selection among populations could be just a snapshot of temporally variable, potentially environment-dependent, selection, as suggested by other studies in the pied flycatcher (Sirkiä *et al.*, 2010, 2013) and in other systems (Chaine & Lyon, 2008; Morris *et al.*, 2010; Punzalan *et al.*, 2010; Roulin *et al.*, 2011). The factors driving selection remain partly unknown, although we suggest that indirect effects and temporally variable, possibly environment-dependent selection coupled with gene flow may play an important role in the wide diversity of male phenotypes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Correlation matrix for traits of male pied flycatchers used in analyses of selection differentials and gradients. Spearman's correlation coefficient and sample size are given (***$P < 0.0001$). Dorsal coloration is expressed with Drost scores, in which low values represent black males and high values brown males.

Table S2. Mean selection differentials (s) and selection gradients (β) on male coloration before and after correction for the effects of the male age. The differences between the two estimates are compared with a paired t-test where sample size (N) is the number of populations in the analysis. In addition, the correlation between mean values across populations before and after correction for age is analyzed using Spearman's correlation (r_s).

Table S3. The associations between latitude and longitude and selection differentials (s) and selection gradients (β) on male coloration traits in the pied flycatcher.

Table S4. The associations between age-corrected selection differentials (s) and selection gradients (β) on male dorsal coloration and ultraviolet reflectance of the wing patch.