



Taxonomy of the European Pied Flycatcher *Ficedula hypoleuca* (Aves: Muscicapidae)

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Abstract

The convoluted taxonomy of the European Pied Flycatcher, *Ficedula hypoleuca* ([Pallas], 1764) (Aves: Passeriformes: Muscicapidae) might present a challenge for researchers working in other areas of biology. We present here a historical review of this species' nomenclature, discuss its generic allocation, type locality, and all its named subspecies. Its purpose is to help to mitigate errors in application of names in other contexts, and also to point out areas in which future work is needed.

Key words: *Ficedula hypoleuca*, Passeriformes, *Motacilla hypoleuca*, type locality

Introduction

Birds are the animal group with perhaps the most resolved taxonomy. However, a plethora of unresolved questions remain, many of which can affect other fields of study if species identification and delimitation are imprecise and unreliable (Dick *et al.* 2015). One example of such problems is the European Pied Flycatcher, currently *Ficedula hypoleuca* ([Pallas], 1764), a migratory passerine of the family Muscicapidae (the so called “Old World flycatchers”). This species is one of the most studied European passerines and has recently become a high-profile model for ecological studies, especially concerning issues of climate change (*e.g.*, Both & Visser 2001; Both *et al.* 2012). Consequently different populations of this species have been studied separately to resolve different ecological questions (*e.g.*, Both & Visser 2001, in The Netherlands; Laaksonen *et al.* 2006, in Finland; Sanz *et al.* 2003, in the Mediterranean region).

Yet the taxonomy of *F. hypoleuca* is far from settled, which raises the question of whether researchers are referring to the same taxa when they compare works on different populations of Pied Flycatchers. For instance, are they the same subspecies or even the same species? If not, then different results might actually reflect real differences between populations (rather than the unreliability of previous methodology, for instance). Here we expose problems surrounding the taxonomy of *F. hypoleuca* by: presenting a historical review of its nomenclature; discussing its generic allocation; reviewing its subspecies and their type localities; and pointing to complications that might arise in the many non-taxonomic works dealing with this species. This revision should help to mitigate errors in application of names in other contexts, and also to point out areas in which future work is needed.

The genus *Ficedula*

Ficedula Brisson, 1760 is a genus with a complex taxonomy since its inception (Brisson 1760). The overall similarity between muscicapid genera, together with a fair amount of variation in finer morphological traits,

resulted in many poorly defined genera. As such, the species of *Ficedula* have been classified in more than 20 other genera, some of which have since been synonymized (e.g., Vaurie 1953; Mayr & Cottrell 1986). This even led to more drastic “lumping” by simply declaring *Ficedula* a synonym of *Muscicapa* Brisson, 1760 (e.g., Delacour 1946; Delacour & Mayr 1946; Deignan 1947).

Vaurie (1953) conducted a thorough revision of the flycatchers and more clearly defined the genera and their species; a classification that, with some modifications by Mayr & Cottrell (1986), is still largely accepted today (for an overview, see Outlaw & Voelker 2006). Vaurie (1953) reestablished the genus *Ficedula* based on differences in proportions of the tarsus and first primary feather, the shape of the wing tip (in migratory species) and the bill, the rictal bristles, the color patterns, occurrence of sexual dimorphism (in some species) and ecological and behavioral traits. This allowed a clearer distinction from *Muscicapa*, the genus that most closely resembles *Ficedula* (Vaurie 1953).

Nevertheless, diagnostic characters for the genus remained somewhat tenuous and a good deal of variation could be seen among its species. Vaurie (1953) himself acknowledged that *Ficedula* was defined by its overall generalized morphology and that it might serve as a waste-basket taxon in Muscicapidae. Other muscicapid genera (e.g., *Muscicapa*) were more diagnosable (Vaurie 1953; Glutz von Blotzheim & Bauer 1993; Outlaw & Voelker 2006). As such, the problems within the genus remained unsettled. Some recent works (Outlaw & Voelker 2006; Lei *et al.* 2007; Zuccon & Ericson 2010) claim that *Ficedula* is not monophyletic (but that *Muscicapa* perhaps is), but Sangster *et al.* (2010) recovered it as monophyletic. Such works, however, are hardly thorough (for instance, some do not even include the type species of genera) and are far from being definitive, but they do point to some inconsistencies in the classification that need to be further addressed.

If *Ficedula* is indeed recognized according to Outlaw & Voelker (2006) and Lei *et al.* (2007), *F. hypoleuca*, as its type species, would remain in this genus. When only *F. hypoleuca* and its closely allied species [*F. semitorquata* (Homeyer) and *F. albicollis* (Temminck); see discussion below] are taken together, the genus *Ficedula* is more easily diagnosable (Mayr & Cottrell 1986; Outlaw & Voelker 2006). Presently, *Ficedula* includes 34 species (Clements *et al.* 2016).

Disentangling the taxonomical history of *Ficedula hypoleuca*

We present below a historical review of the taxonomy of the European Pied Flycatcher, with the most important nomenclatural acts, their authors and their reasons.

The European Pied Flycatcher was described in Linnaeus’s *Fauna Svecica* (1746), a work that was not binomial and that is therefore unavailable nomenclaturally. Later, in the tenth edition of the *Systema Naturae* (Linnaeus 1758) and the next edition of *Fauna Svecica* (Linnaeus 1761), this flycatcher was confounded with the Eurasian Blackcap (currently *Sylvia atricapilla* Linnaeus) and the Whinchat (currently *Saxicola rubetra* Linnaeus). Linnaeus probably thought that the flycatcher was a seasonal form of these other species (Lundberg & Alatalo 1992). To this point, the European Pied Flycatcher still lacked a proper valid binominal name.

Eventually, the species was named available as *Motacilla hypoleuca* by Pallas (1764). Peter Simon Pallas (1741–1811) was a renowned German scientist who worked in The Netherlands (mainly in Leiden and The Hague) from 1763–1767 (Wendland 1992). However, he described (anonymously) this species in the appendix of a sales catalogue of the collection of Adriaan Vroeg; for an explanation of Pallas’s claim to authorship, see Richmond (1905), Stone (1912) and Rookmaaker & Pieters (2000). This appendix is popularly known simply as the “Adumbratiunculæ” among ornithologists. It lists 38 bird species supposedly unknown to Linnaeus. Luckily, this extremely rare appendix (only four copies, one of them incomplete, are known; Jansen 2011) was republished in full by Sherborn (1905).

However, as pointed out by van Oort (1911), all 38 names from Pallas’s appendix appear in the main body of the catalogue. As argued by Rookmaaker & Pieters (2000), the catalogue’s author is Arnout Vosmaer (1720–1799). Nevertheless, Rookmaaker & Pieters (2000) conclude that the names given by Pallas (1764) have precedence over those given by Vosmaer (1764). In such circumstances, Recommendation 51D of the International Code of Zoological Nomenclature (1999; hereafter the Code) advocates that Pallas’s name should appear enclosed in square brackets to indicate the original anonymity of the publication and the inferred authorship by external evidence, such that the correct name of the European Pied Flycatcher is *Ficedula hypoleuca* ([Pallas], 1764).

Nevertheless, Pallas's (1764) "Adumbratiunculae" remained unknown until the beginning of the 20th century. Up to that point, the valid name of the European Pied Flycatcher was the one from the 12th edition of Linnaeus's *Systema Naturae*, namely *Muscicapa atricapilla* Linnaeus, 1766 (e.g., Sharpe 1879). Still, Pallas's "*hypoleuca*" preceded Linnaeus's "*atricapilla*" by two years and thus had priority. After Sherborn's (1905) republication of the "Adumbratiunculae", Richmond (1905) related Pallas's new species to Linnaeus's names, putting *Muscicapa atricapilla* into the synonymy of *Motacilla hypoleuca*. We infer that the auctioned type specimen(s) of *F. hypoleuca* (from Vroeg's collection) has been lost.

Type locality

The Pied Flycatcher was expressly described by Pallas (1764) from a specimen or specimens captured in the Netherlands. Therefore, the Netherlands ("Holland", in the original, meaning either Holland province or the whole country) should be considered the type locality of the species, in accord with Article 76 of the Code (1999). This takes precedence over the choice of Sweden as type locality by Glutz von Blotzheim & Bauer (1993: 165), which was based on the supposition that the black (rather than brown) male described by Pallas (1764) should have come from the Scandinavian (or Fennoscandian) population, where the males are usually blacker. This act is not valid because the place of capture is the type locality according to the Code (*l.c.*), regardless of the form of the type.

It is, however, likely that Pallas's specimens were Fennoscandian migrants, for the following reasons. First, their darker color is consistent with Fennoscandian birds, while the Central European population is brown (e.g., Dunajewski 1938; Glutz von Blotzheim & Bauer 1993). Secondly, although the Netherlands did not have a resident breeding population of *F. hypoleuca* at the time, birds from elsewhere in Europe have always been a common passage migrant in the country (Bijlsma *et al.* 2001); Fennoscandian birds, in particular, are commonly caught mid-migration in the Netherlands (see the Appendix).

The subspecies

Ficedula hypoleuca has four currently recognized subspecies, which are listed below alongside synonymized names and an unnamed population, with commentary on their taxonomy, type localities and current status. Circumscribing them morphologically is beyond the scope of this paper, but they are diagnosed in del Hoyo *et al.* (2006). Figure 1 shows a map with the geographic distribution of the currently valid subspecies.

***F. h. hypoleuca* ([Pallas], 1764)**

Motacilla hypoleuca [Pallas], 1764: 3.

Type locality Netherlands. Type material now lost. As explained above, nominate *hypoleuca* was probably described from migrant Fennoscandian birds. This subspecies, including also *muscipeta* Bechstein, 1792 (see below), occurs from the British Isles and western France to western Siberia and from Scandinavia to northern Italy, wintering in west and central Africa (del Hoyo *et al.* 2006; Clements *et al.* 2015).

***F. h. atricapilla* (Linnaeus, 1766)**

Muscicapa atricapilla Linnaeus, 1766: 326.

Type locality Europe. Type material (since lost) from the Scandinavian population was described by Linnaeus as *Muscicapa atricapilla*. Its original type locality (Europe) was restricted to Sweden by Hartert (1907). With a type locality within the range of nominate *hypoleuca*, *atricapilla* is a junior subjective synonym of *hypoleuca*.

F. h. muscipeta (Bechstein, 1792)

Muscicapa muscipeta Bechstein, 1792: 530.

Type locality Thuringia, Germany. The type material of Bechstein could not be traced in any of the likely German collections and is thus considered lost (Mey, personal communication; see also Mey 2003). It is usually considered a synonym of nominate *hypoleuca*, although a few Central European authors (e.g., Dunajewski 1938; Glutz von Blotzheim & Bauer 1993) consider it valid. The latter authors also find that southern Central European populations, to which the type of *muscipeta* would likely belong, are morphologically diagnosable from nominate Fennoscandian *hypoleuca* (e.g., Drost 1936; Dunajewski 1938; Lundberg & Alatalo 1992; Glutz von Blotzheim & Bauer 1993). Hence *muscipeta* might actually be a valid subspecies.

The present Dutch population is of the browner *muscipeta* stock, which expanded from Germany to the Netherlands in the mid-20th century, assisted by artificial nest boxes placed in forests (Haverschmidt 1973; Cramp & Perrins 1993; see also the Appendix).

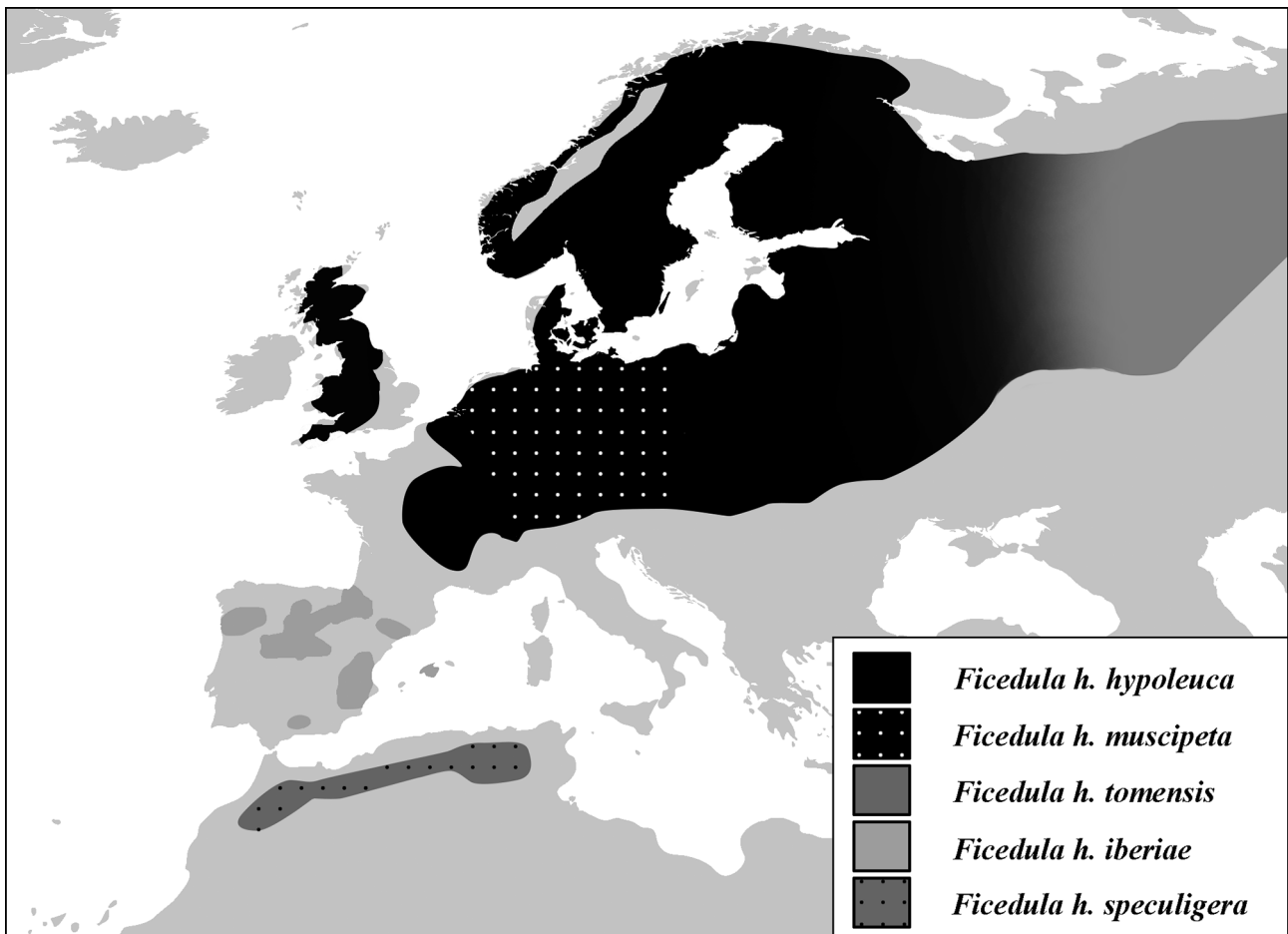


FIGURE 1. Map showing the approximate geographic distribution of the currently valid subspecies of *F. hypoleuca* (*sensu del Hoyo et al.* 2006) in their breeding grounds. The likely distribution of the population recognized as *F. h. muscipeta* by some authors is also indicated. It should be noted that the actual border between *F. h. hypoleuca* and *F. h. tomensis* is not clearly known; this is shown on the map by intergrading shades of grey.

F. h. speculigera (Bonaparte, 1850)

Muscicapa speculigera Bonaparte, 1850: 317.

Type locality Algiers, Algeria. The type material is expected to be a mount in the Muséum National d'Histoire

Naturelle (MNHN, Paris, France), but recent searches there failed to locate it (Fuchs, personal communication). The “Atlas Flycatcher”, as it is popularly known, was long considered a subspecies of *F. hypoleuca* (e.g., Mayr & Cottrell 1986; Howard & Moore 1994), but was recently distinguished at species rank by Sætre *et al.* (2001) (see also Sangster *et al.* 2004). Nevertheless, since Sætre *et al.* (2001) did not compare *F. h. speculigera* with the morphologically and geographically intermediate form *F. h. iberiae*, his assessment was widely rejected (e.g., Dickinson 2003; del Hoyo *et al.* 2006; Taylor & Christie 2013); few major works accepted it (e.g., Clements *et al.* 2015). More recently, Corso *et al.* (2015) and Robb & The Sound Approach (2015) have analyzed, respectively, variation in plumage characters and song, which show that it clearly differs from nominate *hypoleuca*, but not consistently from *iberiae*. Since then, Potti *et al.* (2016) re-analyzed morphological characters, leading him to conclude that *speculigera* is specifically distinct from *iberiae*.

The “Atlas Flycatcher” is distributed across Morocco (south to the middle Atlas Mountains), northern Algeria and northern Tunisia, and winters in western Africa (del Hoyo *et al.* 2006; Clements *et al.* 2015). There are also recent unconfirmed reports of it in Italy and Malta (Corso *et al.* 2015).

***F. h. sibirica* Khakhlov, 1915**

Muscicapa atricapilla sibirica Khakhlov, 1915: 315.

Type locality Tomsk, Russia. The type specimens (ZMMU R-29257, lectotype, female; ZMMU R-29253, paralectotype, female) are deposited at the Zoological Museum of the M. V. Lomonosov Moscow State University (Moscow, Russia). A third female specimen used in the original description is lost (Pavlinov & Borissenko 2001). This name is invalid as a junior primary homonym of *Muscicapa sibirica* Gmelin, 1789 (Mayr & Cottrell 1986), and the subspecies it denotes is now *Ficedula hypoleuca tomensis* (Johansen, 1916) (see below).

***F. h. tomensis* (Johansen, 1916)**

Muscicapa atricapilla tomensis Johansen, 1916: 101 [new name for *Muscicapa atricapilla sibirica* Khakhlov, 1915].

Type locality and material: as for *sibirica* (see above). The name *tomensis* Johansen, 1916 is a replacement name for *sibirica* Khakhlov, 1915, the latter having been published in *Muscicapa* where it is a junior primary homonym of *Muscicapa sibirica* Gmelin, 1789 and so permanently invalid (Article 57.2 of the Code). This subspecies is considered to be clearly diagnosable from nominate *hypoleuca* (e.g., Johansen 1954), although the location of and circumstances in their contact zone is poorly understood. It occurs in the taiga of west Siberia, from the Ural Mountains to the Yenisey River, wintering in east Africa (Clements *et al.* 2015).

***F. h. iberiae* (Witherby, 1928)**

Muscicapa hypoleuca iberiae Witherby, 1928: 591.

Type locality Segovia, Spain. The holotype (male; NHMUK 1929.1.15.1) is deposited at the Natural History Museum (Tring, UK). This subspecies is sometimes not recognized because it is geographically and morphologically intermediate between *F. h. hypoleuca* and *F. h. speculigera* (Bonaparte, 1850) (von Jordans & Steinbacher 1942; Vaurie 1954; del Hoyo *et al.* 2006). There is also disagreement as to whether it should be treated as a synonym of *F. h. hypoleuca* (e.g., Vaurie 1954; Mayr & Cottrell 1986) or of *F. h. speculigera* (e.g., Curio 1960). This subspecies breeds in the Iberian Peninsula, wintering in western Africa (Clements *et al.* 2015).

Unnamed population

According to Löhrl (1965), an Alpine (southern Germany and Switzerland) population of *F. hypoleuca* is

diagnosable morphologically from the northern German *muscipeta* by darker plumage and eco-physiologically by differences in average clutch size. This matter should be further investigated, although features such as clutch size are often related to altitude (Sanz 1997).

Is *Ficedula hypoleuca* a single species?

Here we follow del Hoyo *et al.* (2006), who accept *hypoleuca*, *iberiae*, *tomensis* (as *sibirica*) and *speculigera* as valid subspecies. Despite some populations being seemingly easy to diagnose on plumage coloration, taxon identification is complicated by hybridization. All subspecies hybridize with the nominate *F. h. hypoleuca* (including Central European *muscipeta*) where their geographical ranges meet (del Hoyo *et al.* 2006; Taylor & Christie 2013).

Furthermore, *F. h. iberiae* is considered an intermediate between nominate *hypoleuca* and *speculigera*. Some recent works treat *speculigera* as a separate species, but without confronting the problem with *iberiae* (e.g., Sætre *et al.* 2001; Corso *et al.* 2015). Potti *et al.* (2016) distinguished *speculigera* and *iberiae* as species based on statistical differences in morphological traits, but without a comparison with type material and topotypes, and no deposition of vouchers nor the required comparison with nominate *hypoleuca*. Moreover, these authors, echoing Curio (1960), suggested that *speculigera* and *iberiae* were more closely related to each other than to *hypoleuca*, but did not expressly compare them to the latter.

Further factors, still partly related to hybridization, might also come into play. First, these birds are migrants, implying that their populations are philopatric in their breeding. This may drive differentiation between the nuclei of the populations, even if the populations hybridize at the periphery. Secondly, despite males being morphologically diagnosable, females are not. Accordingly, song and behavior, which are less studied characters than plumage, might have a more prominent role in delimiting subspecies. For instance, Robb & The Sound Approach (2015) attempted differentiating nominate *hypoleuca* from *iberiae* and *speculigera* by song, with a reasonable degree of success.

There are two species considered to be closely related to *F. hypoleuca*, namely the Collared Flycatcher *F. albicollis* (Temminck), known to hybridize with *F. hypoleuca* (e.g., Qvarnström *et al.* 2010; Sætre & Sæther 2010), and the Semicollared Flycatcher *F. semitorquata* (Homeyer); the latter is often considered a subspecies of the former in the literature (e.g., Mayr & Cottrell 1986; Cramp & Perrins 1993). These three species have an as yet-unresolved evolutionary history, having diverged around 1–2 Ma ago (Lundberg & Alatalo 1992; Nadachowska-Brzyska *et al.* 2016). Both *F. albicollis* and *F. semitorquata* have long been accepted as distinct species from *F. hypoleuca* (e.g., Dunajewski 1938; del Hoyo *et al.* 2006; Uebbing *et al.* 2016). However, some authors consider *F. semitorquata* a subspecies of *F. hypoleuca* (e.g., Hartert 1907; Lundberg & Alatalo 1992) and *F. h. speculigera* an intermediate between *F. h. hypoleuca* and *F. albicollis* (e.g., Corso *et al.* 2015). Consequently, any thorough systematic work dealing with the circumscription of *F. hypoleuca* should include the relationships and status of these taxa as well.

Prospects for future research

Species (or subspecies) delimitation in cases such as this is best conducted using the full potential of phenotypic characters, *i.e.*, not only morphometric and plumage coloration characters, but also vocal and ecological/behavioral characters (Tobias *et al.* 2010). For instance, differences in migratory patterns have been reported as key characters for the taxonomy of some bird species (e.g., Rolshausen *et al.* 2009), further corroborated by the unviability of hybrids between distinct migratory types (Price 2008, and references therein). Different populations of *F. hypoleuca* (from Fennoscandia, the Netherlands and UK) were recently found to consistently have distinct migration patterns and wintering grounds (Ouweland *et al.* 2015). Molecular studies should also be used in defining population groups and their divergence (and gene flow in hybrid zones), but need to be conducted in conjunction with analyses of phenotypic characters (e.g., Qvarnström *et al.* 2010 for *F. hypoleuca* and *F. albicollis*) and not as a self-sufficient methodology, as it is often the case.

The subspecies concept, when properly applied, is a valuable tool for all fields in ornithology (Mayr &

Ashlock 1991; Patten & Unitt 2002). It identifies populations with incipiently divergent gene pools, which are the building blocks of evolution, and it allows for synthesis of information and study of questions involving distinct populations, their local selection pressures, and behaviors. Populations with subspecific or specific status are seen differently by conservation policy, a concern that might become urgent in the near future, as some flycatcher populations have been declining recently (Both *et al.* 2006; BirdLife International 2012). Geographical ranges also play important roles, since taxon range size is a major factor in deciding their conservation status (BirdLife International 2012).

Despite “internal” issues of relationship and status, the *hypoleuca/albicollis* group of *Ficedula* seems to form a cohesive taxonomic grouping. Nevertheless, its relationships with other species currently classified in this genus remain problematic. The genus clearly needs to be better defined, as many studies have recovered it as para- or even polyphyletic. These studies are all molecular using only a handful of loci, which, besides the usual problems (see, for instance, Tobias *et al.* 2010; Wilkins & Ebach 2014), have largely disregarded the importance of geographical representation in their sampling. In the studies dealing more specifically with the *hypoleuca/albicollis* group or with the genus *Ficedula*, none examined specimens from all populations, nor did they include specimens from many type localities, even when comparing subspecies. For instance, Sætre *et al.* (2001) used *hypoleuca* specimens only from Norway; Outlaw & Voelker (2006) from Russia and Norway; Sangster *et al.* (2010) from Sweden; Barve & Mason (2015) from Sweden, Norway, Czech Republic and a few without provenance; Nadachowska-Brzyska *et al.* (2016) from Sweden, Czech Republic and Spain; Dong *et al.* (2015) from Russia; and specimens used by Ellegren *et al.* (2012) lack geographical data altogether. More problematically, Zuccon & Ericson (2010), in their phylogeny of the whole chat/flycatcher complex, did not include *F. hypoleuca*, which is the type species of the genus.

The majority of these works included GenBank/NCBI data in their species sampling without regard for geographical source (if any) and subspecies rank. Moreover, the identification of the samples and their vouchers are often also questionable (Vilgalys 2003). Such disregard might not be so problematic in a very broad phylogeny (*e.g.*, Barve & Mason 2015), but they greatly diminish the value of studies focused on species-subspecies relationships, such as those on *Ficedula hypoleuca* and related species (*e.g.*, Ellegren *et al.* 2012).

To conclude, studies in areas other than systematics, especially physiology and ecology (and often also molecular systematics) rarely observe two other very important practices. The first is to state clearly which taxonomic classification they are following (Hyam 2015). Since different checklists and systematists can apply different circumscriptions in a given species complex, disclosing which definition one is using is crucial for sound comparison among published studies (Hyam 2015). The second practice concerns the deposition of voucher material. Every study should deposit voucher material—the whole specimen, not only tissue samples—in museum collections, which allows future researchers to check and re-analyze the material used (Huber 1998; Funk *et al.* 2005). Such voucher material should be accompanied by standard, comprehensive label data, including locality, collection date, sex, age, etc. This is critical, since the specimens themselves are the primary data (Schilthuizen *et al.* 2015) and failure to retain them makes research unverifiable, a serious flaw in any scientific endeavor (Turney *et al.* 2015).

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APPENDIX. Composition and exchanges in the Dutch Pied Flycatcher population

The Dutch Flycatcher population

European Pied Flycatchers did not breed in the Netherlands until very recently, although there is anecdotal information of possible occasional nests found there from the end of the 19th to the beginning of the 20th centuries (Dunajewski 1938; Haverschmidt 1973). The first actual breeding pair observed and recorded in The Netherlands was found in 1903, in the town of Denekamp, very close to the German border (Knolle *et al.* 1998). The population only really became established in the country in the mid-20th century (Haverschmidt 1973; Cramp & Perrins 1993; Bijlsma *et al.* 2001).

Before that, flycatchers caught in the Netherlands (such as Pallas's types) would have been caught during their migration. Fennoscandian birds, in particular, are presently commonly caught mid-migration in the Netherlands, as shown below.

Ringling data

Based on roughly 60 years of ringling data (from the Dutch Centre for Avian Migration and Demography), 306,031 individuals ringed in the Netherlands and individuals ringed elsewhere (14 in the UK and 48 in Fennoscandia) and then recaptured in the Netherlands, it was possible to assess the composition (Table 1) and exchanges between the Dutch and other Pied Flycatcher populations (Table 2). This data support the idea that birds ringed in Fennoscandia rarely breed in the Netherlands and that birds born in the Netherlands rarely disperse to Fennoscandia. The majority of dispersal of birds born in the Netherlands happens within the “*F. h. muscipeta*” distribution: either Germany or Belgium (but not Poland). This information gives further support to the classification of the present Dutch flycatcher population in the “*F. h. muscipeta*” stock, consisting of an expansion of the German population. Also, as explained in the main text of the body, the type material of nominate *F. hypoleuca* caught in the Netherlands very likely was composed of Fennoscandian individuals caught mid-migration.

TABLE 1. Population of destination of birds born in the Netherlands but recovered breeding in other countries. These numbers were based on 74 ring recoveries and do not include birds breeding in the Netherlands that correspond to the majority (99.63%, 19975 recoveries) of all flycatchers ringed as nestlings in the Netherlands and subsequently caught as breeding birds.

Breeding population	Countries with recoveries from NL	Proportion of recoveries
<i>F. h. hypoleuca</i>	UK, Ireland, Norway, Sweden, Finland	0.00
<i>F. h. ibereae</i>	Portugal, Spain	0.00
" <i>F. h. muscipeta</i> "	Belgium, Germany, Poland	93.24
<i>F. h. speculigera</i>	Tunisia, Algeria, Morocco	1.35
<i>not defined</i>	Hungary, Italy, France, Turkey	5.41

TABLE 2. Origin and situation of *F. h. hypoleuca* caught in the Netherlands; birds of foreign origin caught in the Netherlands were either breeding there or simply passing through during migration. Here are shown the individuals of *F. h. hypoleuca*, which stem from either the United Kingdom (total = 14 birds) or Fennoscandia (total = 48).

Country of origin	Proportion breeding in NL	Proportion caught during migration
United Kingdom	57.14	42.86
Fennoscandia	2.08	97.92