Morphological and sexual traits in Atlas and Iberian Pied Flycatchers Ficedula hypoleuca speculigera and F. h. iberiae: a comparison

Jaime Potti, José Luis Copete, Carlos Gutiérrez-Expósito & Carlos Camacho

To cite this article: Jaime Potti, José Luis Copete, Carlos Gutiérrez-Expósito & Carlos Camacho (2016) Morphological and sexual traits in Atlas and Iberian Pied Flycatchers Ficedula hypoleuca speculigera and F. h. iberiae: a comparison, Bird Study, 63:3, 330-336, DOI: 10.1080/00063657.2016.1188879

To link to this article: http://dx.doi.org/10.1080/00063657.2016.1188879

Published online: 01 Jun 2016.

Submit your article to this journal

Article views: 93

View related articles

View Crossmark data
Morphological and sexual traits in Atlas and Iberian Pied Flycatchers *Ficedula hypoleuca* speculigera and *F. h. iberiae*: a comparison

Jaime Pottia, José Luis Copeteb, Carlos Gutiérrez-Expósitoc and Carlos Camachoa

aDepartment of Evolutionary Ecology, Estación Biológica de Doñana – CSIC, Seville, Spain; bIndependent Researcher, Spain; cDepartment of Conservation Biology, Estación Biológica de Doñana – CSIC, Seville, Spain

**ABSTRACT**

**Capsule:** There are significant biometric differences between Pied Flycatchers from Iberian and north African populations which are consistent with proposals to classify the two forms into separate species.

**Aims:** To determine the similarities and differences in the main biometrical and plumage sex traits between populations of the Iberian Pied Flycatcher *Ficedula hypoleuca iberiae* and the Atlas Flycatcher *Ficedula hypoleuca speculigera*.

**Methods:** Biometric and plumage traits of 193 breeding individuals of Iberian Pied Flycatchers and 43 Atlas Flycatchers were measured in 2014 with standardized protocols.

**Results:** Both sexes of Atlas Flycatchers were larger than Iberian Pied Flycatchers in skeletal (tarsus) and wing size and also differed in bill morphology, which was wider but shallower in *speculigera* than *iberiae*, with females (but not males) having shorter bills than *iberiae* females. Males differed in mantle colour and forehead patch size, with *speculigera* males being darker and displaying larger forehead patches than *iberiae* males. As in populations of *iberiae*, some *speculigera* females also expressed a white forehead patch.

**Conclusion:** We demonstrate significant phenotypic differences between Iberian Pied Flycatchers and Atlas Flycatchers with respect to size and traits of ecological and evolutionary relevance, supporting the recently proposed scenarios on their independent evolution.

Black-and-white European flycatchers in the genus *Ficedula* (Collared Flycatcher *Ficedula albicollis*, Pied Flycatcher *Ficedula hypoleuca* and Semi-collared Flycatcher *Ficedula semitorquata*), comprise a group of similar, ‘sister’ species which have become models in the study of avian ecology, sexual selection and the processes leading to speciation (Lundberg & Alatalo 1992, Newton 2003, Price 2008, Sætre & Sæther 2010). These flycatchers occupy forested habitats across most of the European continent, even reaching the northern ranges of Africa, from Tunisia to Morocco, populated by what has been long considered a distinctive subspecies of the Pied Flycatcher, known as the Atlas Flycatcher *Ficedula hypoleuca speculigera*. The other accepted subspecies of the Pied Flycatcher, which are restricted to the European subcontinent, are *iberiae*, restricted to the Iberian Peninsula, and nominate *hypoleuca* in the rest of the area (Cramp & Perrins 1993). The subspecies *iberiae* is commonly regarded as the more differentiated with respect to other Pied Flycatcher populations in the continuous part of the breeding range, due to its geographic isolation and the distinctiveness of genetic (Lehtonen et al. 2012) and male plumage (Lehtonen et al. 2009, Sirkiä et al. 2015) characteristics.

Sætre et al. (2001) were the first to suggest, mainly on the basis of molecular genetic data, that the Atlas Flycatcher should be elevated to the status of a full species. They found that *speculigera* flycatchers were genetically as distinct from nominate *hypoleuca* as these were from Collared Flycatchers. Furthermore, plumage measurements in males provided additional evidence that *speculigera* should be regarded as a separate species, the Atlas Flycatcher *Ficedula speculigera*, which seems nowadays widely accepted (Crochet et al. 2010, Clements et al. 2015). However, BirdLife International has yet to accept the Atlas Flycatcher as a valid species, on the grounds that ‘Sætre et al. (2001) fail to compare speculigera with the geographically and morphologically intermediate form *iberiae* […] we find that *iberiae* appears to be more closely allied to *speculigera* than *hypoleuca* and overall
these forms do not warrant specific status’ (BirdLife International 2016, see also Collar 2013; but see Dickinson & Christidis 2014, emphasis by author). This tentative conclusion sums up to the increasing consensus among ornithologists that Iberian Pied Flycatcher and Atlas Flycatcher are similar in appearance (Cramp & Perrins 1993, Taylor 2006; see below), though they may or may not belong to the same lineage. However, to date, there has not been any corroboration or quantitative test of this issue.

Although the literature on plumage differences among Ficedula flycatchers has proliferated in recent years (Mild 1994, Mild & Shirihai 1994, van den Berg & the Sound Approach 2006, Copete et al. 2010, Corso et al. 2015) there is surprisingly little published information comparing biometrical measurements of iberiae and speculigera males, and most previous work (Curio 1960) has relied on museum specimens or small sample sizes to draw conclusions on plumage similarities and differences between the two ‘races’ (a term we will use henceforth only for convenience). Further, females have been largely ignored, although variation in at least Iberian Pied Flycatchers may be extensive, including the expression of secondary ‘male’ plumage sex traits such as the white forehead patch (Potti 1993) and overall plumage mantle colour (Potti et al. 2014), which seems to parallel the well-researched extensive variation in males (Lehtonen et al. 2009). Here, we aim to fill some of these gaps by providing a contemporary, rigorous comparison of the biometry of the two sexes in both flycatcher races. Until more extensive, comparative analyses of genetic variation (Bruvik 2007, Nadachowska-Brzyska et al. 2016, Nater et al. 2016) and more data on African populations settle the issue, comparative phenotypic data may contribute to the debate on the species/subspecies classification and phenotypic differentiation between the Iberian Pied Flycatcher and the Atlas Flycatcher.

**Study areas and methods**

Fieldwork was conducted during June 2014 in Central Spain (La Hiruela, Madrid province; 41°04’ N 3°27’ W) and northern Morocco, near the cities of Ifrane (33°31’ N 5°06’ W) and Azrou (33°26’ N 5°13’ W). The Spanish study site is an old Pyrenean Oak Quercus pyrenaica forest at 1250 m above sea level (asl), located in the core of the distribution range of the Iberian Pied Flycatcher. This forest is provided with 156 nest boxes, where Pied Flycatchers have been studied since 1984 (see Camacho et al. 2013 for a recent overview). Moroccan capture sites lie in the westernmost part of the Atlas Flycatcher distribution area and consist of forests of Portuguese Oaks Quercus faginea, either pure or mixed with Holm Oaks Quercus ilex or, at higher elevations, with many tall Atlas Cedar Cedrus atlantica trees interspersed, at altitudes ranging from 1400 to 1650 m asl. From April to July, coinciding with the flycatcher breeding season, average long-term temperatures in La Hiruela and Ifrane are 7°C, 11°C, 16°C, 20°C, and 8°C, 12°C, 16°C and 21°C, respectively. Rainfall regimes differ between localities, being much rainier in April (when first arrivals occur in Morocco and Spain; Boudeffa et al. 2014) in Ifrane (130 mm) than in La Hiruela (62 mm). Further, the Moroccan sites are much drier on average in June (28 mm), when most chicks hatch and fledge, than our Spanish study area (48 mm).

In Spain, birds were captured with a swing trap within their nest boxes while feeding nestlings. In Morocco, we used mist nets and spring traps near sites where we saw flycatchers perching and feeding, or tree holes being frequently accessed by adults. All Moroccan birds were ringed and measured by JP following the same long-term (Camacho et al. 2015), standardized protocols being simultaneously used by CC and field collaborators in the Spanish population, where the repeatability of measurements among observers is highly standardized with JP. Each bird was aged as first-year (EURING age code 5) or older (EURING age code 6) following criteria in Karlsson et al. (1986) and Potti & Montalvo (1991a), and measured for wing length (flattened chord; Svensson 1992). Dial callipers (to the nearest 0.05 mm) were used for measuring tarsus length (bent toes method; Alatalo and Lundberg 1986), skull length to bill tip, bill (culmen) length, height and width, extent of white (cream in females) on the outer vane in primary feathers of the extended left wing, and height and width of the forehead patch. The three bill dimensions were taken at the level of the nostrils by placing one end of the calliper on the distal edge of the external nostril as an anchor reference point, as measurement repeatability increases with this method (J. Potti & C. Camacho unpubl.). Forehead patch area was calculated as height × width (mm²). The outermost primary feather with its basal part showing white in the outer vane beyond the primary coverts was also recorded. We summed all the lengths of those white/cream ‘extensions’ in the primary feathers (from the primary where white/cream started till the tenth primary feather) to obtain a surrogate measure of the wing (primaries) patch area (Török et al. 2003). In addition, the percentage of non-black feathers on the dorsal mantle of males was visually estimated (Potti & Montalvo 1991a, Lundberg & Alatalo 1992, Sirkiai et al. 2015) and we also noted whether males had any trace
of a white/brown neck collar (Potti & Merino 1995). Birds were weighed to the nearest 0.1 g with a spring balance.

**Statistical methods**

We used one-way ANOVAs to assess most differences between *iberiae* and *speculigera* males and females. Mann–Whitney tests were used to test for differences in mantle colour scores and in the outermost primary feather where the wing primary patch starts. Allometric differences between both races were tested with analyses of covariance (ANCOVA), with race as main factor and tarsus length as the predictor variable. All tests are two-tailed.

**Results**

We measured 94 males and 99 females of Iberian Pied Flycatchers (3–30 June 2014) and 24 males and 19 females of Atlas Flycatchers (7–13 June 2014). Both populations were apparently in very similar phenological state, that is, feeding nestlings in the second half of the nestling period, as judged by observations of nestlings being fed by parents in tree holes in the Moroccan population. This is not surprising, as we planned our trip to Morocco on the basis of the recent work on the breeding ecology of Atlas Flycatchers in the Algeria mountains, where reported spring arrival dates and breeding phenology are extremely similar to those in our Spanish population (Potti & Montalvo 1991b, Boudeffa et al. 2014).

The relative age composition of both populations differed, with 20% of males and 26% of females of the Moroccan sample being aged as first-year, the corresponding figures being 16% and 15% in the Spanish population. Table 1 summarizes the biometry and differences of the flycatcher populations in Central Spain and Morocco. Figure 1 shows an example of male forehead patch variation between populations and two *speculigera* females differing in age and mantle colour. One male escaped before being scored for dorsal colour in Spain, hence the different sample size for this trait.

**Discussion**

Our analyses indicate that both male and female Atlas Flycatchers had larger skeletal size than the Iberian Pied Flycatcher (indexed by tarsus length; Alatalo & Lundberg 1986) and they also differed in bill morphology: bills were wider but shallower in *speculigera* compared to *iberiae*, and female, but not male, *speculigera* had shorter bills than *iberiae* birds. Also, as previously reported, but never confidently compared quantitatively apart from Curio’s (1960) limited sampling of a mixture of male *speculigera* skins and live *iberiae*, males of both races differed in dorsal mantle colour and size of the white forehead patch: male *speculigera* were darker and displayed larger forehead patches on average than male *iberiae*. These differences can hardly be explained by age differences between the sampled populations, as age-related variation in well studied traits would go opposite to the trends observed, for example, in wing size or male dorsal colour (Lundberg & Alatalo 1992). In addition, this study confirms that in *speculigera*, as in *iberiae*, a few males (1 out of 24; 4%) and females (2 out of 19; 11%) also expressed neck collar traces (van den Berg & the Sound Approach 2006, Bruvik 2007) or a white forehead patch (Figure 1), respectively. Our measurements of wing patch size limited to the primary feathers indicated a slightly more extended primary white/cream patch in *speculigera* than in *iberiae* flycatchers. However, there were no overall differences in wing (primaries) patch overall size between races, suggesting that it is the large conspicuous patch formed by the inner greater coverts, rather than the primary patch, what underlies the general appreciation in the literature that the Atlas Flycatcher has larger wing patches than the Iberian Pied Flycatcher. Unfortunately, however, this feather tract is difficult to measure in the field in a standardized way, so that was not attempted.

The larger skeletal size and wing length of *speculigera* compared to *iberiae* flycatchers is contrary to the expectation following Bergmann’s rule, which predicts larger body size in northern, colder locations (McNab 1971). However, it is likely that altitudinal differences between the study populations somewhat cancel out the pattern, as the African population occupies higher elevations than the Iberian population studied, resulting in a similar climate, in terms of average temperatures, in most of the breeding season. The two races inhabit humid oak and coniferous forests in the relatively cold (supra) Mediterranean montane climate belt that may impose very similar thermoregulatory demands. Hence, heat conservation cannot reasonably be invoked to explain the size differences between the races.

The pattern of differences between races in skull and bill dimensions is complex. In contrast with the Iberian Pied Flycatchers, Atlas Flycatchers have smaller heads with broader but shallower bills, and their beak length averages longer in females but not in males. These relationships stood once the allometric relationship between overall body size (tarsus length) and skull and bill measurements had been accounted for in the
Table 1. Biometrics of Atlas Flycatchers and Iberian Pied Flycatchers. Shown are means ± sd (medians for variables marked with *), range of variation and sample sizes (N). P-values are from one-way analyses of variance, except for those marked with *, which are derived from Mann-Whitney two-tailed tests.

<table>
<thead>
<tr>
<th></th>
<th>Atlas Flycatcher</th>
<th>Iberian Pied Flycatcher</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Mean ± sd (median*)</td>
<td>Range</td>
</tr>
<tr>
<td>(a) Males</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%Non-black feathers*</td>
<td>24</td>
<td>2*</td>
<td>0–90</td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>24</td>
<td>20.38 ± 0.47</td>
<td>19.35–21.40</td>
</tr>
<tr>
<td>Bill length (mm)</td>
<td>24</td>
<td>7.23 ± 0.45</td>
<td>6.20–8.10</td>
</tr>
<tr>
<td>Bill width (mm)</td>
<td>24</td>
<td>4.53 ± 0.32</td>
<td>3.70–5.00</td>
</tr>
<tr>
<td>Bill height (mm)</td>
<td>24</td>
<td>3.25 ± 0.09</td>
<td>3.10–3.40</td>
</tr>
<tr>
<td>Skull length (mm)</td>
<td>24</td>
<td>29.40 ± 0.64</td>
<td>28.60–30.60</td>
</tr>
<tr>
<td>Forehead patch width (mm)</td>
<td>24</td>
<td>10.03 ± 0.86</td>
<td>8.80–11.80</td>
</tr>
<tr>
<td>Forehead patch height (mm)</td>
<td>24</td>
<td>8.27 ± 1.10</td>
<td>6.20–10.10</td>
</tr>
<tr>
<td>Forehead patch area (mm²)</td>
<td>24</td>
<td>83.08 ± 13.77</td>
<td>56.42–117.16</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>24</td>
<td>80.63 ± 1.62</td>
<td>77.5–84.0</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>24</td>
<td>12.20 ± 0.63</td>
<td>11.2–13.3</td>
</tr>
<tr>
<td>White on wing begins on primary no.*</td>
<td>24</td>
<td>4*</td>
<td>2.0–6.0</td>
</tr>
<tr>
<td>Wing patch (mm)</td>
<td>24</td>
<td>43.73 ± 17.70</td>
<td>9.80–70.40</td>
</tr>
<tr>
<td>Longest white on primaries patch (mm)</td>
<td>24</td>
<td>7.65 ± 2.22</td>
<td>3.30–11.50</td>
</tr>
<tr>
<td>(b) Females</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tarsus length (mm)</td>
<td>19</td>
<td>20.34 ± 0.50</td>
<td>19.40–21.20</td>
</tr>
<tr>
<td>Bill length (mm)</td>
<td>19</td>
<td>6.88 ± 0.67</td>
<td>5.70–7.90</td>
</tr>
<tr>
<td>Bill width (mm)</td>
<td>19</td>
<td>4.51 ± 0.32</td>
<td>3.80–4.90</td>
</tr>
<tr>
<td>Bill height (mm)</td>
<td>19</td>
<td>3.29 ± 0.14</td>
<td>3.0–3.90</td>
</tr>
<tr>
<td>Skull length (mm)</td>
<td>19</td>
<td>29.23 ± 0.68</td>
<td>28.10–30.60</td>
</tr>
<tr>
<td>Forehead patch width (mm)</td>
<td>2</td>
<td>6.78 ± 1.38</td>
<td>5.80–7.75</td>
</tr>
<tr>
<td>Forehead patch height (mm)</td>
<td>2</td>
<td>4.30 ± 0.71</td>
<td>3.80–4.80</td>
</tr>
<tr>
<td>Forehead patch area (mm²)</td>
<td>2</td>
<td>29.63 ± 10.72</td>
<td>22.04–37.20</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>19</td>
<td>78.77 ± 1.49</td>
<td>76.0–81.5</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>19</td>
<td>12.64 ± 0.67</td>
<td>11.80–14.30</td>
</tr>
<tr>
<td>White on wing begins on primary no.*</td>
<td>19</td>
<td>4*</td>
<td>3.0–7.0</td>
</tr>
<tr>
<td>Wing patch (mm)</td>
<td>19</td>
<td>27.88 ± 8.73</td>
<td>14.70–39.60</td>
</tr>
<tr>
<td>Longest white on primaries patch (mm)</td>
<td>19</td>
<td>5.44 ± 1.25</td>
<td>3.0–7.30</td>
</tr>
</tbody>
</table>

Figure 1. Iberian Pied Flycatcher and Atlas Flycatcher: (a) a *speculigera* male; (b) an *iberiae* male; (c) a *speculigera* female aged as first-year, showing brownish dorsal plumage colour and (d) a *speculigera* female aged as older than first-year, showing forehead patch (inset) and greyish dorsal plumage colour. Note that both males were chosen as comparable instances of birds displaying some of the smallest forehead patches in their respective populations. Photos © José Luis Copete.
ANCOVAS (for brevity, results from these tests are not shown). Possibly, some of these between-race differences in overall size and bill shape could be driven by size-related habitat or environmental variation, which we have recently shown to be operating in our Iberian population even at very small spatial scales (Camacho et al. 2013, 2015). The differences in bill morphology are particularly interesting as, besides their well-known role in determining feeding niches and sizes of food consumed (Grant & Grant 2008), they can have large effects on the structure of vocal tracts and the acoustic properties of mating signals (Podos 2001, Badyaev et al. 2008). In fact, songs of Atlas Flycatchers, which are used by males to attract females, are also very distinctive from Iberian Pied Flycatchers, being richer in motifs and more complex and sounding lower-pitched to trained ears (JLC & JP, pers. obs.), although comparative sonogram analyses remain to be done (for calls, see Robb & The Sound Approach 2015). In addition, there likely exist differences between populations in the average size of their main insect prey (Lundberg et al. 1981), which can affect the strength and directionality of selection pressures on functionally important traits (Grant & Grant 2008). We have no clear explanation for the lack of significant differences between populations in male, but not female, bill length but population differences in the degree of sexual dimorphism could be involved (Selander 1966).

Mainly on the basis of differences between males in the size of the forehead patch and dorsal plumage colour, Curio (1960) suggested that speculigera and iberiae are more closely related to each other than they are to hypoleuca. Our results here, combined with the wide-ranging analyses of male Pied Flycatchers by Lehtonen et al. (2009) and Sirkiä et al. (2015), support the alternative scenario that, lacking previous reliable phenotypic data, has been increasingly assumed by most researchers working on the molecular biology of Ficedula flycatchers, despite some reservations (Collar 2013, BirdLife International 2016). That is, that speculigera and iberiae races are different enough to be considered as belonging to different lineages. Males of both races display the largest forehead patches among Ficedula flycatchers formerly included in the hypoleuca group. Furthermore, there is a pronounced coarse, latitudinal size gradient (nominate hypoleuca < iberiae < speculigera), so that Mediterranean flycatchers approach the even greater patches displayed by Collared Flycatchers in central and northern Europe (Sirkiä et al. 2015, this study). A proportion of females, on the other hand, also express the ‘male’ forehead patch in iberiae and speculigera populations, and male expression of an almost complete neck collar (Potti & Merino 1995) is also common to both races. However, both of these age-related traits are likely to be of little use in separating the taxa as complete collar expression is not frequent, and the displaying of a forehead patch by females has been neglected and is likely under-reported in other Pied and Collared Flycatcher populations (Potti & Canal 2011, L.Z. Garamszegi, pers. comm.; see also Zötli et al. 2007). Finally, although not measured objectively in this study, female plumage colour probably also varies rather subtly with age in speculigera as it does in iberiae (Figure 1; Potti et al. 2014). However, there is no information on age and geographical variation of female plumage colour in non-Mediterranean populations of Ficedula flycatchers.

To conclude, results presented here demonstrate significant phenotypic differences between Iberian Pied Flycatchers and Atlas Flycatchers with respect to size and traits of ecological and evolutionary relevance (Alatalo & Lundberg 1986, Lehtonen et al. 2009, 2012, Camacho et al. 2015), supporting the recently proposed scenarios on independent evolution of Ficedula flycatchers of the north African and Iberian lineages (Sætre & Saether 2010, Nadachowska-Brzyska et al. 2016).

Acknowledgements
We thank Mohamed Dakki for kindly providing the Moroccan rings and Abdeljebar Qinba for managing administrative permits. Ernesto Gómez helped with field work in Morocco and Tomás Redondo, Javier Manzano, David Ochoa and Fran Romero helped CC with catching birds in Spain in the absence of JP. We gratefully acknowledge the constructive comments of Malcolm Burgess and an anonymous reviewer for improving an earlier draft of this work.

Funding information
The work was made with funds provided by the EBD-CSIC through the Severo Ochoa Programme for Centres of Excellence in R&D&I [grant number SEV-2012-0262]. Field work in Spain was funded by project [grant number CGL2011-29694]. During writing, JP was funded by project [grant number CGL2014-55969-P]. CC is funded by the Severo Ochoa Program for Centres of Excellence of the Spanish Ministry of Economy and Competitiveness [grant number SVP-2013-067686].

ORCID details
Jaime Potti http://orcid.org/0000-0002-2284-0022
José Luis Copete http://orcid.org/0000-0001-8542-0351
Carlos Gutiérrez-Expósito http://orcid.org/0000-0002-2907-7998
Carlos Camacho http://orcid.org/0000-0002-9704-5816
References


