Using age-ratios to investigate the status of two Siberian *Phylloscopus* species in Europe

PAUL DUFOUR,*[1,2] MAGNUS HELLSTRÖM,[3] CHRISTOPHE DE FRANCESCHI,[2] MARC ILLA,[4]
GABRIEL NOREVIK,[5] PAUL CUCHOT,[2] STEPHAN TILLO,[1] MARK BOLTON,[6] DAVID PARNABY,[6]
ALEX PENN,[6] VINCENT VAN DER SPEK,[7] PETER DE KNIJFF,[8] VRS CASTRICUM,[†]
SOPHIE DAMIAN-PICOLLET, WILLY RAITIERE, SEBASTIEN LAVERGNE, PIERRE-ANDRE CROCHET &
PAUL DONIOL-VALCROZE

[1]*Tour du Valat, Le Sambuc, Arles, France*
[2]*CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France*
[3]*Ottenby Bird Observatory, Ottenby 401, Degerhamn, S-386 64, Sweden*
[4]*Institut Català d'Ornitologia, Barcelona, Catalunya, Spain*
[5]*Department of Biology, Lund University, Lund, 223 62, Sweden*
[6]*Fair Isle Bird Observatory Trust, Fair Isle, ZE2 9JU, UK*
[7]*Naturalis Biodiversity Center, Postbus 9517, Leiden, 2300 RA, The Netherlands*
[8]*Department of Human Genetics, Leiden University, Medical Center, Leiden, The Netherlands*
[9]*58 avenue du lieutenant Duverger, Pontenx-les-forges, France*
[10]*62 Rougerand, St Vincent-des-landes, 44590, France*
[11]*Université Grenoble Alpes, CNRS, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Écologie Alpine, Grenoble, France*

Distinguishing between vagrancy and regular migration has proved to be challenging as vagrants may, in theory, act as pioneers in the establishment of new migration routes. Because migratory songbirds tend to follow the same orientation and migration route throughout their lives, age assessment can help to distinguish individuals which have already used a route (i.e. adults) from those using it for the first time (i.e. juveniles). The presence of a significant proportion of adult individuals would suggest the presence of regular migrants in a vagrancy context. To decipher the status of two species of Siberian warblers in Europe, the Yellow-browed Warbler *Phylloscopus inornatus* and the Siberian Chiffchaff *P. tristis*, we assessed the age-ratios of (respectively) 324 and 117 individuals captured at different sites during the last decade. We compared whether the estimated age-ratios differed from those estimated in Common Chiffchaff *P. collybita*, a common and widespread breeding and migrating species in Europe, used here as a control species. With 1.8% of birds being adult (one confirmed, five probable), the vast majority of Yellow-browed Warblers occurring in Europe each autumn appear to be mostly, if not only, vagrants, implying that the species does not migrate regularly in Europe. These results are consistent with the very few spring records but still invite further research to unravel this remarkable phenomenon of large-scale vagrancy. Conversely, we estimated that 9.4% and 29.7% of Siberian Chiffchaffs captured, respectively, during migration in Sweden and on regular wintering sites in southern France are adult birds, suggesting that the species could migrate towards southern

*Corresponding author.
Email: paul.dufour80@gmail.com

Europe to winter, using a migration route in a markedly different direction from those known previously. These results urge more research to explore the origin, selection and causes of orientation variability in songbird species at the start of their first migration.

Keywords: Europe, migration route, orientation, seasonal migration, songbird, vagrancy, warbler, winter.

With billions of individuals travelling twice a year, sometimes over tens of thousands of kilometres between their breeding and non-breeding grounds, migratory birds are arguably among the most vagile group of terrestrial organisms on earth (e.g. Egevang *et al.* 2010). In addition to their regular movements, some species of migratory birds also frequently engage in surprising long-distance movements, far from their normal breeding ranges, migration routes or wintering ranges (Åkesson & Helm 2020, Lees & Gilroy 2021a). This phenomenon, called vagrancy, is defined as the appearance of an individual outside the normal geographical distribution range of its species (Dufour *et al.* 2024). Vagrancy is, by definition, rare and is expected to be generally costly, and often lethal, as most vagrancy events take the individuals far from any conspecifics, into potentially unsuitable habitats where they could likely die without reproducing. Yet, these vagrancy events can have important evolutionary and ecological implications (Dufour *et al.* 2024). Among them, it has been hypothesized that vagrancy may foster the evolution of new migration routes (Dufour *et al.* 2021, Lees & Gilroy 2021b). In species where migration is under strong genetic control (e.g. in songbirds; Berthold *et al.* 1992, Liedvogel & Delmore 2018) or is transmitted through social learning (e.g. in geese; Madsen *et al.* 2023), a vagrant following a novel route that survives, returns to its breeding grounds and successfully reproduces could transmit its novel migration phenotype to the next generation. If such atypical movements then increase in populations, so that more individuals survive these journeys and return to the breeding area in the following years, vagrancy could in theory permit the emergence of new migratory routes (see Bearhop *et al.* 2005).

An increase in the number of vagrants of a particular species in a specific region and in a short period is sometimes interpreted as suggesting that the species is establishing a new migration route (as proposed by Gilroy & Lees 2003). However, in the early stages of this process, distinguishing between vagrancy and regular migration remains challenging. Dufour *et al.* (2022) proposed a series of empirical tests to disentangle the relative contribution of vagrancy and migration, using the occurrence of the Yellow-browed Warbler *Phylloscopus inornatus* in Europe as a case study. One of these tests relies on the assessment of age-ratios (i.e. the proportion of adult and young birds) after the post-breeding migration (Dufour *et al.* 2022, see also Ralph 1981).

In migratory passerines, juveniles follow a migration 'map' (orientation, duration of flight and sometimes changes in orientation) that is genetically inherited from their parents (Liedvogel *et al.* 2011). They also learn from multiple cues during their first journey and use them to navigate during their subsequent migrations (see Chernetsov *et al.* 2017). This combination of inherited information and learned cues ensures that they generally follow the same migration routes throughout their lives (e.g. Stanley *et al.* 2012, Hasselquist *et al.* 2017). The existence of a migratory population in a given area outside the breeding range thus implies that the species' occurrence there is made of both young birds (<1 year old) and returning adult birds. A lack of adults of a given species in a location thus implies that the species is still a vagrant there. Conversely, the mere occurrence of adult birds (>1 year) does not demonstrate that the species is a regular migrant: even if vagrancy movements are most often lethal, vagrants can in rare cases survive their first winter and returning spring migration, and repeat their atypical movements as adults after the breeding period. For regular migration to be the most plausible hypothesis, the proportion of adult and juvenile birds would need to be similar to that of other species with comparable life-history traits and demography that are regular migrants in the same area. While such data may not always be available, using closely related species for comparison is a reasonable approach, even though it is important to acknowledge this limitation and the rationale for this choice.

In this paper, we aimed to investigate the status of two *Phylloscopus* species that are typically treated as vagrants in Europe: the Yellow-browed Warbler and the Siberian Chiffchaff *Phylloscopus tristis*. We used the *Handbook of the Birds of the World* (HBW) & BirdLife Taxonomic Checklist and recent taxonomic recommendations by treating *tristis* as a separate species and not as a subspecies of the Common Chiffchaff *Phylloscopus collybita* (del Hoyo *et al.* 2016, Talla *et al.* 2017, Doniol-Valcroze 2024). These two species are nevertheless very close phylogenetically (Shipilina *et al.* 2017, Talla *et al.* 2017, Raković *et al.* 2019) and can be difficult to distinguish in the field (see Genetic Identification and Dean & Svensson 2005).

Phylloscopus is a genus of predominantly Eurasian songbirds which comprises several long-distance migratory species (Cramp 1992, Sokolovskis *et al.* 2018, 2023). Among the species breeding in Siberia, the Yellow-browed Warbler (*inornatus* hereafter) and the Siberian Chiffchaff (*tristis* hereafter) regularly occur in Europe during the autumn migration (and the wintering period for *tristis*), even if neither species is traditionally regarded as migrating through Europe (see Fig. 1). Indeed, these two species breed mainly between the Urals and the Pacific Ocean with wintering grounds in southeast Asia for *inornatus*, and in the Indian subcontinent and marginally in the Middle East for *tristis* (Fig. 1). However, the numbers of individuals of these two species have significantly increased in recent decades in Europe (Dean & Svensson 2005, Dubois 2015, Dufour *et al.* 2022), leading ornithologists to question their status (see the 'pseudo-vagrancy' hypothesis described by Thorup 1998, Gilroy & Lees 2003, de Juana 2008, Barnagaud & Issa 2011). Using age-ratios, this study aims to determine whether *inornatus* and *tristis* individuals occurring during autumn and winter in Europe are mostly vagrants or if regular migration is also involved. To do so, we collected standardized pictures to assess the age-ratios of 324 *inornatus* and 117 *tristis* captured in different locations across Europe between 2010 and 2023. We compared these data with age-ratio data of the Common Chiffchaff (*collybita* hereafter), a similar species which breeds and migrates in Europe, as a control species. We therefore compared whether the estimated age-ratios for the two vagrant species were statistically different from those estimated for *collybita*. Because of the difficulties in ageing *inornatus* and identifying *tristis*, we relied on expert ringers to assess age in both species and used molecular identification to confirm the identity of some *tristis* individuals.

METHODS

Data collection

Between 2010 and 2023, 324 *inornatus* were captured in different locations across Europe, during the autumn (post-breeding) migration (September–November). Birds were captured during sessions dedicated to the capture of this species and during regular migration ringing sessions. Capture sites from the same geographical region were grouped together into seven large areas: Sweden, the Netherlands, Scotland, western France, southwestern France, southern France and Spain. Note that *inornatus* was never captured during spring migration at sites monitored in both seasons. Playback of calls and songs was used at most of the capture sites to specifically target the species.

In total, 117 *tristis* were captured and photographed in two locations: Ottenby Bird Observatory (Öland, Sweden; 56.19°N, 16.40°E) between 2010 and 2023, and Mireval (Occitanie, France; 43.51°N, 3.82°E) between 2021 and 2024 (of the 117, a few birds also were caught in satellite sites in southern France). Birds were captured during the migration period (autumn: September–November, $n = 45$; spring: March–June, $n = 8$) in Sweden and during the winter period (November–March, $n = 64$) in France. Birds captured in France were fitted with a two-character alphanumeric Darvic ring to increase the probability of subsequent controls (i.e. inter-annual return of birds). Most birds caught in France after February (March and April) were in active moult and were thus discarded from the age assessment because they could not be safely aged. The birds were identified as *tristis* based on calls heard in the field or in hand, and from several coloration criteria recorded in hand, such as the absence of olive in the crown and mantle, the absence of yellow away from the underwing, and the presence of a grey-brown or pale brown hue in the upper parts (Dean & Svensson 2005 and see Genetic Identification). Playback of calls and songs was used to capture the birds in France.

As a control group, 11 048 *collybita* were captured between 2010 and 2024 and aged in
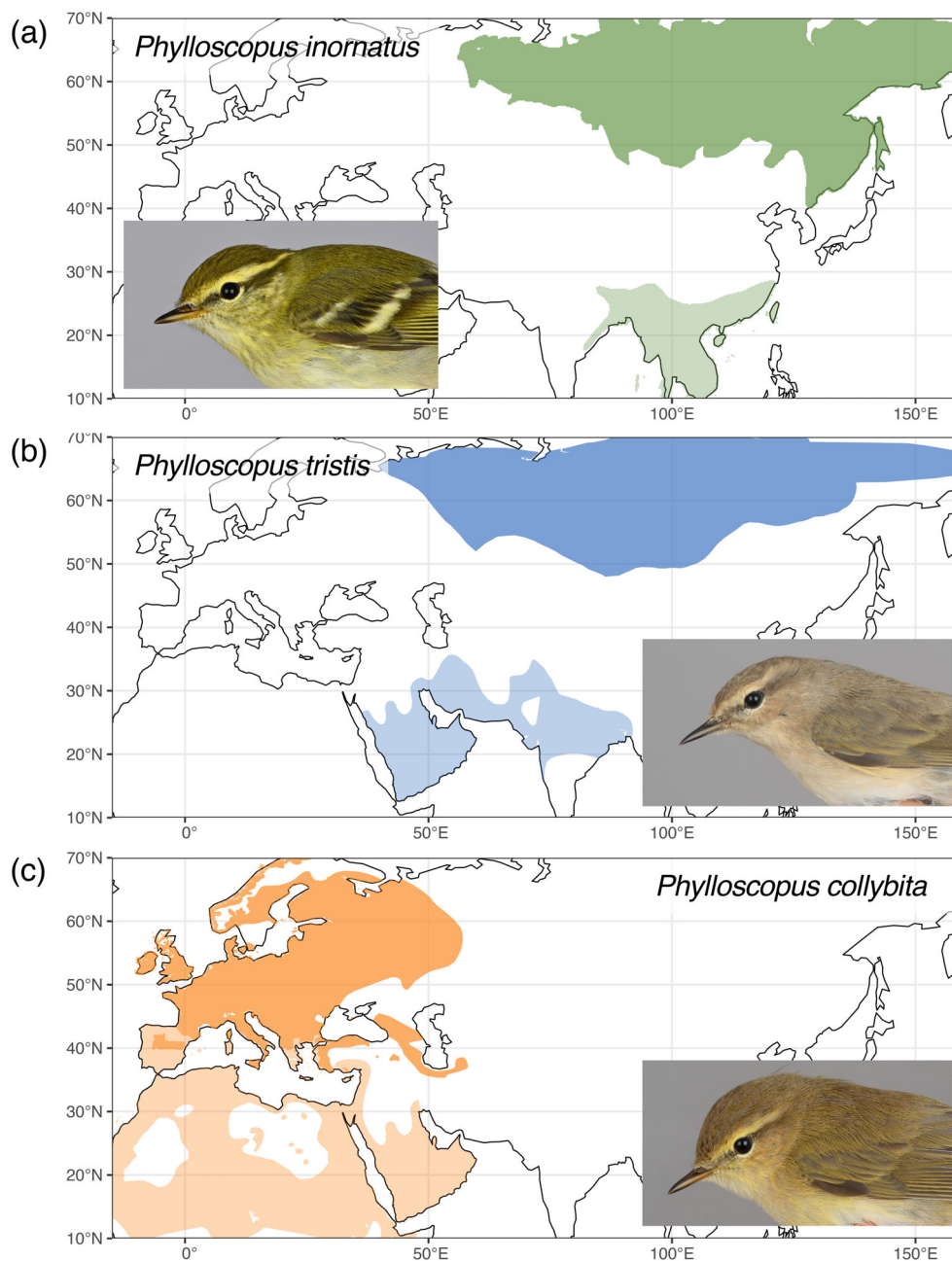
Figure 1. Distribution ranges of the Yellow-browed Warbler (*Phylloscopus inornatus*), the Siberian Chiffchaff (*Phylloscopus tristis*) and the Common Chiffchaff (*Phylloscopus collybita*). Breeding and non-breeding ranges are taken from BirdLife International. On each map, the pale part corresponds to the non-breeding distribution. The distribution of *P. collybita* mapped here includes several subspecies (*collybita*, *abietinus*, *menzbieri*, *caucasicus* and *brevirostris*) but only *collybita* and *abietinus* (in Sweden) are supposed to occur in locations studied here (see Shirihai & Svensson 2018 for more details). Furthermore, note that *P. collybita* can be seen all-year in the southernmost part of its 'breeding distribution' indicated on the map, even if these all-year distributions are likely to concern different populations occupying the same locations at different times of the year. Pictures: Ottenby fågelstation.

different locations in autumn: western France, southwestern France; in autumn and spring in Sweden; and in winter in southern France.

For the three species, all captured birds were measured and ringed with a metal ring. For *inornatus* and *tristis*, ringers were asked to take a series of

standardized and high-quality pictures showing different parts of the bird. For *tristis*, two or three body feathers were taken for genetic analysis (see below). All birds were released after c. 5–10 min of handling. There is no reliable way to determine the sex in these species and we thus have no information on sex (but see *Genetic Identification*). *P. collybita* individuals were aged by the ringers from in-hand examination but not systematically photographed.

Age-assessment

Birds were sorted into two age-categories based on plumage characteristics where *juveniles* (or first-time migrants) were separated from *adults* (birds expected to have migrated at least once) by the presence of juvenile feathers.

Adults of the three studied *Phylloscopus* species (i.e. *collybita*, *tristis* and *inornatus*) perform their complete moult during late summer (Shirihai & Svensson 2018, Jenni & Winkler 2020), and are therefore less easy to age during the autumn than some of their related species (Demongin 2016). The reason for this is that in adults and young birds the plumage is of similar age (just a few months old) and does not differ markedly in wear. This makes the feather generations more difficult to separate and any moult contrast (created by the partial post-juvenile moult in the young bird) more difficult to spot. We agree with Svensson (2023) that a cautious approach is required, and that any intermediate bird should be left un-aged. However, by building experience and by combining several characters, the number of birds apprehended as intermediate can be significantly reduced.

For *inornatus* the knowledge relating to ageing has in large part been built by some of the authors (MH and GN) during several seasons of fieldwork in China and Mongolia during which more than 4000 individuals were handled in the period August–November. Of these, several tens of individuals were known adults based on still actively growing inner secondaries during early autumn (which is an irrefutable proof of a soon-to-be-completed complete moult). Similarly, we handled c. 200 birds that, based on clear moult contrasts (e.g. in the tail), were easily recognized as being young. From such birds, we extrapolated the general method for ageing the species. Not surprisingly, our work showed that the method for ageing *inornatus* is in fact very similar to *collybita* and *tristis*

(see Svensson 2023), with the exception being that *inornatus* rarely show a detectable moult contrast among the wing coverts. The findings were published in Norevik *et al.* (2020) proposing that adult birds typically have a blackish ground colour on their wings and tail. Additionally, the structure of the greater and primary coverts, primaries and tail-feathers is generally denser (i.e. thicker, more compact) than in juvenile birds, with tail-feathers often featuring broader and blunter tips. Furthermore, for *collybita* and *tristis*, the difference of shape of the tail-feathers between juveniles and adults is often more apparent for these two species, making age assessment generally easier than for *inornatus* (Demongin 2016, Svensson 2023).

For *inornatus*, the age assessment of all individuals was performed by a single observer (MH) who has been ringing and ageing the species for a long time, both in Europe and along the regular migration flyway of this species in Asia (the most complicated birds also were discussed with GN). For the other two species, the age assessment was performed by a few expert ringers who have handled and aged many *collybita* in the context of their regular migration, namely MH, GN and PDV for *tristis*, and MH, PDV, ST, WR and CDF for *collybita*. Note that approximately 20 *tristis* were examined jointly by several experts to ensure the consistency of the used methods and criteria as well as the estimated ages.

Each bird was therefore assigned to one of four possible age categories, as follows: *1A* for a juvenile (first-year) bird (fledged the previous summer); *1A?* for a bird assumed to be a juvenile (first-year) but with doubt; *+1A* for an adult bird; and *+1A?* for a bird assumed to be an adult but with doubt. Note that we discarded from the sample one *tristis* and five *inornatus* that were considered impossible to age from the set of pictures available and some individuals for which the sets of pictures were judged to be of insufficient quality to ensure age-estimation.

Genetic identification

As a consequence of past uncertainties in the identification and status of *tristis* in Western Europe (see Dean & Svensson 2005), especially regarding the separation of *tristis*, *P. c. abietinus* and their potential hybrids, a sample of our birds identified as *tristis* from in-hand examination (56 individuals) were genotyped using feathers collected during the captures.

First, we sequenced a short fragment (309 bp) of the mitochondrial cytochrome B gene to verify the taxon-specific field-identification. This short fragment easily allows the mitochondrial DNA (mtDNA)-based identification of *abietinus*, *tristis* and nominate *collybita* (see van der Spek & de Knijff 2021). Sequencing of fragments is described in full detail in de Knijff (2024). Second, each individual was sexed using a DNA-based method that targets the avian sex chromosomes (Z and W), using the same PCR primers 2550F/2718R (Fridolfsson & Ellegren 1999) as in Collinson *et al.* (2018).

Recent studies demonstrated that *abietinus* and *tristis* hybridize, and that an unknown number of individuals cannot reliably be attributed to either of these taxa by means of mtDNA only (Shipilina *et al.* 2017, Talla *et al.* 2017). These contact zone studies found that hybrid individuals were relatively easy to identify by means of autosomal single-nucleotide polymorphism (SNP) genotypes and reciprocally fixed SNPs notably proved to be sensitive and ideally suited to identify F_1 hybrids, F_2 hybrids and lower-order backcrosses (McFarlane & Pemberton 2019). We developed and relied on a single multiplex assay of c. 300 fixed SNPs to assess the level of potential introgression in the *tristis* individuals captured for this study. To develop this assay, we used the VCF-files of 1695 SNPs that were found to be reciprocally fixed (Shipilina *et al.* 2017, Talla *et al.* 2017) between *abietinus* and *tristis*, kindly supplied by N. Backström (Uppsala University, Sweden), as reference sequences. The full protocol (detailed in de Knijff 2024) allowed us to screen 294 SNPs in each of the analysed *tristis* samples. The homozygous *abietinus*-specific genotype was scored as 0 and the *tristis*-specific homozygous genotype was scored as 1. Heterozygous genotypes were scored as 0.5 and summed values were averaged over all SNPs of a single individual, with the average score 0 indicating a 100% pure *abietinus* and a score of 1 indicating a 100% pure *tristis*. We considered pure *abietinus* as any bird with a hybrid score of 5% or less, and a pure *tristis* is defined as any bird with a hybrid score of 95% or higher.

Statistical analysis

Differences in age-ratio between species were explored using generalized linear mixed models (package *lme4*; Bates *et al.* 2015). We tested for statistical differences between *collybita* (control

species) and the two others (*inornatus* and *tristis*). Age-ratio was modelled as a binary variable, with juveniles (first time migrants) = 1 and adults = 0.

We first modelled age-ratios for the migration period (birds caught during spring and autumn), thus including the three species and birds caught in all locations (Scotland, Sweden, Netherlands, western France, southwestern France, southern France and Spain; see Fig. 2a). Then, we modelled the age-ratios for the wintering period including only *tristis* and *collybita* caught during winter in southern France (see Fig. 2b; no *inornatus* were captured during winter). We ran each model twice, first including individuals with uncertain ages in their respective categories, and then excluding them from the analysis. We included Species ($n = 3$) as a fixed effect, and Year ($n = 15$), Season (autumn/spring/winter) and Location ($n = 7$) as random intercepts.

Finally, we investigated whether there could be a relationship between the hybrid score and age. To assess this, we used Student's *t*-tests to compare the hybrid scores between the two age-groups, both with and without individuals of uncertain age.

RESULTS

In *inornatus*, only one bird of 324 caught during autumn migration was aged as a confirmed adult (0.3%), with a further five individuals determined as +1A? (probably adult), leading to a maximum likely proportion of adult birds in Western Europe in winter of 1.8% (Fig. 2a; Table 1). In *tristis* and *collybita*, we estimated respectively 7.5% and 17.2% of adult birds during the migration period including individuals with uncertain age, and 9.4% and 17.2% without (Fig. 2b; Table 1). We found significantly different age-ratios between *collybita* and *inornatus*, but not between *collybita* and *tristis* (Table 2).

During the wintering period, we estimated 29.7% and 37.7% of adult birds for *tristis* and *collybita*, respectively, including probable adults, and 10.9% and 28.3% with only confirmed adults (Fig. 2b). We did not find any significant difference between *collybita* and *tristis* age-ratios (Table 2). The estimated age-ratios are plotted for each species and for both migration and wintering periods in Figure S1.

Additionally, monitoring of the wintering population of *tristis* in southern France and the use of
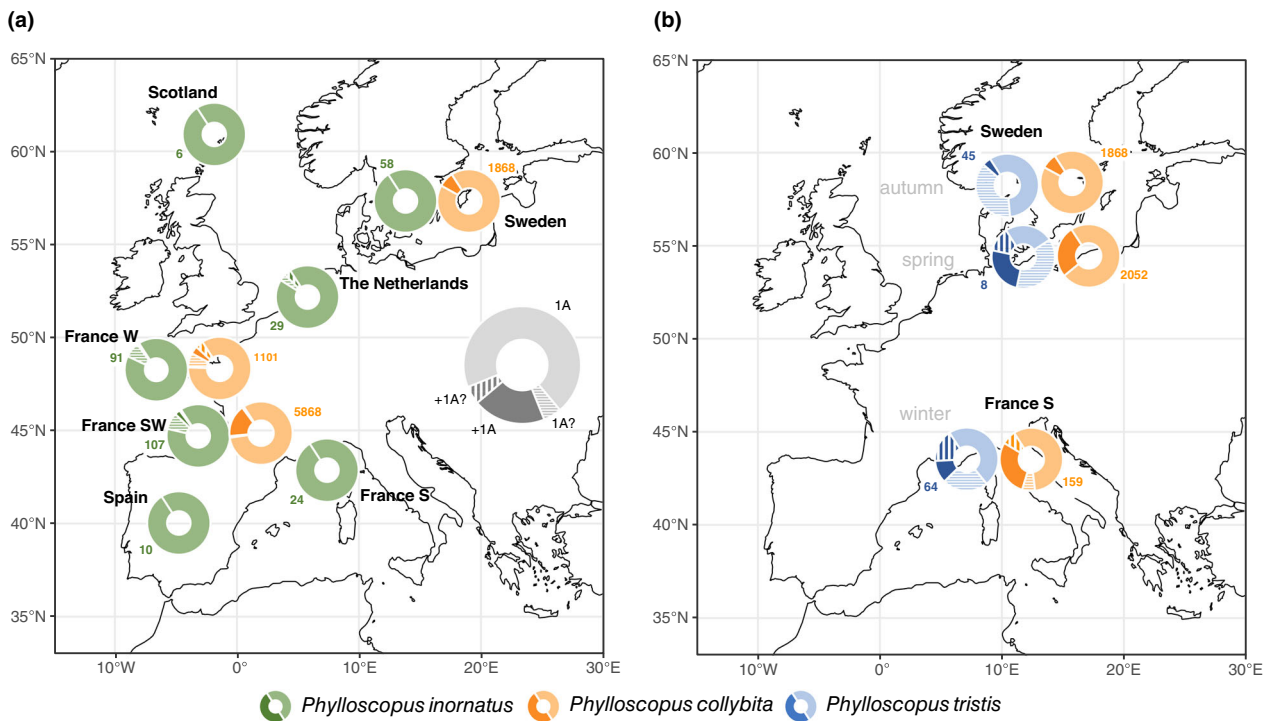
Figure 2. Age-ratios of *Phylloscopus inornatus*, *P. tristis* and *P. collybita* caught in Europe. In (a), the age of 324 *inornatus* caught in seven areas is presented, in comparison with the age of 8964 *collybita* (control) caught in three areas. For both species, birds were caught during the autumnal migration period (September–November). In (b), the age of 117 *tristis* caught in two locations (Ottenby, Sweden; and Mireval, France) is presented, in comparison with the age of 11 048 *collybita* (control) caught in the same locations. Birds were captured during the winter period in France (November–March) and during the migration period in Sweden (autumn: September–November; or spring: March–June). A key indicating the depiction of the different age categories is shown in (a); see details in the Material and Methods section. Proportions <1% do not appear in pie charts.

Table 1. Numbers of *Phylloscopus inornatus*, *P. tristis* and *P. collybita* caught in Europe per locations with their age assessments. Birds considered impossible to age by the expert ringers (five *inornatus* and one *tristis*) do not figure in the counts.

	Location	Period	+1A	+1A?	1A	1A?	Total
Phylloscopus inornatus							324
	France S	Autumn	0	0	24	0	24
	France SW	Autumn	1	3	94	9	107
	France W	Autumn	0	1	82	7	90
	Holland	Autumn	0	1	27	1	29
	Scotland	Autumn	0	0	6	0	6
	Spain	Autumn	0	0	10	0	10
	Sweden	Autumn	0	0	58	0	58
Phylloscopus tristis							117
	France S	Winter	7	12	31	14	64
	Sweden	Autumn	2	0	26	17	45
	Sweden	Spring	2	1	2	3	8
Phylloscopus collybita							11 048
	France S	Winter	45	15	88	11	159
	France SW	Autumn	955	57	4808	48	5868
	France W	Autumn	57	58	907	79	1101
	Sweden	Autumn	145	0	1723	0	1868
	Sweden	Spring	548	0	1504	0	2052

Table 2. Parameter estimates of generalized linear mixed models for age-ratio comparisons between *Phylloscopus collybita* and both *P. inornatus* and *P. tristis*.

(a) Including uncertainly aged individuals

		Est.	se	z-value	P-value
	collybita = 11 048, tristis = 53, inornatus = 324				
Migration	Fixed				
	collybita (Intercept)	1.45	0.6	2.41	0.02
	inornatus	2.13	0.42	5.07	<0.001
	tristis	0.03	0.48	0.06	0.95
	Random				
	Year	0.3			
	Area	0.49			
	Period	0.77			
	collybita = 160, tristis = 64				
Winter	Fixed				
	collybita (Intercept)	0.9	0.37	2.44	0.01
	tristis	−0.22	0.48	−0.47	0.64
	Random				
	Year	0.46			

(b) Excluding uncertainly aged individuals

		Est.	se	z-value	P-value
	collybita = 10 780, tristis = 32, inornatus = 302				
Migration	Fixed				
	collybita (Intercept)	1.68	0.67	2.49	0.01
	inornatus	3.7	0.95	3.84	<0.001
	tristis	−0.4	0.56	−0.75	0.45
	Random				
	Year	0.3			
	Area	0.68			
	Period	0.79			
	collybita = 134, tristis = 38				
Winter	Fixed				
	collybita (Intercept)	0.87	0.37	2.36	0.02
	tristis	0.31	0.58	0.53	0.59
	Random				
	Year	0.48			

The species model underwent two runs: initially, with no distinction made between uncertainly aged and confirmed aged individuals (a), and subsequently, considering only confirmed individuals (b). We looked for differences between *P. collybita* (here considered as a control species) and the two Siberian species (*P. tristis* and *P. inornatus*); different results compared to *P. collybita* indicate a potentially different status for the species in Europe. Est., estimate; se, standard error. Significant estimates ($P < 0.05$) for the intercepts indicate biased age-ratios in the reference species, here *P. collybita*.

alphanumeric rings resulted in the observation of seven inter-annual returns of different individuals (out of the 78 birds ringed between 2021 and 2023; the age of some birds was not determined because they were caught during the active moult period in March–April).

Of the 56 samples of *tristis* genotyped, we found that all birds carried a *tristis* mtDNA haplotype, and that these samples were composed of 25 females and 31 males. Regarding the hybrid score, all our birds were composed of largely dominant *tristis* ancestry with an average of 94% of *tristis* ancestry, excluding one individual with no reliable results (minimum score 64%, maximum score 100%). In detail, we found 36 pure *tristis* with a score >95% and 19 individuals with a score <95% (Fig. 3). Note that we did not find a significant link between hybrid score and age, both when including (Student's *t*-test; $P = 0.84$) and excluding (Student's *t*-test; $P = 0.85$) uncertainly aged individuals.

DISCUSSION

A puzzling pattern of vagrancy across Europe for *Phylloscopus inornatus*

The increasing occurrence of several thousands (probably tens of thousands) of *inornatus* each autumn in Europe (Dufour *et al.* 2022) has been discussed repeatedly, with several papers suggesting that this change in occurrence may result from the emergence of a new migration route (see Gilroy & Lees 2003). As reviewed in Dufour *et al.* (2022), no evidence has yet been provided in favour of this hypothesis but the regular occurrence of adult birds in autumn would support the contribution of regular migration to this pattern of occurrence. However, information on the age-ratio of *inornatus* in Europe has long been lacking because the species is notoriously difficult to age.

Here, we provide the first comprehensive assessment of the age-ratio in a large sample of *inornatus* in autumn in Western Europe, demonstrating that the vast majority of birds observed each autumn in Europe are juvenile (first-year) birds, and hence vagrants following an erroneous direction at the start of their first migration (Thorup 2004, Thorup *et al.* 2012). Thus, the species does not migrate regularly to Europe or if it does, the number of individuals involved remains extremely small and difficult to detect.

Overall, these results are consistent with the very low numbers of *inornatus* observed during spring migration in Europe (and the absence of
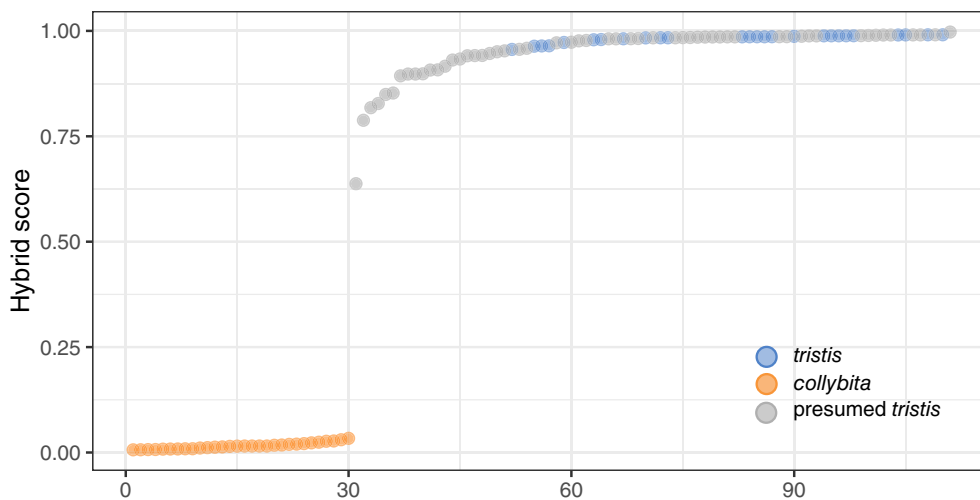
Figure 3. Proportion of genomic ancestry in 56 samples of presumed *Phylloscopus tristis* collected during winter in southern France (grey) compared with reference samples of *P. collybita abietinus* (orange; *n* = 30) and *P. tristis* (blue; *n* = 26). Each dot represents an individual and all individuals are sorted according to their hybrid score.

birds caught during spring migration at the same capture sites), suggesting that very few birds survive the winter after they arrive in Europe in autumn or die in/over the Atlantic Ocean. A single case of inter-annual control in southern Spain in 2019 (Tonkin & Gonzalez Perea 2019) proves that some birds can survive the winter in Europe to return the following year, but it remains the only case of inter-annual control despite hundreds of individuals ringed every autumn in Europe (de Juana 2008, Zucca 2017) and it remains compatible with the vagrancy hypothesis. Indeed, this bird may have been (1) part of an extremely small westward migrating population, (2) migrating back to the breeding grounds without being part of a westward-migrating population or (3) not migrating back to any breeding ground. Several cases of returning vagrants have showed that they can use a different migratory system for several years without returning to their breeding ranges (Ottens 2007). Some may even reproduce with other vagrants or hybridize with other species far from their usual breeding ranges (Dufour *et al.* 2017). Finally, as shown in Richard's Pipits *Anthus richardi* tagged in southern France that travel through Central Europe (Dufour *et al.* 2021), we cannot exclude the possibility that autumn adult *inornatus* and spring individuals might also take a similar route, making them less easily detectable. We consider this hypothesis unlikely given the general and extreme rarity of *inornatus* in Europe during spring migration.

A regular westward migration route for *Phylloscopus tristis*

In contrast to our findings for *inornatus*, we found numerous adult birds among *tristis* wintering in southern France, and this population exhibited an age-ratio similar to that of *collybita*, a closely related species that winters commonly in the same region. The age-ratio we estimated in *tristis* in southern France in winter also was similar to that of another songbird species wintering in the Iberian Peninsula, the European Robin *Erithacus rubecula* (c. 30–40%; Catry *et al.* 2004). Additionally, several individuals, including some adult birds, were caught in Sweden during the spring migration, suggesting that at least some of the birds arriving in Europe in autumn return towards their breeding grounds after wintering in Europe.

These findings suggest that *tristis* could migrate on a regular basis in southern Europe from its breeding grounds in Siberia, and undertakes a migration in a direction markedly different from the previously documented and presumably ancestral migration routes towards South Asia and the Middle East (BirdLife International 2020). This idea also is largely supported by several inter-annual controls in southern France between 2021 and 2024 (seven recaptured or controlled individuals; 84 birds caught in total between 2021 and 2024). Additionally, the genetic identification of several birds caught in Britain and the Netherlands mostly during migration (and some during

the winter period) has recently shown that this taxon is more abundant than thought previously (de Knijff *et al.* 2012, Collinson *et al.* 2018, van der Spek & de Knijff 2021). The under-detection of this taxon probably results from misinterpretation of the identification literature, but also from the fact that some individuals may display characteristics considered not to belong to *tristis* (van der Spek & de Knijff 2021).

Because of this, it is difficult to know how long *tristis* has been wintering in southern France (and elsewhere in Europe) and how often it appears each autumn in Europe (see Dean *et al.* 2010 for a review of the past identification of this taxon in Europe). However, it seems that this taxon was already wintering in Italy in the province of Vincenza (northeastern Italy) in the 1990s (Farronato *et al.* 1995) and this may still be the case, as suggested by regular contemporary sightings in northern Italy. Conversely, the species is still relatively rare in the Iberian Peninsula, and it is possible that France (and Catalonia) constitute the western limits of the regular winter distribution of this taxon in southern Europe (Gutiérrez *et al.* 2013). We may hypothesize that *tristis* benefited from an increase in winter temperatures to increase its winter survival and colonize new territories. The same hypothesis has been proposed to explain the colonization of new wintering territories for the Richard's Pipit (Dufour *et al.* 2021), and it also has been shown that *collybita* might be benefiting from increased temperatures to colonize new breeding territories to the north (Howard *et al.* 2023). A niche-modelling approach could help to understand the extent of the suitability of the wintering range of *tristis* in Europe, but it would require a better understanding of what constitutes the 'classic' wintering range of this taxon (see Babbington *et al.* 2024).

Interestingly, genomic results showed that all our sampled birds were composed of dominant *tristis* ancestry but that a significant proportion were intergrade individuals (i.e. with a hybrid score <95%) suggesting past-hybridization and introgression. This would suggest that at least some of the birds breed in the west of the *tristis* distribution close to the contact zone between *abietinus* and *tristis* (Shipilina *et al.* 2017). Furthermore, this raises new hypotheses concerning the emergence of new migration routes, with hybridization possibly leading to the introgression of genes or genomic regions involved in the orientation of migration (but see Delmore & Irwin 2014).

In summary, with the data that we currently have, we cannot know whether the westward migration route used by *tristis* is new or whether it has been used for some time before it was detected. Either way, it represents a route that was unknown previously. Identifying the breeding sites of these birds is the next step in investigating the evolution and maintenance of this migratory route. Progress will require the use of isotope-tracing analyses or small geolocators (Hobson 1999, Bridge *et al.* 2011).

LIMITATIONS AND CONCLUSIONS

Age-ratio stands as a simple and useful tool to determine the routes used by migratory species (Ralph 1981). However, the distribution of young, migratory, inexperienced birds can be biased by various factors. The coastal effect describes the accumulation of young, inexperienced birds on the coast owing to the wider range of orientation at the start of their migration and the fact that young birds generally prefer to follow the coastline for some distance rather than crossing immediately over the sea (Alerstam & Pettersson 1977, Åkesson *et al.* 2021). Because most of our capture sites are close to the coast, we may have captured higher proportions of juveniles than would have been found further inland. However, the use of *collybita* as a control gives us a comparison of the age-ratios expected at these same sites. Juveniles also may have a greater response to play-back than adults (i.e. experienced individuals; Oñate-Casado *et al.* 2021). For example, it has been found that experienced birds do not approach the sound sources as closely as naïve birds (de Lima & Roper 2009). However, we do not believe that these effects could have influenced the age-ratios that we observed in *inornatus* as several capture sites do not use playback systems to lure the birds. Finally, we acknowledge that age estimation, particularly for *inornatus*, is not infallible, and some birds may have been aged incorrectly. Ideally, the accuracy of the ageing made by the two of us who are expert on ageing this species (MH and GN) should have been tested using in-hand photos obtained during the post-nuptial in Asia and comprising individuals from both age classes. In practice, such photos do exist, but they were produced

by MH and GN themselves, which would make this test circular and therefore not relevant. We have allowed for some uncertainty in ageing in our statistical tests, and a low rate of mistakes in ageing would not affect our overall pattern, but our conclusions still rest on the overall effectiveness of our ageing process. Most of the ageing of *inornatus* was carried out by MH, who is arguably one of the most experienced experts in ageing passerines in-hand in Asia and Europe, including from photographs, and who has extensive experience with the two age-classes of species in-hand. Difficult cases also were referred to GN, who also has first-hand experience with the species in Asia and co-authored with MH the only source offering ageing criteria for the species (Norevik *et al.* 2020). We are thus entirely confident that the vast majority of *inornatus* reaching western Europe are first-calendar birds. We also acknowledge that ageing birds correctly from photographs is decidedly more difficult than in-hand, although the benefit of the approach in this study is that the analyses of the same images can be repeated in the future.

To conclude, we found contrasting support for the importance of seasonal migration in explaining the occurrence of two Siberian passerines in Western Europe. Both species breed predominantly east of the Ural Mountains (and hence mostly outside Europe) and normally winter in South-East Asia (*Phylloscopus inornatus*) or the Indian Subcontinent (*P. tristis*). For *P. inornatus*, our results show that the vast majority of the individuals reaching Western Europe are vagrants. The number of birds involved thus constitutes an intriguing evolutionary paradox, as we still do not understand why tens of thousands of individuals fly every autumn towards a near-certain death. This calls for further research to investigate the proximate mechanisms behind these large-scale misorientation patterns (Dufour *et al.* 2022, Bensch *et al.* 2024). For *P. tristis*, our results suggest that, at least in southern France in winter, the occurrence of the species might be best explained by seasonal migration. Of course, further research is needed to confirm the migration hypothesis. The first step would be to prove that the birds wintering in France return to reproduce in the breeding range of the species and transmit their migratory phenotype (i.e. orientation) to their offspring (see Dufour *et al.* 2021). The use of geolocators could help validate this hypothesis (Schaffner *et al.* 2023), which would support the discovery of yet another newly emerged or previously overlooked migration route towards Europe for another Siberian species, in a markedly different direction from the presumed ancestral one.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICS STATEMENT

All birds captured during this study were handled in strict accordance with ethical capture guidelines. On average, birds were released after c. 5–10 min of handling. All ringers involved in this study held valid ringing permits issued by the national ringing authority of their respective countries.

AUTHOR CONTRIBUTIONS

Paul Dufour: Conceptualization; writing – review and editing; writing – original draft; investigation; formal analysis; data curation. **Magnus Hellström:** Investigation; data curation; writing – review and editing. **Christophe de Franceschi:** Investigation; data curation. **Marc Illa:** Data curation; investigation; writing – review and editing. **Gabriel Norevik:** Writing – review and editing; investigation; data curation. **Paul Cuchot:** Formal analysis; writing – review and editing. **Stephan Tillo:** Investigation; data curation. **Mark Bolton:** Investigation; writing – review and editing. **David Parnaby:** Investigation. **Alex Penn:** Investigation. **Vincent van der Spek:** Investigation; formal analysis; data curation. **Peter de Knijff:** Writing – review and

editing; formal analysis; investigation; data curation. **Sophie Damian-Picollet:** Investigation. **Willy Raitiere:** Investigation. **Sébastien Lavergne:** Writing – review and editing; conceptualization. **Pierre-Andre Crochet:** Conceptualization; writing – review and editing. **Paul Doniol-Valcroze:** Conceptualization; investigation; formal analysis; data curation; writing – review and editing.

DATA AVAILABILITY STATEMENT

A file containing all of the information used to produce this paper is available online as Data S1.

REFERENCES

Åkesson, S. & Helm, B. 2020. Endogenous programs and flexibility in bird migration. *Front. Ecol. Evol.* **8**: 78.

Åkesson, S., Bakam, H., Martinez Hernandez, E., Ilieva, M. & Bianco, G. 2021. Migratory orientation in inexperienced and experienced avian migrants. *Ethol. Ecol. Evol.* **33**: 206–229.

Alerstam, T. & Pettersson, S.-G. 1977. Why do migrating birds fly along coastlines? *J. Theor. Biol.* **65**: 699–712.

Babbington, J., Roberts, P., Senfeld, T. & Collinson, J.M. 2024. Subspecies of common chiffchaff in Saudi Arabia. *Br. Birds* **117**: 438–455.

Barnagaud, J.-Y. & Issa, N. 2011. The post-breeding passage of the yellow-browed warbler *Phylloscopus inornatus* in France: Phenology and spatial variation. *Alauda* **79**: 221–232.

Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**: 1–48.

Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P. & Farnsworth, K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* **310**: 502–504.

Bensch, S., Duc, M. & Valkiūnas, G. 2024. Brain parasites and misorientation of migratory birds. *Trends Parasitol.* **40**: 369–371.

Berthold, P., Helbig, A.J., Mohr, G. & Querner, U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* **360**: 668–670.

BirdLife International. 2020. IUCN Red List for birds.

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., Robinson, W.D. & Wikelski, M. 2011. Technology on the move: Recent and forthcoming innovations for tracking migratory birds. *Bioscience* **61**: 689–698.

Catry, P., Campos, A., Almada, V. & Cresswell, W. 2004. Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. *J. Avian Biol.* **35**: 204–209.

Chernetsov, N., Pakhomov, A., Kobylkov, D., Kishkinev, D., Holland, R.A. & Mouritsen, H. 2017. Migratory Eurasian

reed warblers can use magnetic declination to solve the longitude problem. *Curr. Biol.* **27**: 2647–2651.e2.

Collinson, J., Murcia, A., Ladeira, G., Dewars, K., Roberts, F. & Shannon, T. 2018. Siberian and Scandinavian common chiffchaffs in Britain and Ireland – A genetic study. *Br. Birds* **111**: 384–394.

Cramp, S. 1992. *The Birds of the Western Palearctic*, Vol. **6**. Oxford: Oxford University Press.

Dean, A.R. & Svensson, L. 2005. 'Siberian chiffchaff' revisited. *Br. Birds* **98**: 396–410.

Dean, A., Bradshaw, C., Martin, J., Stoddart, A. & Walbridge, G. 2010. The status in Britain of 'Siberian chiffchaff'. *Br. Birds* **103**: 320–338.

Delmore, K.E. & Irwin, D.E. 2014. Hybrid songbirds employ intermediate routes in a migratory divide. *Ecol. Lett.* **17**: 1211–1218.

Demongin, L. 2016. *Identification Guide to Birds in the Hand*: 392. Privately published.

Doniol-Valcroze, P. 2024. On the taxonomic status of the Siberian chiffchaff *Phylloscopus [collybita] tristis* (Phylloscopidae). *Zootaxa* **5432**: 145–150.

Dubois, P.J. 2015. Identification, taxonomie, statut en France du Pouillot de Sibérie *Phylloscopus collybita tristis*. *Ornithos* **22**: 16–38.

Dufour, P., Pons, J.-M., Collinson, J.M., Gernigon, J., Ignacio Dies, J., Sourrouille, P. & Crochet, P.-A. 2017. Multilocus barcoding confirms the occurrence of elegant terns in Western Europe. *J. Ornithol.* **158**: 351–361.

Dufour, P., de Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., Lavergne, S. & Crochet, P.-A. 2021. A new westward migration route in an Asian passerine bird. *Curr. Biol.* **31**: 5590–5596.e4.

Dufour, P., Åkesson, S., Hellström, M., Hewson, C., Lagerveld, S., Mitchell, L., Chernetsov, N., Schmaljohann, H. & Crochet, P.-A. 2022. The yellow-browed warbler (*Phylloscopus inornatus*) as a model to understand vagrancy and its potential for the evolution of new migration routes. *Mov. Ecol.* **10**: 59.

Dufour, P., Lees, A.C., Gilroy, J. & Crochet, P.-A. 2024. The overlooked importance of vagrancy in ecology and evolution. *Trends Ecol. Evol.* **39**: 19–22.

Egevang, C., Stenhouse, I.J., Phillips, R.A., Petersen, A., Fox, J.W. & Silk, J.R.D. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc. Natl. Acad. Sci. USA* **107**: 2078–2081.

Farronato, I., Valente, S., Cappellaro, R. & Farinello, F. 1995. Lo svernamento del lui siberiano *Phylloscopus collybita* gruppo tristis nella provincia di vicenza. *Riv. Ital. Ornitol.* **65**: 3–13.

Fridolfsson, A.K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **30**: 116–121.

Gilroy, J. & Lees, A. 2003. Vagrancy theories: Are autumn vagrants really reverse migrants? *Br. Birds* **96**: 427–438.

Gutiérrez, R., Lorenzo, J.A., Elorriaga, J., Gorospe, G., López-Velasco, D., Martí-Aledo, J., Rodríguez, G. & Sales, S. 2013. Observaciones De Aves Raras En España, 2011. *Ardeola* **60**: 437–506.

Hasselquist, D., Montràs-Janer, T., Tarka, M. & Hansson, B. 2017. Individual consistency of long-distance migration in a songbird: Significant repeatability of autumn route,

stopovers and wintering sites but not in timing of migration. *J. Avian Biol.* **48**: 91–102.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia* **120**: 314–326.

Howard, C., Marjakangas, E.-L., Morán-Ordóñez, A., Milanesi, P., Abuladze, A., Aghababyan, K., Ajder, V., Arkumarev, V., Balmer, D.E., Bauer, H.-G., Beale, C.M., Bino, T., Boyla, K.A., Burfield, I.J., Burke, B., Caffrey, B., Chodkiewicz, T., Del Moral, J.C., Mazal, V.D., Fernández, N., Fornasari, L., Gerlach, B., Godinho, C., Herrando, S., Ieronymidou, C., Johnston, A., Jovicevic, M., Kalyakin, M., Keller, V., Knaus, P., Kotrošan, D., Kuzmenko, T., Leitão, D., Lindström, Å., Maxhuni, Q., Mihelič, T., Mikuska, T., Molina, B., Nagy, K., Noble, D., Øien, I.J., Paquet, J.-Y., Pladevall, C., Portolou, D., Radišić, D., Rajkov, S., Rajković, D.Z., Raudonikis, L., Sattler, T., Saveljić, D., Shimmings, P., Sjenicic, J., Šťastný, K., Stoychev, S., Strus, I., Sudfeldt, C., Sultanov, E., Szép, T., Teufelbauer, N., Uzunova, D., van Turnhout, C.A.M., Velevski, M., Vikstrøm, T., Vintchevski, A., Voltzit, O., Voříšek, P., Wilk, T., Zurell, D., Brotons, L., Lehikoinen, A. & Willis, S.G. 2023. Local colonisations and extinctions of European birds are poorly explained by changes in climate suitability. *Nat. Commun.* **14**: 4304.

del Hoyo, J., Collar, N.J., Christie, D.A., Elliott, A., Fishpool, L.D.C., Boesman, P. & Kirwan, G.M. 2016. *HBW and BirdLife international illustrated checklist of the birds of the world. Volume 2: Passerines*: 1013. Barcelona, Spain and Cambridge, UK: Lynx Edicions and BirdLife International.

Jenni, L. & Winkler, R. 2020. *Moult and Ageing of European Passerines*, 2nd edn. London: Helm editions.

de Juana, E. 2008. Where do Pallas's and yellow-browed warblers (*Phylloscopus proregulus*, *Ph. inornatus*) go after visiting northwest Europe in autumn? An Iberian perspective. *Ardeola* **55**: 179–192.

de Knijff, P. 2024. Genetic research protocols for studying Chiffchaff *Phylloscopus collybita* s.l. taxa (version VS01). *Zenodo*. https://doi.org/10.5281/zenodo.11472174

de Knijff, P., van der Spek, V. & Fisher, J. 2012. Genetic identity of grey chiffchaffs trapped in The Netherlands in autumns of 2009-11. *Dutch Bird.* **34**: 386–392.

Lees, A.C. & Gilroy, J.J. 2021a. *Vagrancy in Birds*. London: Christopher Helm.

Lees, A.C. & Gilroy, J.J. 2021b. Bird migration: When vagrants become pioneers. *Curr. Biol.* **31**: R1568–R1570.

Liedvogel, M. & Delmore, K. 2018. *(Micro) Evolutionary Changes and the Evolutionary Potential of Bird Migration*. Cham: Springer International Publishing.

Liedvogel, M., Åkesson, S. & Bensch, S. 2011. The genetics of migration on the move. *Trends Ecol. Evol.* **26**: 561–569.

de Lima, A.M.X. & Roper, J.J. 2009. The use of playbacks can influence encounters with birds: An experiment. *Rev. Bras. Ornitol.* **17**: 37–40.

Madsen, J., Schreven, K.H.T., Jensen, G.H., Johnson, F.A., Nilsson, L., Nolet, B.A. & Pessa, J. 2023. Rapid formation of new migration route and breeding area by Arctic geese. *Curr. Biol.* **33**: 1162–1170.e4.

McFarlane, S.E. & Pemberton, J.M. 2019. Detecting the true extent of introgression during anthropogenic hybridization. *Trends Ecol. Evol.* **34**: 315–326.

Norevik, G., Hellström, M., Dongping, L. & Petersoon, B. 2020. *Ageing & Sexing of Migratory East Asian Passerines*. Avium Förlag.

Oñate-Casado, J., Porteš, M., Beran, V., Petrusek, A. & Petrusková, T. 2021. An experience to remember: Lifelong effects of playback-based trapping on behaviour of a migratory passerine bird. *Anim. Behav.* **182**: 19–29.

Ottens, G. 2007. Lost and found: Laughing Gull 'Atze' in Europe. *Dutch Bird.* **29**: 288–291.

Raković, M., Neto, J.M., Lopes, R.J., Koblik, E.A., Fadeev, I.V., Lohman, Y.V., Aghayan, S.A., Boanno, G., Pavia, M., Perlmann, Y., Kiat, Y., Ben Dov, A., Collinson, J.M., Voelker, G. & Drovetski, S.V. 2019. Geographic patterns of mtDNA and Z-linked sequence variation in the common chiffchaff and the 'chiffchaff complex'. *PLoS One* **14**: e0210268.

Ralph, C. 1981. Age ratios and their possible use in determining autumn routes of passerine migrants. *Wilson Bull.* **93**: 164–188.

Schaffner, F., Hallworth, M., Jimenez, M., Rodríguez-Colón, I. & Seavy, N. 2023. Light-level tracking of northern Waterthrush (*Parkesia noveboracensis*): Lessons learned from wintering ground deployments. *J. Field Ornithol.* **94**: art5.

Shipilina, D., Serbyn, M., Ivanitskii, V., Marova, I. & Backström, N. 2017. Patterns of genetic, phenotypic, and acoustic variation across a chiffchaff (*Phylloscopus collybita abietinus/tristis*) hybrid zone. *Ecol. Evol.* **7**: 2169–2180.

Shirihai, H. & Svensson, L. 2018. *Handbook of Western Palearctic Birds*, Volume 1: Passerines: Larks to Warblers. London: Bloomsbury Publishing.

Sokolovskis, K., Bianco, G., Willemoes, M., Solovyeva, D., Bensch, S. & Åkesson, S. 2018. Ten grams and 13,000km on the wing - route choice in willow warblers *Phylloscopus trochilus yakutensis* migrating from Far East Russia to East Africa. *Mov. Ecol.* **6**: 1–10.

Sokolovskis, K., Lundberg, M., Åkesson, S., Willemoes, M., Zhao, T., Caballero-Lopez, V. & Bensch, S. 2023. Migration direction in a songbird explained by two loci. *Nat. Commun.* **14**: 165.

van der Spek, V. & de Knijff, P. 2021. Migrating chiffchaff taxa in The Netherlands: A 10-year genetic study. *Dutch Bird.* **120**: 120–131.

Stanley, C.Q., MacPherson, M., Fraser, K.C., McKinnon, E.A. & Stutchbury, B.J.M. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS One* **7**: e40688.

Svensson, L. 2023. *Identification Guide to European Passerines*, 5th edn: 448. Stockholm: Lullula Förlag.

Talla, V., Kalsoom, F., Shipilina, D., Marova, I. & Backström, N. 2017. Heterogeneous patterns of genetic diversity and differentiation in European and Siberian chiffchaff (*Phylloscopus collybita abietinus*/*P. tristis*). *G3* **7**: 3983–3998.

Thorup, K. 1998. Vagrancy of yellow-browed warbler *Phylloscopus inornatus* and Pallas's Warbler *Ph. proregulus* in north-west Europe: Misorientation on great circles? *Ringing Migr.* **19**: 7–12.

Thorup, K. 2004. Reverse migration as a cause of vagrancy. *Bird Study* **51**: 228–238.

Thorup, K., Ortvad, T.E., Holland, R.A., Rabøl, J., Kristensen, M.W. & Wikelski, M. 2012. Orientation of

vagrant birds on The Faroe Islands in the Atlantic Ocean. *J. Ornithol.* **153**: 1261–1265.

Tonkin, S. & Gonzalez Perea, J.M. 2019. Ringing recovery of yellow-browed warbler in Andalucia confirms overwintering in consecutive winters. *Br. Birds* **112**: 686–687.

Zucca, M. 2017. Évolution récente du statut du Pouillot à grands sourcils *Phylloscopus inornatus* en France. *Ornithos* **4**: 201–223.

APPENDIX A

Members of VRS Castricum: Tim van der Meer, Andre van Loon, Arnold Wijker, Guido Keijl, Henk Levering, Jan Visser, Leo Heemskerk, Luc Knijnsberg, Marc van Roomen, Paul Ruiters, Piet Admiraal, Piet Veldt, Richard Reijnders & Walter Beentjes.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Age estimates and related information for all the individuals used to produce this paper.

Figure S1. Parameter estimates of the four models comparing age-ratio between each species during *spring and autumn migration* (a,b) or *wintering* (c,d).