

1 Running title: Spatial variation in selection on multiple traits

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6

7 Fecundity selection on multiple male colouration traits does not vary

8 along large geographical cline of trait means in a passerine bird

9

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37

38 ***Abstract***

39 Local environmental and ecological conditions are commonly expected to result in local adaptation,  
40 but there are few examples of variation in phenotypic selection across continent-wide spatial scales.  
41 We collected standardised data on selection on the highly variable plumage colouration of pied  
42 flycatcher (*Ficedula hypoleuca* Pall.) males from 17 populations across the species' breeding range.  
43 The observed selection on multiple male colouration traits via annual number of fledged young was  
44 generally relatively weak. Our main aim, however, was to examine whether the current directional  
45 selection estimates are associated with distance to the sympatric area with the collared flycatcher  
46 (*Ficedula albicollis* Temminck), a sister species with which the pied flycatcher is showing character  
47 displacement. This pattern was expected as plumage traits in male pied flycatchers are changing  
48 with the distance to these areas of sympatry. However, we did not find such a pattern in current  
49 selection on colouration. There were no associations between current directional selection on  
50 ornamentation and latitude or longitude either. Interestingly, current selection on colouration traits  
51 was not associated with the observed mean plumage traits of the populations. Thus there do not  
52 seem to be geographic gradients in current directional fecundity selection on male plumage  
53 ornamentation. Our results do not support the idea that constant patterns in directional fecundity  
54 selection would play a major role in the maintenance of colouration among populations in this  
55 species. On the other hand, the tendency for relatively weak mosaic-like variation in selection  
56 among populations could reflect just a snapshot of temporally variable, potentially environment-  
57 dependent, selection suggested by other studies in this system. Such fine-grained variable selection  
58 coupled with gene flow could maintain extensive phenotypic variation across populations.

59  
60 Keywords: cline, geographic variation, multiple signals, phenotypic variation, sexual selection  
61

## 1 ***Introduction***

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

13  
14 Studies investigating spatial variation in phenotypic selection across large geographic scales are still  
15 scarce, and the understanding of patterns of selection and of the selective agents behind phenotypic  
16 patterns remains poor. Such studies have been conducted in relation to behavioural traits (Soler et  
17 al., 1999, Soler et al., 2001), morphology (Blanckenhorn et al., 1999, Svensson & Sinervo, 2004,  
18 Gosden & Svensson, 2008, Møller et al., 2006) and other phenotypic traits, including animal  
19 colouration (Calsbeek et al., 2010, Weese et al., 2010, Svensson & Waller, 2013). However, rather  
20 few studies assess geographic variation in contemporary selection on sexually selected colour  
21 ornaments. This is surprising, not least given the importance of sexual selection in animal  
22 colouration in many different taxonomic groups (Andersson, 1994, Hill, 2006).

23  
24 We investigated current selection pressure on the plumage ornaments of male pied flycatchers  
25 across a continent-wide spatial scale. The pied flycatcher is a small hole-nesting passerine bird that

26 has sexually dimorphic plumage colouration, with males displaying multiple apparent ornaments,  
27 such as a white forehead patch and conspicuous white wing and tail patches (Lundberg & Alatalo,  
28 1992). Despite the fact that sexual selection in this species has been extensively studied across  
29 much of their breeding range for decades (von Haartman, 1985, e.g. Alatalo et al., 1984, Slagsvold  
30 & Lifjeld, 1988), the patterns of selection on male ornaments still remain largely unknown.

31  
32 The most conspicuous colouration trait in male pied flycatchers is the melanin based dorsal  
33 colouration that varies from completely brown to black (Lundberg & Alatalo, 1992, Drost, 1936).  
34 Melanin colouration is often linked with reproduction (reviewed in Meunier et al., 2011), stress  
35 sensitivity (Almasi et al., 2012), parasite resistance (Lei et al., 2013) and costs of parasite infections  
36 (Karell et al., 2011a). Several studies have found context-dependent selection on melanin based  
37 colouration (e.g. Dreiss et al., 2010, Dreiss et al., 2012, Roulin et al., 2008, Karell et al., 2011b).  
38 This is the case also in an allopatric population of the pied flycatcher where breeding success of  
39 different melanin phenotypes has been found to be dependent on current weather conditions (Sirkiä  
40 et al., 2010, Sirkiä et al., 2013). Melanin-based colouration typically shows high heritability in birds  
41 (Roulin & Ducrest, 2013); also in the pied flycatcher the black-brown melanin-based colouration  
42 has been shown to be highly heritable in different populations (reported  $h^2$  values varying from 0.6  
43 to 0.9) (see Alatalo et al., 1994, Lehtonen et al., 2009a, Grinkov, 2000). There is much more  
44 phenotypic variation in the dorsal black-brown coloration of pied flycatchers among populations  
45 than predicted by neutral genetic variation (Lehtonen et al. 2009a), similar to heritable melanin  
46 colouration of barn owls (*Tyto alba*) (Antoniazza et al., 2010). Such patterns are commonly  
47 interpreted as indirect signals of divergent selection on a trait (Leinonen et al., 2008).

48  
49 The distributions of the pied flycatcher and the closely related collared flycatcher overlap in Central  
50 and Eastern Europe (Fig. 2). In the areas of sympatry, male pied flycatchers are mostly brown,

51 probably due to avoidance of interspecific competition and hybridization with the black-and-white  
52 collared flycatcher (Král et al., 1988, Lundberg & Alatalo, 1992, Sætre et al., 1997, Sætre &  
53 Sæther, 2010, Qvarnström et al., 2010). There is selection for brown dorsal colouration in males in  
54 the sympatric area (Sætre et al., 1997). In allopatric areas both colour types occur, but the frequency  
55 of darker males – and thus the level of sexual dichromatism – seems to increase with distance from  
56 the Central European breeding areas (Lundberg & Alatalo, 1992, Lehtonen et al., 2009a, Røskaft et  
57 al., 1986). This has often been assumed to be associated with sexual selection for conspicuous  
58 colouration, while gene flow from sympatric and nearby areas is expected to be the main factor  
59 maintaining variation in male phenotype in allopatric areas. Some studies have found sexual  
60 selection for black male colouration in allopatric areas (Sætre et al., 1994, Røskaft & Järvi, 1983,  
61 Dale & Slagsvold, 1996, Sætre et al., 1997). However, there are also several studies conducted in  
62 single allopatric populations that have not found any clear benefits for black males in mate choice  
63 (e.g. Sirkiä & Laaksonen, 2009, Potti & Montalvo, 1991a, Alatalo et al., 1990, Alatalo et al., 1986,  
64 Lehtonen et al., 2009b) or breeding success (e.g. Røskaft & Järvi, 1983) and there have been no  
65 attempts to analyse selection acting on plumage colouration in multiple populations. In addition,  
66 selection on male dorsal colouration has been found to be context-dependent, depending on current  
67 temperatures (Sirkiä et al., 2010). In the light of current evidence, there is thus no consensus that  
68 black colouration per se is sexually or naturally selected in the allopatric area in all contexts. Spatial  
69 pattern of selection on melanin colouration thus remains unknown in allopatry.

70

71 Another aspect of avian plumage colouration is reflectance at near-ultraviolet light wavelengths  
72 (UV-A; 320–400 nm), which is visible to birds (Cuthill et al., 2000). The UV reflectance is sexually  
73 selected for in the pied flycatcher, at least in some allopatric populations (Siitari et al., 2002,  
74 Lehtonen et al., 2009b, Sirkiä & Laaksonen, 2009), but spatial variation in selection on the trait is  
75 unknown. The remaining plumage traits studied are conspicuous white ornamental patches in the

76 forehead, wing and tail that all vary greatly in size and shape. Most males have a white forehead  
77 patch, the size of which has a heritable component (Potti & Canal, 2011; but see Dale et al. 1999).  
78 Sexual selection has been found to act on forehead patch size in some allopatric populations (Potti  
79 & Montalvo, 1991a, Sirkiä et al., 2010, Canal et al., 2011, Järvisto et al., 2013). Sexual selection  
80 has also been indicated to act on wing patch size (Sirkiä & Laaksonen, 2009, Sirkiä et al., 2010),  
81 but not on tail patch size (Sirkiä & Laaksonen, 2009), which has been little studied. Spatial  
82 variation in selection on wing and tail patches remains unknown. Common for all the plumage  
83 ornamentation traits is that the mean conspicuousness increases with the distance from the  
84 sympatric area (Sirkiä, 2011; Laaksonen T. et al. in prep.). Although selection on male plumage  
85 ornaments has been widely studied in the pied flycatcher, most studies have concentrated on only  
86 one or few phenotypic traits at a time and no study has compared selection acting on plumage traits  
87 across populations. When studying ornamentation it is important to examine multiple attributes  
88 simultaneously (e.g. Candolin, 2003, Laczi et al., 2011). We analysed selection on five different  
89 plumage traits, which cover the main axis of male colour variation in this species. As the studied  
90 colouration traits are correlated (Table S1; Ivankina et al., 2007, Sirkiä & Laaksonen, 2009; but see  
91 Moreno et al. 2011) we were particularly interested to compare the roles of indirect and direct  
92 selection as indirect selection on correlated traits may potentially drive the evolution of some of the  
93 studied traits.

94  
95 We estimated selection on plumage traits of male pied flycatchers via fecundity (here defined as the  
96 number of fledglings produced). Males gain fitness benefits through producing a higher number of  
97 fledglings. This may occur due to pairing with a female in good condition (Fisher, 1930), or  
98 indirectly if female investment in the clutch is dependent on the attractiveness or quality of the male  
99 (Burley, 1986, Sheldon, 2000). Selection can also be differentially acting on male phenotype during  
100 the nestling period (Sirkiä et al. 2010). The intensity of selection caused by annual fecundity can be

101 investigated by comparing the standardised number of fledged young in relation to the standardised  
102 male plumage trait.

103

104 On the basis of the previous evidence, it can be hypothesized that there should be an association  
105 between ongoing directional selection on the plumage traits of the pied flycatcher and the distance  
106 to the sympatric area with the collared flycatcher. In allopatric areas selection is often expected to  
107 be towards black plumage colouration and for large ornaments while gene flow from sympatric  
108 areas can be expected to be the main factor maintaining phenotypic variation in allopatry (Fig. 1A).  
109 In this case wide variation in male phenotype in allopatric populations would be maintained mainly  
110 by gene flow from sympatric populations. On the other hand selection for conspicuous colouration  
111 can be expected to get stronger with increasing distance from the sympatric area (Fig. 1B).  
112 Alternatively, populations can be primarily locally adapted and selection landscape can thus be  
113 more variable. In this case selection is expected to be balancing within populations and no  
114 association is expected between selection and distance to the sympatric area (Fig. 1C). One  
115 alternative for such fine-scaled and spatially variable selection is that selection on colouration is  
116 context-dependent (Sirkiä et al., 2010, Sirkiä et al., 2013) and variation in male colouration  
117 represents colour polymorphism in which different male types may eventually gain same fitness via  
118 different routes. A fourth option is that there is no selection operating on male ornamentation; in  
119 this case no association between selection and distance to the sympatric area can be expected either  
120 (Fig. 1D). However, in case of no selection on male phenotype, variation between populations  
121 should decrease with time, which is not supported by the wide geographical variation among  
122 populations and earlier studies observing selection on male colour phenotype.

123

124

125

126 The aim of this study was to examine spatial variation in fecundity selection pressure on plumage  
127 colouration of male pied flycatchers. We used data from 17 different study populations well  
128 distributed across the species breeding distribution, to calculate standardised linear fecundity  
129 selection coefficients. We were particularly interested to see if selection on conspicuous male  
130 plumage colouration strengthens with distance from the sympatric area with the collared flycatcher.  
131 In addition to see if there are other large scale geographical patterns in selection, we tested whether  
132 latitude or longitude of the sampled populations affect selection patterns on male plumage  
133 colouration. We further determined the relationship between selection acting on the phenotype and  
134 the observed mean phenotypes among populations. Overall we aim to increase understanding of  
135 mechanisms that maintain phenotypic variation at large spatial scales.

136

## 137 **Methods**

138

### 139 *Study areas*

140

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

146

147 The distance from each study area to the closest edge of the Central and Eastern European breeding  
148 range of the collared flycatcher was estimated on the basis of the map in the Birds of the Western  
149 Palearctic (Cramp & Simmons, 2006) and complemented with more local information of the  
150 authors. We neglected the populations of the collared flycatcher on the Swedish islands Gotland and

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

158

### 159 *Phenotypic measurements*

160

161 The data were collected by different persons in each study population but all contributors recorded  
162 male plumage traits, took photographs and collected feather samples in a prescribed way. Feather  
163 samples and photographs were sent to PS who measured the UV reflectance and the sizes of  
164 ornamental patches as described below. Detailed description of male phenotypic variation across  
165 the breeding distribution will be reported elsewhere (Laaksonen T. et al. in prep.).

166

#### 167 *a) Dorsal colouration*

168

169 The dorsal colouration of the head and back of males was estimated by Drost scores (Drost, 1936)  
170 in the field by the observer. Drost scores I and II represent males with a black head and back, but in  
171 group I the rump of a male is black whereas in group II it is more or less light. In group VII males  
172 have a completely brown dorsal colouration, thus representing 0 % of black (Lundberg & Alatalo,  
173 1992, Glutz von Blotzheim & Bauer, 1993, for a detailed description, see Drost, 1936). Although  
174 dorsal colouration was estimated in the field, it was also photographed in most of the sampling sites  
175 (not in the Tomsk, Moscow region or Courish spit populations (Russia)). If Drost scores were not

176 estimated in the field, PS estimated it based on the photographs (La Hiruela (Spain) and some  
177 occasional cases in other populations). A sample of 20 photographs per sampling site was checked  
178 by PS in order to verify the consistency of colouration estimation between different observers in  
179 different populations. If the sample of 20 checked males included any disagreement between the  
180 colouration score of the observer and PS, the rest of the photographed individuals were re-examined  
181 too. In general the colouration estimation between observers was very consistent as corrections  
182 were made to only 3 % of all colour estimations. Differences in estimations between populations do  
183 not affect the calculation of selection estimates as male traits were standardised within populations  
184 (see below).

185

186 *b) UV measurements of white wing patch*

187

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

201

202 The repeatability of measurements from the same feather samples and it was measured as an intra-  
203 class correlation (Lessells & Boag, 1987) was  $r = 0.89$  ( $N = 30$ ,  $F_{9,20} = 25.83$ ,  $p < 0.0001$ ). Samples  
204 from one population per study year were measured mainly at the same measuring bout. If, however,  
205 the samples were measured during two measuring sessions, we checked that the calibration of the  
206 equipment did not cause differences between measuring occasions ( $p > 0.10$ ). The UV reflectance  
207 measurements were done during 2008–2010 and there were minor differences between some of the  
208 measuring sessions due to differences in calibration of the equipment. These differences do not  
209 influence selection estimates because the male traits were standardised within populations (see  
210 below). However, to be able to compare mean UV reflectance values between sampled populations,  
211 ten samples (individuals) of each set of samples measured at a time (i.e. ten samples per population  
212 and year) were re-measured in one session. The mean difference between the first measurements  
213 and the re-measurements done in one session were used to correct the differences between  
214 measuring bouts in the original values. The corrected values were used when looking at variation in  
215 phenotypic traits among populations and when comparing selection estimates to the mean  
216 reflectance values among populations. It is known that structural colouration may erode over time  
217 (Delhey et al., 2010). Feather samples were collected mainly during the nestling period; however in  
218 the Oslo population (Norway), samples were mainly collected during pairing at the beginning of the  
219 breeding season. This difference does not affect the analyses of our study because the  
220 measurements were standardised within populations for calculation of selection estimates (see  
221 below). However, when analysing the amount of variation in UV reflectance among populations  
222 and when comparing selection estimates to the mean observed UV reflectance of white wing patch,  
223 the analyses were done with and without the population of Oslo.

224

225 *c) Non-pigmented ornament patches*

226

227 Forehead, wing and tail patches were photographed in the field. A ruler was held at the same  
228 distance from the camera as the target ornamental patch. Area of white was later measured from the  
229 photographs with ImageJ -software (Abramoff et al., 2004). The forehead patch was photographed  
230 directly from the front, the wing patch directly from the side when the wing was in resting position.  
231 If the forehead patch consisted of two separate patches, the area of both patches was summed and  
232 this value used as a variable in the analyses. In the Tomsk population (Russia) the size of the  
233 forehead patch was measured with a calliper in the field according to a long-term protocol of the  
234 study. In the Valsaín-Lozoya population (Spain) the wing patch was photographed from slightly  
235 different angle than in other populations. These differences do not affect the selection analyses of  
236 our study because the measurements were standardised within populations (see below). However,  
237 when analysing variation in plumage traits among populations and comparing between selection  
238 coefficients and mean observed phenotype of a population, analyses were done with and without the  
239 Tomsk and Valsaín-Lozoya populations in respect to forehead patch size and wing patch size,  
240 respectively. Tail feathers were photographed with the outermost feathers on one side of the tail  
241 fanned from each other; thus the total area of white was visible. Tail patch area was calculated as a  
242 sum of these white areas.

243

#### 244 *Reproductive variables*

245

246 All populations used nest boxes for breeding in and were checked at least weekly to determine  
247 laying date, clutch size, and the number of nestlings and fledglings. Fecundity was defined as the  
248 number of fledged young per male in one year. Number of fledged young is affected by several  
249 factors including e.g. timing of breeding, clutch size and nestling mortality, but the effect of  
250 different components on fecundity were not separated in this study.

251

252 All nests that were involved in experiments that could have affected breeding date or the number of  
253 fledglings were excluded from the analysis (443 nests in six populations). Males may also gain  
254 higher fecundity by being polygynous or by fertilising extra-pair females, but selection acting via  
255 polygyny (Huk & Winkel, 2006) and via extra-pair copulations seems to be weak in the pied  
256 flycatcher (see below). In general, polygyny occurs in the pied flycatcher at a low rate. However, in  
257 many of the populations no polygamous males were reported, mainly because it is usually difficult  
258 to identify polygamous males without detailed observations during the pairing and nestling phases.  
259 In a fraction of populations some of the males were known to be polygamous and the second nests  
260 of the polygamous males were omitted from the analyses (74 nests in ten populations). As the  
261 information on polygamous males was available only in a small fraction of populations, it was not  
262 possible to take polygamy into account when considering patterns of selection among populations.  
263 Furthermore, it was not possible to obtain information on possible extra-pair paternity due to the  
264 amount of work required for sampling and genotyping the number of broods included in the study.  
265 However, the frequency of extra-pair paternity (% of offspring) in the pied flycatcher is low in most  
266 of the populations (Finland 4,4 % (Lehtonen et al., 2009b); Germany 5,1 % (Lubjuhn et al., 2000) ;  
267 Norway 4–7 % (Ellegren et al., 1995, Lifjeld et al., 1991); Spain 7,5–20 % of offspring (Moreno et  
268 al., 2013, Moreno et al., 2010, Canal et al., 2012). Thus we consider that a lack of extra-pair  
269 information should not greatly influence the results.

270

### 271 *Selection analyses*

272

273 It is important to be able to describe selection in standardised terms, to be able to quantitatively  
274 compare selection in different populations (and across studies). In the analysis of selection, we used  
275 the approach developed by Lande and Arnold (1983) and Arnold and Wade (1984), in which linear

276 regression models are used to calculate estimates of selection pressure. The dependent variable is a  
277 measure of fitness (number of fledged young), which is standardised by dividing by its mean value.  
278 Explanatory variables are standardised to a mean of zero and variance of one. The resulting  
279 standardised selection coefficients represent proportional change in fitness for a proportional  
280 change in the trait in question, which makes it possible to compare selection across different  
281 populations and more generally with other studies and species. When there was data for more than a  
282 single year, both the standardisation of male traits and fitness variable were done separately for each  
283 year. By doing this we avoid bias caused by possible between-year variation in male traits or fitness  
284 variable. However, as the aim of this study was to compare variation in selection pressure among  
285 populations, the overall selection estimates were calculated from data pooled over years so that a  
286 single selection estimate was derived for each population and male colouration trait.

287

288 Selection acts rarely on single traits in isolation and correlational selection seems to be common  
289 (Blows & Brooks, 2003, Phillips & Arnold, 1989). *Selection differentials* represent overall  
290 selection, which consist of both direct and indirect selection acting via correlated traits. Male  
291 colouration traits are correlated in the pied flycatcher (Table S1; Ivankina et al., 2007, Sirkiä &  
292 Laaksonen, 2009; but see Moreno et al. 2011). To be able to control for indirect selection on a trait  
293 due to selection on other correlated traits, partial selection coefficients (*selection gradients*) were  
294 calculated. This was done by using partial selection differentials estimated by multiple linear  
295 regression, where the standardised fitness component was the dependent variable and standardised  
296 phenotypic traits the explanatory variables (Lande & Arnold, 1983, Arnold & Wade, 1984). Partial  
297 selection coefficients were not calculated for sites where more than one of the male traits was  
298 missing (3 sites). Calculation of non-linear selection gradients was considered, but as the magnitude  
299 of quadratic selection is often relatively small and large sample sizes are needed to detect it

300 (Kingsolver et al., 2001), we considered our data inadequate for revealing any spatial patterns of  
301 quadratic selection.

302

### 303 *Statistical analyses*

304

305 The analyses were performed with SAS 9.2. The associations between selection estimates and  
306 distance to the sympatric area, latitude, longitude and trait means were analysed with linear  
307 regressions. It is known that selection coefficients can be heavily influenced by sample size  
308 (Kingsolver et al., 2001, Hersch & Phillips, 2004). Very small sample sizes can produce  
309 overestimates of selection estimates, and therefore only standardised selection differentials and  
310 gradients that are based on more than 15 individual observations are reported (see Tables 2 and 3)  
311 and used in analyses. In addition we used weighted regressions so that sample sizes of each  
312 selection coefficient were taken into account when comparing selection estimates with distance to  
313 the sympatric area, latitude, longitude and trait means. Using weighted regression models (results  
314 presented) did not change the results compared to the linear regressions without weighted term. We  
315 used Morans *I* to check whether there is spatial autocorrelation in our selection estimates. Moran's *I*  
316 coefficients were all  $P > 0.10$  and thus there is no evidence of spatial autocorrelation.

317

318 Male age may confound selection estimates when there are differences in the phenotypes between  
319 young and old males. Old males tend to be darker than young ones, as a modest (ca. one Drost  
320 score) change occurs between the ages 1 and 2 years (Lundberg & Alatalo, 1992, Gálvan &  
321 Moreno, 2009). In addition, the size of the tail patch depends on age at least in a Russian population  
322 (Belskii, 2006). Males were aged in some populations as young (1 yr) or old (> 1 yr) on the basis of  
323 several aspects of feather wear (Karlsson et al., 1986, Lundberg & Alatalo, 1992, Svensson, 1992).  
324 However, age determination is not easy in all populations and information on age was therefore

325 missing in several populations, and for some populations it was mainly based on recapturing ringed  
326 birds (a subset of birds). Due to this large amount of missing data, the effect of age on selection  
327 estimates was analysed separately with the subset of data in which it was possible (Table S2). The  
328 selection coefficients were re-calculated with these data by including age (1 yr or older) as an  
329 explanatory factor in the regression analyses. To be able to assess the effect of age on the selection  
330 estimates, the selection differentials and selection gradients were compared before and after the  
331 correction for age. Age was found to affect the selection gradients on dorsal colouration and on UV  
332 reflectance of wing patch (Table S2). Taking age into account weakened these selection estimates  
333 (Table S2). Despite the differences, selection coefficients before and after the age-correction were  
334 strongly positively correlated in all cases (Table S2). The age-corrected estimates were not available  
335 for all populations and in most of the populations where they were available, the correction for age  
336 decreased sample size substantially. However, the subsequent analyses considering selection  
337 estimates that changed significantly when taking age into account (see above) were repeated by  
338 using age-corrected selection coefficients.

339

340 Although male traits were standardised among populations, differences in the measurements of UV  
341 reflectance, forehead patch size and wing patch size in populations of Oslo, Tomsk and Valsaín-  
342 Lozoya (respectively) were taken into account when analysing the amount of variation in  
343 colouration traits among populations and when comparing selection estimates to the average of  
344 observed traits across populations. Analyses were conducted both with and without these  
345 populations, but as the results of both models were similar, we present the results of the models  
346 with these populations included.

347

348 Our main interests were the possible patterns in selection, rather than any single selection estimate,  
349 and we have thus not applied any multiple test correction to the estimates of selection. To gain more

350 understanding on spatial variation in selection, it is important to pay attention to patterns in  
351 selection between locations rather than testing if selection pressure estimates differ from zero in  
352 certain locations.

353

## 354 **Results**

355

### 356 *Variation in selection estimates among populations*

357

358 There was some variation in directions and magnitudes of both the standardised selection  
359 differentials (Table 2) and gradients (Table 3) on all male plumage traits among populations.  
360 Standardised selection differentials varied between positive and negative in relatively even  
361 frequencies (dorsal colouration: 7/10; UV: 6/11; forehead patch: 11/4; wing patch: 9/5; tail patch:  
362 6/8), as did standardised selection gradients (dorsal colouration: 9/5; UV: 9/5; forehead patch: 6/8;  
363 wing patch: 9/5; tail patch: 8/6). Overall the selection on plumage traits was relatively weak and  
364 most of selection estimates did not differ from zero (see Tables 2 and 3).

365

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

371

### 372 *Distance from the sympatric area, latitude and longitude*

373

374 All the associations between selection estimates and distance from the sympatric area (all  $P > 0.10$ ,  
375 Figure 3, Table 5), latitude or longitude (all  $P > 0.10$ , Figure 3, Table S3) were non-significant. The  
376 associations between age-corrected selection gradients (see methods) on male dorsal colouration  
377 and UV reflectance of the wing patch were also non-significant (all  $P > 0.10$ , Table S4).

378

### 379 *Selection in relation to observed patterns of plumage traits*

380

381 We tested whether current patterns of the observed plumage traits among populations could be  
382 accounted for by the current patterns of selection. However, the relationships between mean male  
383 plumage traits and selection estimates were non-significant (all  $P > 0.10$ , Table 6). This was also the  
384 case for relationships between age-corrected selection differentials with respect to dorsal  
385 colouration (selection gradient: estimate =  $-0.0079 \pm 0.027$ ,  $F_{1,7} = 0.08$ ,  $P = 0.78$ ) and UV  
386 reflectance of the white wing patch (selection gradient: estimate =  $3.77 \pm 3.09$ ,  $F_{1,6} = 1.49$ ,  $P =$   
387  $0.26$ ).

388

## 389 **Discussion**

390

391 Selection acting on plumage colouration has been studied extensively in the pied flycatcher, one of  
392 the model species of evolutionary ecology, but this is the first study on broad scale spatial patterns  
393 of selection on male phenotype in this species. Interestingly, current fecundity selection on male  
394 plumage colouration did not vary along clines of phenotypic variation, as it was not associated with  
395 mean phenotypes, geographical location, or the distance from the sympatric area with the sister  
396 species collared flycatcher. The results thus suggest that the populations along the plumage colour  
397 gradient may be either locally adapted or that the observed spatial pattern of selection is a snapshot  
398 of temporal dynamics of selection driven by fluctuating environmental conditions (Sirkiä et al.,

399 2010, Sirkiä et al., 2013). In the following we also discuss the potential role of indirect selection  
400 and other selection pathways in the maintenance of plumage colour gradients among populations.  
401 However, the factors maintaining the variation remain partly unknown in large geographic scales.

402

403 Quantifying patterns between selection and mean phenotypes across populations is informative  
404 when trying to understand the strength of selection in ecological context (Siepielski et al., 2013).  
405 Surprisingly the among-population variation in selection estimates on male pied flycatcher plumage  
406 traits was not associated with population mean phenotypes with respect to dorsal black-brown  
407 colouration, UV reflectance, forehead patch size, wing patch size or tail patch size. Our results thus  
408 suggest that the increase in the level of sexual dichromatism in dorsal colouration with distance  
409 from the sympatric area with the collared flycatcher, and parallel gradual changes in other male  
410 plumage traits (T. Laaksonen et al. unpublished data; Sirkiä 2011) are not driven by stable  
411 concurrent directional fecundity selection pressure within the gradient. There were neither any  
412 associations between selection and geographical location of populations.

413

414 It is often assumed that clines in phenotypes are products of a smooth change in directional  
415 selection acting on the trait (Slatkin, 1973, Lande, 1982). However, regimes of selection have been  
416 shown to vary in a relatively fine-grained way, even if the phenotype would show a cline (Svensson  
417 & Sinervo, 2004, Gosden & Svensson, 2008). In the pied flycatcher, it has been shown that in areas  
418 of sympatry character displacement has been driving divergence of male pied flycatcher colouration  
419 (reviewed by Qvarnström et al., 2010) but in the rest of the breeding range selection on colour  
420 phenotype seems to be relatively weak and it tends to vary across populations. Earlier results on  
421 selection on male plumage colouration have been variable both in direction and magnitude (see  
422 Introduction for details). Differences in selection on male plumage traits between populations

423 located in close proximity have also been reported earlier for the pied flycatcher (e.g. Gálvan &  
424 Moreno, 2009).

425

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

445

446 The detected current selection on multiple colouration traits in male pied flycatchers is relatively  
447 weak compared to the average reported selection coefficients acting on phenotypic traits

448 (Kingsolver et al., 2001, Kingsolver et al., 2012). Several studies have reported stronger selection  
449 estimates on sexual selection acting on colouration traits, in e.g. insects (Grether, 1996) and birds  
450 (Price & Burley, 1994, Sheldon & Ellegren, 1999, Chaine & Lyon, 2008, but see Hegyi et al., 2006,  
451 Robinson et al., 2012). Power to detect selection coefficients that differ from zero can be influenced  
452 by sample size (Kingsolver et al., 2001). We observed such coefficients also with modest sample  
453 sizes, whereas there were several cases with relatively large sample sizes where we did not detect  
454 selection that would have differed statistically from zero. This suggests that the sample sizes did not  
455 strongly affect the fact that we did not observe patterns in the selection coefficients studied.  
456 However, despite that we applied weighed regressions that take sample size into account, our results  
457 may partly suffer from limited sample size per population. Nevertheless, if selection is consistent  
458 over time, a shift in mean phenotype may occur despite weak selection. A meta-analysis on spatial  
459 variation of selection suggested that when selection is weak there tends to be most variation in the  
460 direction of selection (Siepielski et al., 2013), which seems to apply to selection on male pied  
461 flycatcher colouration. Relatively weak selection might indicate that the populations are close to  
462 selective optima. On the other hand, potential pleiotropic effects may limit the strength of selection  
463 if there are antagonistic effects.

464

465 In general, it should be kept in mind that any description of spatial patterns of selection is a  
466 snapshot of temporal dynamics of selection (Siepielski et al., 2009, Morrissey & Hadfield, 2012).  
467 Temporally fluctuating, for example environment-dependent selection may average to zero across  
468 all conditions in time and end up to stabilising selection across years. Thus temporally variable  
469 selection may appear as spatial variation in selection if the time period of observing is not long  
470 enough (Siepielski et al., 2013). It may be that different male types in the pied flycatcher may gain  
471 the same long-term fitness via different routes. Temporally fluctuating environment-dependent  
472 selection has been shown to occur on male pied flycatcher dorsal colouration in a northern

473 allopatric population (Sirkiä et al., 2010, Sirkiä et al., 2013) in a similar way to selection on  
474 phenotypic traits in several other species (e.g. Chaine & Lyon, 2008, Morris et al., 2010, Punzalan  
475 et al., 2010). Environment-dependent, temporally variable selection could also maintain relatively  
476 wide among population variation in phenotype and colouration gradient among populations. For  
477 example in the barn owl, potentially environment-dependent variable selection in space and time  
478 may account for the maintenance of variation in eumelanic plumage spot size (Roulin et al., 2011).  
479 We suggest that understanding on the environmental factors affecting selection may be the key to  
480 understand fine-scaled spatial structure of selection in our study system. In future studies it will  
481 therefore be essential to bring together the spatio-temporal aspects of selection and environmental  
482 factors potentially driving selection.

483

484 One must bear in mind that ultimately it is the integration of all fitness components that matters.  
485 Although fecundity selection is often stronger than survival selection (Siepielski et al., 2011,  
486 Kingsolver et al., 2012), survival has been found to play an important role on selection on a  
487 melanin-based colouration in the barn owl (Roulin et al., 2010), in the barn swallow (Saino et al.,  
488 2013) and urban feral pigeons (Récapet et al., 2013). In the light of the existing literature it does not  
489 seem very likely that in the pied flycatcher there would be strong consistent association between  
490 male colouration and survival, as several studies have not found any such associations (Lundberg &  
491 Alatalo, 1992, Ivankina et al., 2001, Slagsvold & Lifjeld, 1988, Alatalo et al., 1994) and the ones  
492 that have found an association have been mixed in their direction (see Potti & Montalvo, 1991b,  
493 Belskii & Lyakhov, 2004, Järvi et al., 1987, Slagsvold et al., 1995). In addition, other selection  
494 pathways, such as male-male competition, survival, male polygamy, extrapair paternity and  
495 sexually antagonistic selection could provide new and more accurate views on spatial patterns of  
496 selection and on net selection acting on phenotypes. It must also be taken into consideration that our  
497 data is to some extent biased towards successful males, as we do not have information of those

498 males that do not manage to pair at all and some breeding attempts fail before the male was  
499 captured. The knowledge of the proportion of nonbreeding males is very scarce (but see Sternberg,  
500 1989) and may also differ between populations. In addition, if the expression of the traits is  
501 changing during the breeding season (Adamík & Vaňáková, 2011, Delhey et al., 2010, Griffith &  
502 Sheldon, 2001), the change may to some extent affect the selection estimates. Possible eroding of  
503 the plumage ornaments is however simultaneous with the progression of the breeding season.  
504 Despite these limitations of our selection estimates we believe that we have been able to increase  
505 the understanding on the spatial variation in selection in general.

506

### 507 *Conclusions*

508

509 Selection regimes have often been shown to vary spatially (e.g. Blanckenhorn et al., 1999, Jann et  
510 al., 2000, Møller et al., 2006, Gosden & Svensson, 2008), but few studies have been able to study  
511 patterns of selection across large geographic areas. With this study we are able to add to the  
512 understanding of spatial variation in selection acting on several phenotypic traits simultaneously.  
513 We show that none of the expected patterns in current fecundity selection on male pied flycatcher  
514 plumage were found. Current selection was not associated with the distance to the areas of sympatry  
515 with a sister species where character displacement is taking place, and were not associated with the  
516 observed mean plumage traits of the populations. There do not seem to be geographic gradients in  
517 current directional fecundity selection on male plumage ornamentation. Our results thus do not  
518 support the idea that constant directional fecundity selection would play a major role in the  
519 maintenance of colouration among populations. On the other hand, tendency for weak, mosaic-like  
520 variation in selection among populations could be just a snapshot of temporally variable, potentially  
521 environment-dependent, selection suggested by other studies in the pied flycatcher (Sirkiä et al.,  
522 2010, Sirkiä et al., 2013) and in other systems (e.g. Chaine & Lyon, 2008, Morris et al., 2010,

523 Punzalan et al., 2010, Roulin et al., 2011). The factors driving selection remain partly unknown but  
524 we suggest that indirect effects and temporally variable, possibly environment-dependent selection  
525 coupled with gene flow may play important role in the wide diversity of male phenotypes.

526

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528

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544

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798

799 **Figure legends**

800 **Figure 1.** Conceptual illustration of four different hypotheses about association between selection  
801 on male phenotype and distance from sympatric area. In the left column different lines represent  
802 associations between fitness and male phenotype in different populations. In the right column is the  
803 predicted relationship between selection on male trait among populations in relation to the distance  
804 from sympatric area. Male black-brown colouration is used as an example of the phenotypic traits  
805 studied. Note that ranges of ornamentation among populations may be variable among populations  
806 but are not presented here. A) There is selection on brown male colouration and small ornaments in  
807 mostly brown populations close to sympatric areas with the collared flycatcher whereas in allopatric  
808 areas selection is towards black plumage colouration and for large ornaments. B) There is ongoing  
809 directional selection on phenotype. The direction of selection on male phenotype in relation to  
810 distance from sympatric area is smooth and gradient-like: selection for conspicuous colouration can  
811 be expected to get stronger with increasing distance from the sympatric area. C) Different  
812 populations are locally adapted and there is no association between current selection and distance  
813 from the sympatric area. D) Fitness is not related to phenotype in any of the populations and there is  
814 no association between selection and distance from sympatric area.

815

816 **Figure 2.** Breeding ranges of pied and collared flycatchers and locations of the pied flycatcher  
817 populations studied. Light grey area illustrates breeding range of the pied flycatcher in allopatry, the  
818 middle grey area illustrates the sympatric breeding area of both pied and collared flycatcher and the  
819 dark grey area illustrates the allopatric breeding area of collared flycatcher. This map is modified  
820 from Birds of the Western Palearctic (Cramp & Simmons, 2006) and Flint et al. (1984) using local  
821 information from the authors. The white circles indicate the locations of the study populations: 1 =  
822 Valsáin-Lozoya (Spain), 2 = La Hiruela (Spain), 3 = Vaud (Switzerland), 4 = Harthausen  
823 (Germany), 5 = Moravia and Jeseníky (Czech Republic), 6 = East Dartmoor (United Kingdom), 7 =  
824 Drenthe (the Netherlands), 8 = Courish spit (Russia), 9 = Moscow region (Russia), 10 = Middle  
825 Urals (Russia), 11 = Kraslava (Latvia), 12 = Tomsk (Russia), 13 = Kilingi-Nõmme (Estonia), 14 =  
826 Oslo (Norway), 15 = Ruissalo (Finland), 16 = Karelia (Russia), 17 = Skibotn (Norway).  
827

828 **Figure 3.** Standardised fecundity selection differentials and gradients on male colouration traits in  
829 relation to distance from the sympatric area with the collared flycatcher (km). Selection differentials  
830 ( $s$ ) on a) dorsal colouration, b) UV reflectance, c) forehead patch size, d) wing patch size and e) tail  
831 patch size. Selection gradients ( $B$ ) on f) dorsal colouration, g) UV reflectance, h) forehead patch  
832 size, i) wing patch size and j) tail patch size. High fecundity is associated with higher fitness and  
833 high selection differential values indicate that there is selection for more pronounced trait (darker  
834 dorsal colouration (a, f) and larger trait values (b–e, g–j)).  
835

836 **Tables**

837 **Table 1.** Details of the study populations including coordinates, distance (km) from the sympatric  
 838 area with the collared flycatcher and years of population sampling. If the study was conducted in  
 839 several sub-areas, the mean coordinates are given.

<b>Population</b>	<b>Country</b>	<b>Coordinates</b>	<b>Distance (km)</b>	<b>Years</b>
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 <sup>1</sup>	Russia	55°5' N, 20°44' E	110	2009
Moscow region <sup>2</sup>	Russia	55°44' N, 36°51' E	150	2008
Middle Urals <sup>3</sup>	Russia	56°49' N, 59°39' E	490	2008–2009
Kraslava <sup>4</sup>	Latvia	55°53' N, 27°11' E	310	2008–2009
Tomsk <sup>5</sup>	Russia	56°20' N, 84°56' E	2000	2008–2009
Kilingi-Nõmme	Estonia	58°7' N, 25°05' E	360	2008–2009
Oslo <sup>6</sup>	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

840 <sup>1,2</sup>data on ornamental patch sizes missing, <sup>3</sup>in 2007 data only on dorsal colouration, <sup>4</sup>data on UV reflectance in 2009, <sup>5</sup>  
 841 data on wing and tail patch sizes missing, <sup>6</sup>data on UV reflectance in 2009

**Table 2.** Standardised fecundity selection differentials on male colouration. Male traits referred after following: DC = dorsal colouration, UV = ultraviolet reflectance of white wing patch, FP = forehead patch size, WP = wing patch size, TP = tail patch size. +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ . N is the 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).

Population	s <sub>DC</sub>	se <sub>DC</sub>	N <sub>DC</sub>	s <sub>UV</sub>	se <sub>UV</sub>	N <sub>UV</sub>	s <sub>FP</sub>	se <sub>FP</sub>	N <sub>FP</sub>	s <sub>WP</sub>	se <sub>WP</sub>	N <sub>WP</sub>	s <sub>TP</sub>	se <sub>TP</sub>	N <sub>TP</sub>
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	<b>0.19</b> *	0.078	25	<b>-0.17</b> *	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	<b>-0.090</b> **	0.034	82	-0.045	0.047	30	-0.042	0.043	37	0.053	0.032	37
Courish spit	<b>-0.049</b> *	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	<b>0.13</b> *	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	<b>-0.057</b> *	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	0.065	96
Skibotn	0.083	0.056	90	-0.054	0.054	90	0.050	0.057	86	-0.053	0.059	84	0.078	0.057	86
<b>average</b>	<b>-0.0096</b>	<b>0.045</b>	<b>92</b>	<b>-0.014</b>	<b>0.048</b>	<b>70</b>	<b>0.019</b>	<b>0.052</b>	<b>84</b>	<b>0.0060</b>	<b>0.054</b>	<b>58</b>	<b>0.012</b>	<b>0.055</b>	<b>54</b>

**Table 3.** Standardised fecundity selection gradients on male colouration.  $\beta$  = slope of the regression model and  $\beta$  se = standard error of the slope. Male traits referred after following: DC = dorsal colouration, UV = ultraviolet reflectance of white wing patch, FP = forehead patch size, WP = wing patch size, TP = tail patch size. +  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ . N is the 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).

Population	$\beta_{DC}$	$\beta$ se <sub>DC</sub>	$\beta_{UV}$	$\beta$ se <sub>UV</sub>	$\beta_{FP}$	$\beta$ se <sub>FP</sub>	$\beta_{WP}$	$\beta$ se <sub>WP</sub>	$\beta_{TP}$	$\beta$ se <sub>TP</sub>	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-Jeseniky	-0.088	0.081	-0.0044	0.091	0.099	0.081	<b>-0.19</b> +	0.088	<b>0.19</b> *	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	<b>-0.13</b> *	0.052	0.027	0.051	<b>0.15</b> **	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
<b>average</b>	<b>-0.012</b>	<b>0.085</b>	<b>-0.0085</b>	<b>0.086</b>	<b>0.00083</b>	<b>0.084</b>	<b>0.032</b>	<b>0.077</b>	<b>0.038</b>	<b>0.072</b>	<b>45</b>

1 **Table 4.** Correlations between standardised selection differentials and selection gradients (partial  
2 selection differentials) for different male plumage traits in different populations.  $r_s$  = Spearman  
3 correlation coefficient.

<b>Variable</b>	<b><math>r_s</math></b>	<b>P</b>	<b>N</b>
Dorsal colouration	0.78	0.0009	14
UV 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

4

5 **Table 5.** The associations between distance to sympatric zone with the collared flycatcher and  
6 selection differentials ( $s$ ) and selection gradients ( $\beta$ ) on male colouration traits of in the pied  
7 flycatcher.

Male trait	Selection coefficient	estimate (se)	DF	F	P	N
<b>Dorsal colouration</b>	<i>s</i>	-0.0085 (0.018)	1, 15	0.05	0.83	17
	<i>B</i>	0.000029 (0.00050)	1, 12	0.33	0.57	14
<b>UV reflectance</b>	<i>s</i>	-0.000015 (0.000016)	1, 15	0.89	0.36	17
	<i>B</i>	-0.0000032 (0.000034)	1, 12	0.01	0.93	14
<b>Forehead patch size</b>	<i>s</i>	-0.0000021 (0.000018)	1, 13	0.01	0.91	15
	<i>B</i>	-0.0000038 (0.000046)	1, 12	0.70	0.42	14
<b>Wing patch size</b>	<i>s</i>	-0.00028 (0.000045)	1, 12	0.39	0.54	14
	<i>B</i>	0.0000068 (0.000013)	1,12	0.29	0.60	14
<b>Tail patch size</b>	<i>s</i>	0.000025 (0.000025)	1, 12	1.03	0.33	14
	<i>B</i>	0.0000078 (0.000039)	1, 12	0.04	0.85	14

8

9 **Table 6.** The relationships between male mean plumage traits and selection differentials ( $s$ ) and  
 10 selection gradients ( $\beta$ ) on male colouration traits.

Male trait	Selection coefficient	estimate (se)	DF	F	P	N
<b>Dorsal colouration</b>	<i>s</i>	-0.0047 (0.010)	1, 15	0.23	0.64	17
	<i>B</i>	0.0083 (0.23)	1, 12	0.13	0.72	14
<b>UV reflectance</b>	<i>s</i>	0.13 (1.44)	1, 15	0.01	0.93	17
	<i>B</i>	1.34 (4.37)	1, 12	0.09	0.76	14
<b>Forehead patch size</b>	<i>s</i>	-0.0015 (0.0015)	1, 12	1.11	0.31	14
	<i>B</i>	-0.0022 (0.0015)	1, 12	2.15	0.17	14
<b>Wing patch size</b>	<i>s</i>	-0.000013 (0.00054)	1, 12	0.00	0.98	14
	<i>B</i>	-0.00021 (0.00058)	1, 12	0.13	0.73	14
<b>Tail patch size</b>	<i>s</i>	0.00010 (0.00038)	1, 12	0.07	0.79	14
	<i>B</i>	0.00010 (0.00061)	1, 12	0.03	0.86	14

11